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The structure of ant assemblages in an urban area of Helsinki, southern Finland

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We collected ants in ten replicated habitat types of an urban island and described their assemblages using Non-metric Multidimensional Scaling and Multivariate Regression Trees. *Lasius niger* was the most abundant species, followed by *Myrmica rubra*, *Formica fusca*, *L. flavus* and *L. platythorax*; these species comprised 87% of all 1133 nests of the 16 species found. Ant assemblages changed gradually from open habitats to sites with closed tree canopy. Species most tolerant to urban pressure were *L. niger*, *L. flavus* and *M. rugulosa*, whereas forest-associated species were scarce or absent. Successful urban species had extensive (Palaearctic) or more limited (Euro-Siberian) distribution. Common and abundant habitat generalists were overrepresented relative to rural areas; these were also efficiently dispersing pioneer species with independent colony founding. Lack of suitable (micro)habitat apparently hampered colonization of many species. Competitively superior, territorial species were rare or absent, as were species dependent on dead wood, and many species depending on other ants. The indicated reorganization of interspecific competitive relationships may be due to selective impoverishment of the urban species pool. Comparison with other urban studies suggested that in ants, faunal homogenization has not taken place on a European scale.

Introduction

Urban areas differ from the surrounding rural habitats in many ways, some of which can be either favorable or harsh, depending on the species. Human activities increase temperature peaks and variation and may locally dry the climate, consequently leading to locally unique conditions (Adams *et al*. 2005). A common consensus is that urban environments include an impoverished set of the habitats usually found in the surroundings of the cities, and that the habitat patches tend to be more fragmented (McIntyre *et al*. 2001); the habitats are often small and patchily distributed over a hostile matrix of asphalt, concrete and other man-made structures (Klausnitzer 1993). Urban habitats also include a disproportionally large amount of early successional or frequently perturbed habitats, such as lawns and ruderal fields (Klausnitzer 1993, McKinney 2006). City parks, on the other hand, may represent more stable habitats, though often

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with relatively strong management activity, such as removal of old and decaying trees, and of logs, branches and sticks on the ground — all potential resources for a plethora of organisms.

To comprehend ecological effects of urbanization, it is essential to understand factors which determine the composition of urban faunas and floras. Taxa suitable for urban research should be relatively species-rich, regionally abundant and ecologically well known, and easy to collect with standardized methods. Ants — the focal taxon of this paper — fulfil these criteria, and include species that may be indifferent to, be favoured by, or even avoid urban areas (Saaristo 1995, Ambach 1999, Schlick-Steiner & Steiner 1999). Ants are also known for their multifarious symbiotic relations with other organisms, and their trophic relations with other organisms span the bridge from predators and herbivores to plants (Hölldobler & Wilson 1990). Ants having large territories are organizing centers of ant assemblages (Dlusskij 1981, Vepsäläinen & Pisarski 1982a) and may have a strong impact also on other arthropods (e.g., Kaczmarek 1963, Cherix & Bourne 1980, Martikainen *et al.* 2000, Punttila *et al.* 2004).

Our aims in this study were (1) to describe the structure of ant assemblages of an urban area; (2) to develop and test the approach of Vepsäläinen and Pisarski (1982b), who listed main factors affecting colonization of cities in an ecological, behavioural and biogeographical framework; (3) to explore factors explaining abundances of different ant species in various urban habitats; and (4) to compare our own findings with other European urban ant studies, in order to explore main similarities and differences among the cities — a further test of point (2) above. Next, we expand the theoretical framework of Vepsäläinen and Pisarski (1982b), and formulate hypotheses on successful urban species, to be tested in this study.

Expected main factors affecting colonization

In exploring factors that single out successful urban species from a larger set of regional species, we proceed hierarchically from general to more specific factors. Although here we concentrate on ants, the principles should be valid for most animal and plant taxa. In the approach of Vepsäläinen and Pisarski (1982b), two intertwined aspects of geography are central: the location of the study area relative to zoogeographical regions, and the faunal element to which each species belongs (Pisarski 1982). The more deeply located the city is within a zoogeographical region, the more likely it is to draw species belonging to the faunal (zoogeographical) element characterizing that region. Our study area in Helsinki is located well within the vast Palaearctic region, in the northern part of the Euro-Siberian region, and close to the southern limit of the northern Boreal region.

We thus expect the ant fauna of our study area to reflect zoogeographical principles. Species with an extensive distribution, in our case Palaearctic species with a Transpalaearctic distribution pattern (*sensu* Czechowski *et al.* 2002), are expected to be ecological generalists with broad ecological tolerance. These species are often common and abundant, and hence potential colonizers of various habitats, some of which should be available also in cities — given that the study area is not located at the margin of the distribution of the focal species. Likewise, species belonging to a faunal element with a smaller distribution, in this study Euro-Siberian, have a high potential to colonize cities, given that the city maintains enough of representative common habitats typical of the region. Species of this element originate from the taiga region, but at present often range to mixed forest and deciduous forest biomes of central and western Europe; Helsinki is well within ranges of such species. The Boreal element, on the other hand, covers the forest tundra and taiga biomes. In the Helsinki area, species of this element are outside the core areas of their distribution.

Here, an interesting southern aspect emerges: specialist species with narrow habitat amplitude living at the northern limit of their distribution range with few suitable rural localities available for them, may become successful urban ants, if some urban habitat amplifies special conditions favouring the species. In central and northern

Europe thermophilous, xerothermic species may be favoured, because cities tend to be substantially warmer and drier than the surrounding areas (Klausnitzer 1989). Thus species needing xerothermic habitats should be overrepresented in cities relative to their rural environs.

Many urban habitats resemble habitats of early succession or are frequently perturbed. Hence in cities, pioneer species — which often also are good dispersers with a high number of propagules — should dominate in numbers. In a study on primary succession in the Tvärminne archipelago in the Gulf of Finland, Vepsäläinen and Pisarski (1982a; after taxonomical revisions of *Lasius niger* updated by K. Vepsäläinen unpubl. data) found eight species which occurred even on the smallest islands without tree cover. Of these, *L. niger* was present on all islands studied and was the single species found on the smallest one-species islands. This species and *L. flavus* produce a very large number of propagules able to fly long distances (Vepsäläinen & Pisarski 1982a). We therefore expect *L. niger* to be common and abundant in many urban habitats. *Lasius flavus* is often the second species to colonize small islands in the archipelago (Vepsäläinen & Pisarski 1982a). It is a hypogeal species mainly dependent on root aphids (Seifert 2007), and because urban greens such as lawns and ruderal fields commonly harbour plants with root aphids, we expect also *L. flavus* to be common and abundant in our study area. Other species found on the smallest islands in Tvärminne (Vepsäläinen & Pisarski 1982a) include *Myrmica rubra*, *M. ruginodis*, *M. scabrinodis*, *Leptothorax acervorum*, *L. muscorum* and *Formica fusca*. The main habitats of *F. fusca* are similar to those of *L. niger* (Czechowski *et al*. 2002), and accordingly it is expected to be one of the successful urban ants. The same should be true for each of the above *Myrmica* species, *ceteris paribus*.

Everything else favouring colonization of cities, scarcity of suitable nest sites (microhabitats) may be the limiting resource. Of the above small-island species, *L. acervorum* and *L. muscorum* mostly nest in pieces of decaying wood though also in the ground under stones and moss (Saaristo 1995, Czechowski *et al*. 2002, Seifert 2007). Because remnant wood lots and managed parks in Helsinki tend to be poor in or devoid of even small pieces of decaying wood, in our study these species may be relatively rare. A regionally common dendrobiont (*sensu* Arnol'di 1968), *Camponotus herculeanus*, nests in large pieces of decaying wood and dead trees (Collingwood 1979), and is thus, in spite of its good dispersal capacity (Vepsäläinen & Pisarski 1982a), expected to be rare in our study area.

The territorial, top-dominant wood ant species of the *Formica rufa* group live in forests and forest ecotones (Czechowski *et al*. 2002). The colonies need extensive suitable, unfragmented habitat in order to build large, strong societies and to sustain their longevity; workers of large colonies may visit aphid trees up to 150 m from the mound (Vepsäläinen & Savolainen 1994). Because urbanization causes fragmentation and increasing isolation among suitable wood-ant habitat patches, these ants should be among the first species to suffer from urbanization. For the dramatic fragmentation history of forests adjacent to our study area, *see* Vepsäläinen and Wuorenrinne (1978: fig. 1).

Relaxed competition by wood ants in areas where they are lacking or scarce may raise species belonging to lower levels of the competition hierarchy (*see* Vepsäläinen & Pisarski 1982a, Savolainen & Vepsäläinen 1988) to dominant position in suitable habitats. The interplay of biogeography, colonization potential and habitat requirements of each species is, however, highly complicated. Thus, predicting the success of each species requires deep understanding of species-specific behaviours and ecologies, including life-histories. This is especially true for various social-parasitic relations among species: the dependence of a high proportion of ant species on other ants will interfere with the colonization success of many species. For example, in the Tvärminne archipelago and the adjacent mainland, over one third of the local 43 ant species depend on other ant species at least during some phase of the colony cycle (Vepsäläinen & Pisarski 1982a; updated by K. Vepsäläinen unpubl. data). In central Europe, the proportion of social-parasitic ant species is the same, 35%, i.e., 54 species (Seifert 1996). Consequently, we expect that decreased nest densities of any host species in our study area will affect negatively species which are dependent on them.

Material and methods

Study area

The city of Helsinki is located on the coast of the Gulf of Finland. Its over half a million inhabitants live within an area of 185 km^2, of which the densely constructed urban core area covers about 20 km^2. Our study area, Lauttasaari, is an urban island (60°10´N, 24°53´E) immediately west of the urban core of Helsinki. Bridges and roads connect it to the city centre in the east and to the suburban zone of the sister city of Espoo in the west. The first apartment houses were constructed on the manor fields of the island soon after the first bridge connection was built in 1935. Most of the present housing stock derives from the 1960s. Lauttasaari hosts ca. 19 000 inhabitants and covers < 4 km^2, of which about 70% is constructed. The rest of the island consists of various recreational and, to a lesser degree, open areas. On an urban–rural gradient, Lauttasaari is located between the urban zone (city proper, with ruderal fields and small parks) and the suburban zone, with recreational areas (*sensu* Tonteri & Haila 1990).

Field work

We collected ants from ten habitat types: (1) ruderal land with sparse vegetation and scattered trees; (2) rocky areas with scattered trees and open tree canopy; (3) grassy, narrow roadside verges; (4) meadows alongside rocky areas and outdoor recreation walkways; (5) yards (residential areas) of apartment buildings with managed vegetation and constructed landscape; (6) parks with wide, managed lawns and playgrounds; (7) allotment gardens situated in recreational areas with fairly original bottom and field-layer vegetation, bushes and trees; (8) mixed-wood forests with deciduous dominance ("mixed deciduous"); (9) coniferous forests; and (10) mixed-habitat patches, i.e. consisting of several of the above nine habitat types. Each habitat type was replicated four times (but *see* below), the replicates being scattered as evenly as possible over the study island. Because of difficulties in finding representative habitat patches we obtained only two replicates for each of the meadows and gardens, and three for each of the ruderal and the mixed-habitat patches. Each patch measured at least one hectare, and in each patch a one-hectare core area was sampled (but *see* below). Some patches were smaller than 1 ha: one ruderal and one rocky area, two verges, two meadows, three parks, and one coniferous forest. In these cases, we continued sampling in nearby patches of the same type of habitat so that the one-hectare goal was reached. We also particularly sought xerothermic, rare species in Lauttasaari by adding one more replicate of each of the rocky and residential areas. Our sampling procedure excluded two rare, exotic species living only in heated buildings in Helsinki: *Hypoponera punctatissima* and *Monomorium pharaonis* (Collingwood 1979).

The often-used pitfall-trapping method in urban–rural studies is unreliable for ant sampling for many reasons (Seifert 1990, Vepsäläinen *et al.* 2000, Laeger & Schultz 2005, though *see* Steiner *et al.* 2005). We, therefore, used a direct sampling method (Bestelmeyer *et al.* 2000) which is, despite its subjectivity, a robust and standardized method when used with expertise. We sampled ants between mid-July and early September in 2000 by searching through microhabitats suitable for ant nests. This direct sampling (hand-collecting) involved locating nests by trampling the ground to agitate workers in nests and working through potential nest sites with a knife. Searching was based on published information on ant nest sites (e.g., Collingwood 1979, Seifert 1996) and especially on our personal long-time field experience. Searching included frequent probing of the ground, grass tussocks, moss and earthen mounds, checking dying and dead trees, breaking sticks, tree stumps and logs, and turning stones on the ground and rocks. Additionally we checked for nests (though did not find) in cones and under bark of living trees. While searching, we also utilized foraging workers to locate their nests. We collected up to several tens of individuals from each nest found, and preserved them in vials with 70% ethylene alcohol. We identified the samples to species using a stereomicroscope (maximum magnification 75×) and keys by Dlussky and Pisarski (1971), Kutter (1977), Collingwood (1979), Seifert (1991, 1996), Radchenko *et al*. (1999) and Czechowski *et al*. (2002).

Our aim was to find 30 ant nests within each patch. To determine the cumulative number of ant species as a function of nests, we attached a serial number to each sample, to be identified to species. We used the function to evaluate whether the accumulation of species seemed to saturate satisfyingly before the aim of 30 nests was reached. To keep track of sampling effort, we kept time with a stopwatch while collecting, and stopped it for sampling.

In each patch, we estimated environmental variables that are potentially important for ants (*see* Appendix). These included the percentage cover of the field-layer vascular plants and the percentage canopy cover categorised into five coverage classes as follows: 1 = no or sparse (< 5%) coverage, 2 = 5%–20% coverage, 3 = 21%–50%, 4 = 51%–75%, and 5 ≥ 75% coverage. Because plant and canopy cover both correlate positively with moisture of the soil and negatively with light on the ground, we did not estimate these additional variables separately (though we used them in interpreting the results). We also counted from 10–20 randomly chosen 10 × 10 m squares the amount of easily quantified potential nest sites which were: decomposing wood, sticks and tree stumps separately (our study sites practically lacked large pieces of branches and tree trunks laying on the ground, to be coded separately as nest sites), and stones (all stones large enough for a mature *Myrmica rubra* or *Lasius niger* colony, but still movable by hand). We categorised the abundance of these three nest-site categories into five abundance classes as follows: 1 = 0–2 pieces of given variable within average measured sample square, 2 = 3–4 pieces, 3 = 5–8, 4 = 9–20, and 5 ≥ 20 pieces. We used the categorical variables as environmental data in multivariate analyses (*see* below).

We classified the microhabitat of each nest found as belonging to one of the above three nest site categories or to one of the following categories, here called collectively as “other sites”: mounds constructed of needles or pieces of grass, moss or other vegetative material; earthen mounds; tussocks growing variously moss, grass, shrubs, etc.; and ground nests on bare ground or ground covered by grass, herbs, moss or lichen.

Data analyses

We ran Non-metric Multidimensional Scaling (NMS; e.g., Borg & Groenen 1997) for the ant data to examine the distinctiveness of the ant faunas of different habitat types, and to explore the potential for different environmental variables (*see* above; for a formal test on their significance, *see* below) in explaining these observations. We applied the Bray-Curtis distance measure between samples, Monte Carlo randomization to test the significance of the solution, and used the “thorough” option available in PC-Ord 4.0 (McCune & Mefford 1999). We produced a two-dimensional solution with 400 iterations and 0.00001 as the stability criterion. We then classified the sample scores by their associated habitat type (*see* above), and added to the plot environmental variables as passive ones. We tested the distinctiveness of the resulting habitat-type scatters using Multi-Response Permutation Procedure (MRPP; Zimmerman *et al*. 1985). For MRPP we report the test value (T) with related probability for the similarity of the compared habitat types, and the within-habitat-type heterogeneity of samples (A = 1 if all the samples within a given habitat type are identical; else, $A < 1$).

We added two passive variables to the NMS plot which indicate the main aspects of community diversity, the number of species and the evenness of species distribution. For evenness we used Smith and Wilson’s index (E) which is independent of species richness but sensitive to both abundant and infrequent species in the dataset (Smith & Wilson 1996, Krebs 1999). To study the possible negative effect of territorial wood ants on the patch-specific diversity of ant species (Savolainen *et al*. 1989, Vepsäläinen *et al*. 2000), we estimated the diversity of ant assemblages with the Shannon-Wiener diversity index. We calculated all the indices using Ecological Methodology software (Krebs 1998).

We tested the significance of environmental variables (here, habitat type and variables listed in the Appendix) in shaping the ant assemblages

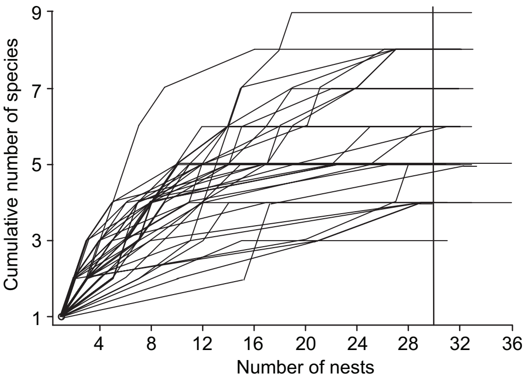

Fig. 1. Cumulative number of species as a function of nests found in each of the 36 study plots; the vertical line indicates the sampling goal of 30 nests per plot.

by using Multivariate Regression Trees (MRT; De'ath 2002). We applied Bray-Curtis pairwise similarities between samples. MRT identifies groups of sites defined by environmental variables and can potentially account for non-linearity (De'ath 2002). The result is usually presented as a tree of dichotomies. Each dichotomy is chosen to minimize the dissimilarity of sites within each branch. We selected the final tree by finding the tree size (number of 'end' branches) that had the lowest cross-validated relative error, following the 1-SE rule (Breiman *et al.* 1998, *see* also De'ath 2002). The tree fit can also be defined using relative error, as it decreases the more variables are included into the model. However, the cross-validated relative error better estimates the predictive accuracy of the resulting model for a new dataset (De'ath 2002). After decreasing to its minimum, the cross-validated relative error curve slightly increases to a plateau, and the predictive power of the model (the number of 'end' branches) does not increase any more. For this analysis we used R 2.1.0 software with vegan and mvpart packages (R Development Core Team 2005).

We performed routine statistical tests with the StataCorp. (2003) software.

Results

We found 16 species with a total of 1133 nests; we recorded one more species after finishing sampling for this study. The number of species per patch varied between three and nine. The most abundant species were *Lasius niger* (343 nests), *Myrmica rubra* (311), *Formica fusca* (123), *L. flavus* (114), and *L. platythorax* (100); these five species occupied 87% of the nests found. The species accumulation as a function of nests found indicated that, in the majority of the study patches, the number of species saturated well before the goal of 30 nests was reached (Fig. 1). Of the studied 36 patches, one meadow patch yielded the maximum of nine species, and a total of eight species was found in six patches: yards (one patch), rocky areas (3), gardens (1), and mixed-habitat patches (1). The species maxima were six for parks and mixed deciduous forests, and seven for coniferous forests. The species-poorest patches (three to four species) were located in ruderal fields, verges of the highway, meadows, parks, and both forest habitats.

The correlation between the patch-specific number of species found and the time needed to locate those nests (usually 30 nests per site) was not significant (Pearson's $r = -0.07$, $p = 0.69$). This result indicates successful avoidance of quick-and-easy search through potential nest sites of locally abundant species.

Assembly patterns

The NMS run produced a two-dimensional solution with final stress 11.61 after 42 iteration runs (Fig. 2). The first two dimensions with real data versus randomized data (Monte Carlo test) had $p = 0.0196$, as had the dimensions 3–6, too (not shown). In the NMS graph, sample scores were classified according to their habitat types; these differed from each other highly significantly (MRPP; $T = -7.10$, $A = 0.35$, $p < 0.0001$). Coniferous and mixed deciduous forests located close to each other on the lower part of the site-score scatter, with allotment gardens next to the forests. There, *Myrmica ruginodis*, *M. rubra*, *Formica polyctena*, and *Lasius umbratus* were most abundant. Also canopy closure, and the numbers of stumps and sticks had their peaks there (Fig. 2). Man-made habitats — yards, parks, road verges and ruderal land — had very different ant faunas, as indicated by the distinctiveness of the site scores of these habitat types (located up in Fig. 2). *Myrmica rugulosa*, *Lasius niger* and *L. flavus* peaked there. Rocky habitats, meadows and mixed habitats, as well as the variables *S* (number of ant species) and *E* (ant community evenness), fell in-between these forested and man-made sites. Ant species apparently thriving in these 'intermediate' sites and — at least partly — in both forested and man-made sites were *Lasius platythorax*, *L. fuliginosus*, *Formica fusca*, *F. truncorum*, *F. rufa*, *Leptothorax acervorum*, *L. muscorum*, *Myrmica lobicornis* and *M. scabrinodis* which all scattered to the centre of the NMS graph (Fig. 2).

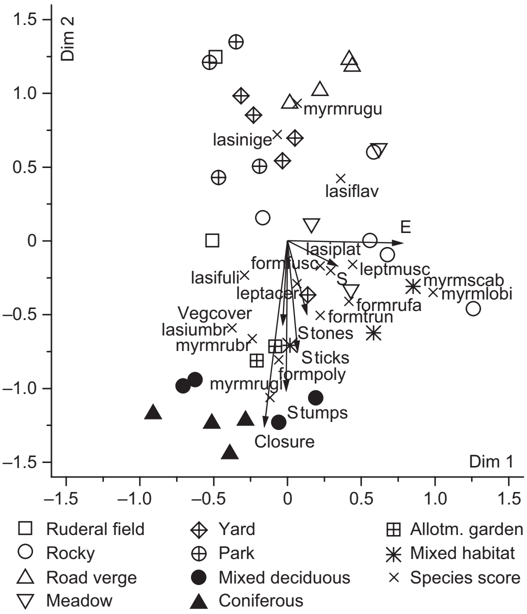

Fig. 2. Non-metric Multidimensional Scaling (Bray-Curtis distance matrix) for the ant data collected in Lauttasaari, Helsinki. The sample scores are sorted according to habitat type (*see* legend). Small crosses indicate species scores (species are indicated by 4 + 4-letter combinations; e.g., formrufa = *Formica rufa*) and arrowheads indicate scores of passive environmental variables (for full variable names, *see* Appendix). Two variables describing community diversity (S = species richness, E = evenness of species abundances) are included. First two NMS dimensions shown.

MRT indicated that the single most important variable explaining variation in ant assemblage composition was habitat type, but that also canopy closure was an important determinant of ant assemblages (Fig. 3). This solution had cross-validated error 0.33 (0.05 SE), indicating good predictive power of the model for a new ant data set (0 = perfect predictor, 1 = poor predictor; De'ath 2002), and explained altogether 76% of the variation in the data. The first node alone explained 55% of the variation and split the sites to open (meadows, parks, rocky habitats, ruderal land, road verges and yards) and forested habitats (allotment gardens, mixed-deciduous and coniferous forests, and mixed habitat types). In the former habitat group, *Lasius niger* (46% of all nests in the 23 plots of these habitats) and *Myrmica rubra* (13%) dominated the ant assemblages, whereas in the forested habitats, *M. rubra* (53% of all nests in the 13 plots of these habitats) and *Formica fusca* (13%) dominated (*see* column charts in Fig. 3). The second node, then, explained 15% and split the open sites according to canopy closure, i.e., the abundance of scattered trees at these sites (left-hand side of Fig. 3). Within the 16 sites with no canopy closure (closure = 1), *L. niger* made up 66% of the ant nests found, and *L. flavus* was the second most often found species (20%). Within the open sites with some canopy closure, *L. niger* and *M. rubra* continued to dominate, with percentages of nests found in these sites being 37% and 18%, respectively. The third node explained another 6% of variation and split the forested sites according to canopy closure (right-hand side of Fig. 3). In the forested sites with more open canopy (2–3), *M. rubra* and *F. fusca* again dominated, their percentages of nests found being 41% and 21%, respectively. Finally, in the forested sites with more closed canopy, *M. rubra* dominated (63% of nests found in these sites), followed by *M. ruginodis* (16%).

Comparisons of abundant species pairs

Lasius niger inhabited all the sampled habitats and was found particularly often in ruderal fields, grassy roadside verges, yards and parks, where urbanization pressure was perhaps most severe. Also *L. platythorax* occurred in most habitats, but was less abundant. This species was completely lacking from the driest and warmest areas, such as ruderal fields and grassy roadside verges. Both species often nested in the vicinity

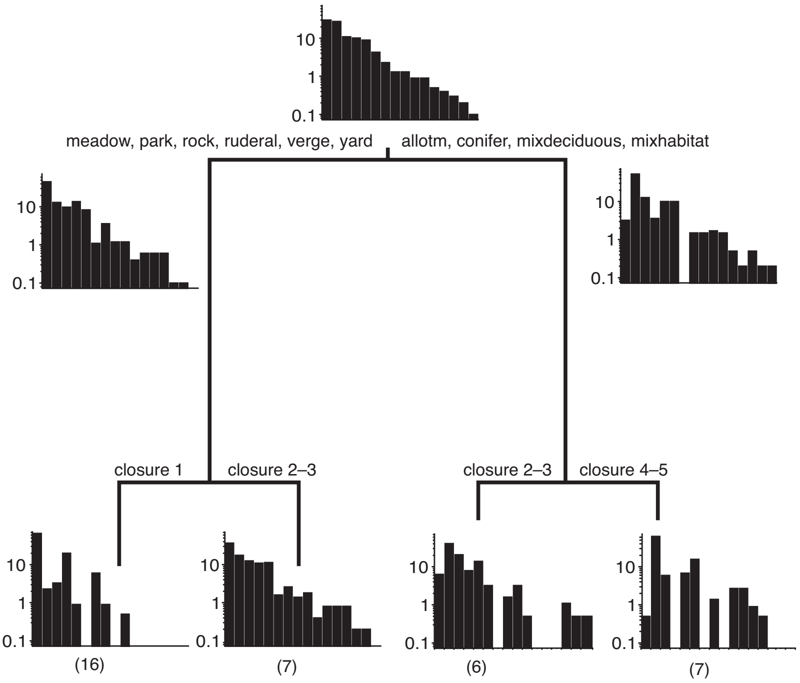

Fig. 3. Multivariate regression tree (Bray-Curtis distance matrix) for the ant data collected in Lauttasaari, Helsinki. The nodes are based on habitat type and canopy closure (for the rest of the variables included in the analysis, *see* text). Values in parentheses below the end nodes show the numbers of sites falling into a given branch. The bar charts show proportional abundances of the 16 ant species collected in the study; all the column orders were defined by the total catch, shown on top of the graph). Horizontal axis = rank abundances of the 16 species, vertical axis = proportional abundance of each species (0%–72%, $\log_{10}$ scale). For species names, consult the rank order of the total catch in Table 1.

of each other, but their abundances peaked in different habitats, *L. platythorax* occurring more abundantly in relatively closed and moist habitats ($r = -0.35$, $p = 0.04$) (Fig. 4).

Myrmica rubra occurred in all the sampled habitats and was most abundant in forests. *Myrmica ruginodis* was less abundant than *M. rubra*, even in forests (Fig. 4). The occurrences of *M. rubra* and *L. niger*, the two most abundant species in our study, complemented each other: habitat patches with high numbers of one of the species had low numbers of the other one ($r = -0.69$, $p = 0.0000$); together they dominated in numbers in almost all study patches. *L. niger* was usually abundant also in sites where we found *M. rugulosa* ($r = 0.41$, $p = 0.01$). On the contrary, the nest numbers of *M. rugulosa* and *M. rubra* correlated negatively ($r = -0.44$, $p = 0.007$), as did those of *F. fusca* and *L. niger* ($r = -0.36$, $p = 0.03$).

Testing predictions on urban species

In section ‘Expected main factors affecting colonization’, we formulated a set of biogeographical, ecological and behavioural attributes which we expect to be crucial in successful colonization of cities. We first tested our prediction on biogeography, using the knowledge on the faunal element to which each species belongs (Table 1). As expected, our urban set of species included a disproportionately large number of regional species belonging to the Palaearctic element, and the species belonging to the Boreo-Montane element were strongly underrepresented in our study (Table 2).

Next we tested the role of ecology by utilizing the information on the habitat amplitude of each species (Table 1). As expected, habitat generalists (eury- or polytopic species) were overrepresented, whereas regional habitat specialists (steno- or oligotopic species) were highly underrepresented (Table 3). The linear regression model relating the range of distribution to habitat amplitude of the species explained only 12% (df-adjusted $r^2 = 0.09$, $p = 0.055$) of the total variation, emphasizing the importance of both zoogeography and ecology in determining the regional set of successful urban species. Of the eight pioneer species selected in section 'Expected main factors affecting colonization', five belonged to the six most abundant species in our study: *Lasius niger*, *L. flavus*, *Myrmica rubra*, *M. ruginodis*, and *Formica fusca*.

Leptothorax acervorum and *L. muscorum* ranked as eighth and 13th species in the abundance list, respectively. Only nine of their 20 nests were found in decaying wood (stumps, none in sticks) — all other nests were located in the ground (under stones and without stones, under moss). Notably, we did not find a single nest of the dendrobiont *Camponotus herculeanus*, a species dependent on dead wood. Apparently dead wood *per se* was not a limiting resource, however. This is evident from the amount and proportion of nests of the four most abundant species (after excluding the hypogeal *L. flavus*) found in dead wood: they occupied 92% of the 61 stick nests and 93% of the 209 stump nests found; the share of *M. rubra* alone was 41% and 55%, respectively.

Unexpectedly we found only one nest of the pioneer species *M. scabrinodis* — in a patch where the combined number of the numerically dominant *M. rubra*, *M. ruginodis*, *L. niger* and *L. platythorax* was low (13 nests; only one patch had a lower number, 10).

As expected, we found an impoverished number of wood ants of the *Formica rufa* group, only two of five potential species, although the nest number of these two species was substantial (Table 1). Contrary to the expected, the combined number of mounds of the two wood-ant species correlated positively with the patch-specific number of ant species and the Shannon-Wiener diversity index (Spearman's $\varrho = 0.46$, $p = 0.005$ and $\varrho = 0.42$, $p = 0.011$, respectively).

We found a total number of four territorial species, five temporary social parasitic species (four of which are territorial), and no slave-making species. The proportion of species dependent on other ant species during some stage of their life cycle was, however, not statistically significantly lower in our study than in the non-urbanized set of species in the vicinity of Helsinki (*see* Table 1). Notably, the temporary social parasite of the numerically dominating *L. niger*, *L. umbratus*, and its temporal social parasite, *L. fuliginosus*, seemed to have settled successfully to our study area (Table 1).

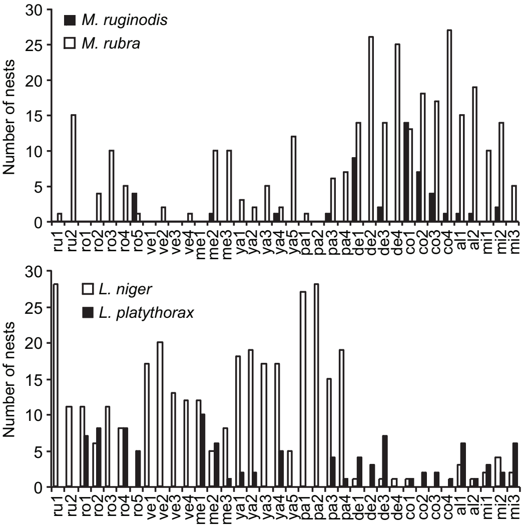

Fig. 4. The occurrence of two species pairs, *Myrmica rubra* and *M. ruginodis*, and *Lasius niger* and *L. platythorax*, in our study sites. Study habitats: ru = ruderal fields, ro = rocks, ve = roadside verges, me = meadows, ya = yards and residential areas, pa = parks, de = mixed deciduous forests, co = coniferous forests, al = allotment gardens, mi = mixed habitats; numbers that follow the abbreviations refer to the replicates within habitats.

Discussion

Studies on the effects of urbanization on animal and plant communities have focussed on a few central themes: impoverishment of species richness, homogenization of urban faunas and floras, and ecological attributes of successful urban species. In the following, we shall relate these main themes to the findings of the present study. Before proceeding with our discussion, we have to note that our study could not address two important aspects of colonization and survival, i.e., the size of the habitat patch, and its age. In a Japanese comparative study on the ants of two towns, Yamaguchi (2004) showed a positive relation between species richness and the size of the parks, a finding in agreement with the theory of island biogeography by Mac Arthur and Wilson (1967). Yamauchi (2004) also detected a negative correlation between species richness and the age of the parks under urban stress, which is an expected finding as urban habitats tend to degrade with age.

Table 1. Classification of urban ant species according to their zoogeographical distribution, habitat amplitude and main habitat association. The list of species is based on Saaristo's (1995) account on Myrmicinae and results of this study, and for Formicinae, on K. Vepsäläinen's (unpubl. data) selection of Collingwood's (1979) enumeration of a larger region, the natural-history province of Nylandia. Species found in Lauttasaari are given first in descending abundance (*n* = number of nests found; * = recorded only after this study). Element = the zoogeographical elements of the myrmecofauna within a radius of about 40 km from Helsinki city centre. The elements are modified and simplified from Czechowski *et al.* (2002). P = Palaearctic, ES = Euro-Siberian, BM = Boreo-Montane; possible occurrence of species in North America omitted. Habitat amplitude = habitat-use specificity for each species. E = eurytopic, P = polytopic, O = oligotopic, S = stenotopic. Main habitats = habitat type(s) from where each species is most often found in the vicinity of Helsinki. The habitat amplitude and main habitat columns are based on Collingwood (1979), Saaristo (1995), Czechowski *et al.* (2002), and are tailored to southern Finland by K. Vepsäläinen (unpubl. data). Species-specific footnotes (1–6) are based on Czechowski *et al.* (2002) and K. Vepsäläinen (unpubl. data).

Species (*n*)	Element	Habitat amplitude	Main habitats
Lasius niger (343)	P	E	Ubiquist/open habitats
Myrmica rubra (311)	P	E	Ubiquist
Formica fusca (123)	P	E	Ubiquist/open habitats
Lasius flavus (114)	P	E	Ubiquist/open habitats
Lasius platythorax (100)	P	E	Forests, rocks with pine
Myrmica ruginodis (49)	P	E	Forests, bogs
Myrmica rugulosa (26)	ES	S	Eskers, urban lawns
Leptothorax acervorum (15)	P	E	Forests, bogs, rocks
Formica rufa[1,2] (15)	P	P	Ecotones, open forests
Lasius umbratus[3] (10)	P	P	Deciduous forests
Formica polyctena[1,2] (10)	P	P	Forests, forest ecotones
Lasius fuliginosus[1,4] (6)	ES	P	Deciduous forests
Leptothorax muscorum (5)	ES	P	Forests, rocks with pine
Myrmica lobicornis (3)	BM	P	Open woodland
Formica truncorum[1,2] (2)	P	P	Ecotones, rocks with pine
Myrmica scabrinodis (1)	ES	O	Bogs
*Formicoxenus nitidulus**	P	P	In *F. rufa* –group mounds
Myrmica sulcinodis	BM	O	Well drained sandy sites
Harpagoxenus sublaevis	BM	O	Obligate dulotic species[5]
Camponotus herculeanus	BM	P	Forests
Formica lemani	BM	O	Forests
Formica aquilonia[1,2]	BM	P	Forests, forest ecotones
Formica lugubris[1,2]	BM	P	Forests, forest ecotones
Myrmica sabuleti	ES	S	Eskers
Temnothorax tuberum	ES	O	Eskers
Myrmica schencki	P	O	Eskers, rocks with pine
Tetramorium caespitum	P	S	Eskers
F. sanguinea[1,2,6]	P	P	Dry, warm habitats
F. pratensis[1,2]	P	O	Open, warm habitats
F. exsecta[1,2]	P	P	Meadows

[1] Territorial species.
[2] Temporary social parasite of *F. fusca*-group species.
[3] Temporary social parasite of *L. niger* and *L. platythorax.*
[4] Temporary social parasite of *L. umbratus.*
[5] Enslaves *Leptothorax acervorum* and *L. muscorum* in decaying (pine) stick nests.
[6] Facultative slave-maker of *F. fusca*-group species.

Main factors affecting colonization

We first tested the importance of biogeography and ecological attributes of species in affecting colonization of cities. Our results on the growing success of colonization as a function of the range of species distribution (characterized by the faunal element to which it belongs) and the habitat amplitude were strongly supported — given that our study area was located clearly within the range of the species. Thus, even though, e.g., *Myrmica schencki*, *Temnothorax tuberum* and, especially, *Tetramorium caespitum* all belong to the Palaearctic faunal element with extensive distribution, we did not find any of them. This absence strengthens the importance of biogeography, as all these species live in southern Finland at their northern limit of distribution, thus being also rare in the vicinity of Helsinki. Our finding is in agreement with those on a large number of family-level taxa studied on the species level in Warsaw and the surrounding Mazovian lowlands, including ants (Czechowski & Pisarski 1981, Czechowski *et al*. 1982a, 1982b), the urban ant study of Sofia (Antonova & Penev 2006), and the urban ant study by Vepsäläinen and Pisarski (1982b) along a long geographical gradient.

Likewise, habitat generalists (eury- or polytopic species) were overrepresented in our urban study, whereas regional habitat specialists (steno- or oligotopic species) were highly underrepresented; again in agreement with findings by Czechowski and Pisarski (1981), Czechowski *et al*. (1982a, 1982b), and Vepsäläinen and Pisarski (1982b). The congruence between the zoogeography and ecology in the species composition of successful urban species (Table 1) is understandable, because the larger the distribution of a species, the more likely it is an ecological ubiquist, and the smaller the area, the more specialized the species tends to be. Ecological ubiquists usually also are common and abundant pioneer species independent of other species during colony founding, which increases their dispersal and colonization capacity.

Dispersal capacity as such is, however, not sufficient to qualify as a good colonizer of cities. On the basis of its powerful dispersal in large numbers, *C. herculeanus* — a Palaearctic species distributed throughout Fennoscandia (Collingwood 1979) and not rare in the forested surroundings of Helsinki (K. Vepsäläinen unpubl. data) — would be expected to be a common city ant, but in this case habitat requirements probably intervene. Our study area harboured relatively plenty of suitable macrohabitat for the species. But dying or dead wood — the necessary microhabitat — when available, was preempted by the four most abundant urban species, emphasizing the nest site requirements of a species. Preemption of nest sites probably also affected the two common Finnish *Leptothorax* species, *L. acervorum* and *L. muscorum*, both among the eight pioneer species found on the early primary-succession islands in the Baltic Sea (Vepsäläinen & Pisarski 1982a). They also mostly nest in decaying wood, sticks usually

Table 2. The number of species recorded in the present study (“Lauttasaari”), and that of additional species known to occur around Helsinki (“Environs”; for details, *see* Table 1), tested for equal representation in three zoogeographical elements: P = Palaearctic, ES= Euro-Siberian, BM = Boreo-Montane (Fisher’s exact p = 0.043). The numbers in parentheses give the contribution of each cell to the total likelihood chi-square statistics (total = 7.08, p = 0.029); “+” indicates that the observed contribution was higher than expected, and “–“ lower than expected.

	P	ES	BM	Total
Lauttasaari	12 (+5.3)	4 (+1.3)	1 (–2.8)	17 (3.8)
Environs	5 (–3.9)	2 (–1.0)	6 (+8.2)	13 (3.3)
Total	17 (1.4)	6 (0.3)	7 (5.4)	30 (7.1)

Table 3. The number of species recorded in the present study (“Lauttasaari”), and that of additional species known to occur around Helsinki (“Environs”; for details, *see* Table 1), tested for equal representation in two main groups of habitat amplitude: E = eurytopic and P = polytopic, versus O = oligotopic and S = stenotopic species (Fisher’s exact two-sided p = 0.007). The numbers in parentheses give the contribution of each cell to the total likelihood chi-square statistics (total = 8.55, p = 0.003); “+” indicates that the observed contribution was higher than expected, and “–“ lower than expected.

	E + P	O + S	Total
Lauttasaari	15 (+8.4)	2 (–4.2)	17 (4.2)
Environs	5 (–5.5)	8 (+9.8)	13 (4.7)
Total	20 (2.9)	10 (5.6)	30 (8.6)

being the predominating nest site of the species (e.g., Seifert 1996, Czechowski *et al*. 2002), but in our study only 45% of their nests were located in stumps and none in sticks.

Of the other small-island species (Vepsäläinen & Pisarski 1982a), *Lasius niger*, *L. flavus*, *M. rubra*, *M. ruginodis* and *Formica fusca* were among the six most abundant species in our study. *M. scabrinodis*, an as abundant species as the two congeners above on the rocky outcrops of the Tvärminne archipelago (Vepsäläinen & Pisarski 1982a, Savolainen & Vepsäläinen 1989), was found only once. *M. scabrinodis* is mentioned to suffer from urbanization (e.g., Saaristo 1995) without any explanation. But because the species is a very poor competitor (Seifert 2007), our results suggest that practically all suitable habitat patches available for it in our study area were preempted by ecologically more tolerant urban and competitively stronger species, mainly *M. rubra* and *L. niger*, but also *M. ruginodis* and *L. platythorax*.

In the context of habitat requirements, *M. rugulosa* gains special attention in Finland. In non-urbanized areas it is a rare species of mainly eskers (Saaristo 1995), but in Finnish cities it seems to be much more successful than in the environs (Saaristo 1995, K. Vepäläinen unpubl. data). Its success as an urban species (seventh in our abundance rank list, nesting often in lawns under strong urban pressure) — in spite of being a weak competitor (Seifert 2007) — is explained by the availability of extreme xerothermic habitat patches in the city. These are habitats too warm and dry for the competitively superior *M. rubra*. In such habitats *L. niger* is often abundant, but this species and *M. rugulosa* seem to avoid conflicts between each other, at least aggressive ones causing losses of workforce (Czechowski 1979).

The impoverished number of wood-ants of the *Formica rufa*-group species (two of five potential ones) and their remarkably lower nest densities in our study compared to the environs of Helsinki (K. Vepsäläinen unpubl. data) and to the Finnish forests overall (Rosengren *et al*. 1979), can best be explained by the strong fragmentation of forests in our study area. Vepsäläinen and Wuorenrinne (1978) found that forest fragmentation leads to abandonment of large mounds and construction of numerous small nests. Such nests located in urban areas had lower inner summer temperatures (even by 10 °C) than nests in more intact areas, probably reducing the production of especially gynes (*see* also Sorvari & Hakkarainen 2005). Although we did not estimate the sizes of wood ant colonies found, indirect evidence indicates weak colonies: the mounds were small and the density of foragers on the ground was low. Notably, we found several mounds of both *F. rufa* and *F. polyctena* within two one-hectare study plots, once together with *F. truncorum*, another territorial species. Also, the number of wood-ant mounds correlated positively with the patch-specific species richness and diversity. Because wood ants are territorial species which exclude weaker colonies of the same species and other territorial ant species within their territory (Pisarski & Vepsäläinen 1989, Savolainen & Vepsäläinen 1989) and generally reduce the species richness and diversity of ant assemblages (Savolainen *et al*. 1989, Punttila *et al*. 1991, 1994, 1996, Vepsäläinen *et al*. 2000), our findings suggest that in our study area wood ant colonies (and their territories) are small and vulnerable to extinction — probably remnants of earlier, healthy populations (cf. Vepsäläinen & Wuorenrinne 1978).

Relaxed competition by wood ants probably has favoured especially *L. niger* and *M. rubra*, both highly successful urban species often with high nest densities. Both species also benefit from the abundance of aphids, the main food stock of many ants, which is exceptionally high in many urban environments (Pisarski & Trojan 1976, Pisarski 1979). Complementary occurrence of these two by far the most and almost equally abundant species in our study is explained by competition between the species (Czechowski 1985), leaving only few study patches with relaxed competition for other, submissive species. Preemption of most habitat patches by these two species probably severely decreases the odds that fundatrix queens by other species (e.g., *C. herculeanus*; *see* above) could settle and start a colony (though *see* examples to the contrary below). Because *Leptothorax acervorum* and *L. muscorum* gain indirectly protection against *Myrmica* and *Lasius* (*s. str*.) species by strong colonies of the *Formica rufa*-group species (Savolainen & Vepsäläinen 1989; *see* also

Rosengren 1986), in our study area *Leptothorax* species probably have suffered from the reorganization of interspecific competition, caused by the shortage of strong wood-ant colonies.

Finally, we predicted poor success of social-parasitic ant species in colonizing cities, when their host densities are low. Of top-dominant territorial species, *Formica rufa*-group species and the facultative slave-maker *F. sanguinea* all are temporary social parasites which during their colony founding rely on species belonging to the subgenus *Serviformica* (Czechowski *et al*. 2002) — in our study area *F. fusca*. Because the host species was locally abundant in suitable habitats for the above territorial species, the reason for the rarity or lack of wood ants is more likely due to lack of large enough suitable habitats (*see* above). The unexpected absence of *F. sanguinea* — a pioneer coloniser of taiga clearcuts (Punttila *et al*. 1991) — could be caused by three factors which may lead to colonization failure: (1) competition pressure by the stronger wood ants in habitats common to the species (Punttila *et al*. 1996, Savolainen *et al*. 1989), (2) elsewhere competition by L. *niger* or *M. rubra*, including predation on fundatrix queens, and (3) scarcity of *F. fusca*, the temporary host during colony founding. The same factors may hold for *F. exsecta*, another temporal social parasite of *F. fusca*, though rarity or lack of undisturbed meadows in our study area is plausibly the most important factor for the absence of this mound-building species.

Of other social-parasitic species known to occur in the vicinity of Helsinki, we did not find the obligatory slave-maker *Harpagoxenus sublaevis*. It needs a high density of nests of *Leptothorax acervorum* or *L. muscorum* (K. Vepsäläinen unpubl. data), a condition not met with in our study. For example in central Europe with a density of > 200 potential host nests/100 m^2, only 6–10 nests are occupied by *H. sublaevis* (Seifert 2007). The guest ant *Formicoxenus nitidulus*, living in wood-ant mounds, was observed only once. On the other hand, we expectedly found many nests of *L. umbratus* which during colony founding requires *L. niger* or *L. platythorax* as host (Seifert 2007), both abundantly available in our study area. Because this temporary social parasite nests between tree roots deep in the ground (Collingwood 1979), its nests are hard to find; consequently the relative nest densities in our data must be gross underestimates of the real ones. Thus it was not surprising to find many nests of *L. fuliginosus*, a temporary parasite of *L. umbratus*, which nests in old or damaged trees. Finally, without special effort we found several times the *microgyne* morph of *Myrmica rubra*, a (practically) workerless intraspecific obligate parasite, known for some time by the species name *M. microrubra* (Seifert 1993, but *see* Savolainen & Vepsäläinen 2003, Steiner *et al*. 2006). The parasite needs high densities of the host (Savolainen & Vepsäläinen 2003); a condition well met with in our study area.

A comparison with other urban ant studies

Urban ant studies have been conducted in many central-European cities; we will compare their results to our own findings (Table 4). Here, a word of reservation is in place. The studies vary in their extensiveness in space and time, degree of urbanization included, the methodological richness or methods applied, and the presentation of the results. Therefore, we had (without knowing the cities studied) to use subjective delimitations of the data to keep within an "urban data set", and to apply quick-and-dirty estimates of abundance relations of the species.

In spite of the above difficulties, main similarities and differences among the cities emerged. *Lasius niger* was the most abundant species in all studies, except in Warsaw where it was the second one, and its prevalence usually increased with urban pressure (though the Warsaw and Leipzig studies could not exclude the possibility of *L. platythorax*). Of the top-seven Finnish urban species, three additional species were in the top-seven list in at least some central-European cities: *L. flavus* (in all six cities, though Mainz had to be evaluated subjectively), *Myrmica rubra* (five cities) and *M. rugulosa* (three cities). *Tetramorium caespitum* was not found in our study. Its absence anywhere in our collections from Helsinki (K. Vepsäläinen unpubl. data) can be understood on the basis of its scarcity in the environs of the city (Saaristo 1995).

The species has been considered one of the most successful urban ants more south (Table 4). It has also invaded North America in ballast soil, and is known there commonly as the pavement ant. In Quebec, the species is one of the most successful urban species, together with *Lasius neoniger* (Lessard & Buddle 2005), the vicariant of *L. niger* in North America. After the revision of the Western Palaearctic *T. caespitum*/*impurum* complex by Schlick-Steiner *et al.* (2006), however, it is evident that the *T.* cf. *caespitum* complex consists of seven species. No revision on the identity of urban *Tetramorium* species is available.

Also *M. rubra* has invaded many areas in eastern and northeastern America, where it has developed very high densities, and consequently locally reduced the abundance of native ants (Groden *et al.* 2005). In Europe, the species is in the middle of the abundance rank list in Vienna, which is understandable as it is a North-Palaearctic species with a southern limit of distribution close to Vienna (Czechowski *et al.* 2002). The same is true for *M. rugulosa* (a Euro-Siberian species) which loses its role as a special urban ant in Vienna. There instead *Solenopsis fugax* (a Mediterranean species) takes the second place in the abundance rank (Schlick-Steiner & Steiner 1999; *see* also Pisarski & Czechowski 1978 for Warsaw, and Dauber & Eisenbeis 1997 for Mainz); a good example of the general trend of cities to favour thermophilic species, thermophilic being here a notion relative to regional temperatures and ant faunas.

The biogeographical location of the city is also emphasized by the six abundant and typical urban ant species of Linz (Ambach 1998): three of them have not been found in Finnish cities, and two have never been found in Finland. There, one of the latter species, *Formica fuscocinerea* (by the name *F. lefrancoisi* in the original), takes the place of *F. fusca* in Helsinki. On the basis of studies on the fauna of Warsaw (Czechowski & Pisarski 1981, Czechowski *et al.* 1982a, 1982b) covering extensively the regional insect taxa and additionally some other inverte-

Table 4. The occurrence of species in Lauttasaari (Lau) and in urban areas of selected central-European cities, sorted according to decreasing latitude: Warsaw (War; Pisarski & Czechowski 1978, Pisarski 1982; suburb excluded), Leipzig (Lei; Richter *et al.* 1986), Cologne (Col; Lippke & Cölln 1991, supplemented with Behr *et al.* 1996), Mainz (Mai; Dauber 1997: table 3), Linz (Lin; Ambach 1998: table 2) and Vienna (Vie; Schlick-Steiner & Steiner 1999). The species list is restricted to that of Lauttasaari; species found only in other areas are thus excluded (except *T.* cf. *caespitum*, but *see* text on its taxonomic revision). Total number of species (*n*) in parentheses; only outdoor-living species are considered. * = the study was conducted before *L. platythorax* was split from *L. niger*. The cipher for each species and city refers to numerical dominance (1 = most abundant; + = recorded).

	Lau (18)	War* (21)	Lei* (11)	Col (24)	Mai (25)	Lin (27)	Vie (38)
Lasius niger	1	2	1	1	1	1	1
Myrmica rubra	2	6	4	2	6	6	20
Formica fusca	3	+		11		21	33
Lasius flavus	4	1	6	3	2	7	4
Lasius platythorax	5						
Myrmica ruginodis	6	+	+	9			22
Myrmica rugulosa	7	4		5	12	5	14
Leptothorax acervorum	8			21		26	
Formica rufa	8	+					
Formica polyctena	10						
Lasius umbratus	10	+	+	23			
Lasius fuliginosus	12	+		14			
Leptothorax muscorum	13					27	
Myrmica lobicornis	14						
Formica truncorum	15						
Myrmica scabrinodis	16	+		10	15	22	19
Formicoxenus nitidulus	+						
Tetramorium cf. *caespitum*		4	8	4	2	2	3

brate taxa, the importance of the biogeographical location and the ecological attributes of successful colonizers of cities, can be generalized (with a few taxa deviating from the trend).

Impoverishment of urban faunas

Our study is in agreement with other urban ant studies in reporting decreased species richness relative to surrounding rural areas (Pisarski 1982, Vepsäläinen & Pisarski 1982b, and references in Table 4). The stronger urbanization is, the more drastic the impoverishment is, a result most clearly seen in central-European studies classifying study patches along increasing urban pressure (references in Table 4), a more preferable approach to using an urban–suburban–rural gradient along which different classes of urban pressure may mix. In stark contrast to the impoverishment of urban ant faunas, the population size of the few highly successful urban ant species may in cities be larger than the pooled population size of all ant species in the rural surroundings (Pisarski & Czechowski 1978). Also, outside Warsaw in a meadow habitat (*Arrhenatheretum*), the ants counted 61% of the ground-layer insect fauna, whereas in urban greens of the city the contribution of ants was 85%–99% (Pisarski & Czechowski 1978).

The decline in ant species richness with urbanization is similar to that reported for large number of other taxa studied. The most extensive set of studies published so far, *Species composition and origin of the fauna of Warsaw*, *Parts 1–3* (Czechowski & Pisarski 1981, Czechowski *et al.* 1982a, 1982b), included 45 taxa, mostly of family rank and identified to species. In most taxa studied and compared with the fauna of the surrounding Mazovian Lowlands, impoverishment by urbanization was clearly demonstrated, though differences in details among the taxa varied as to the consequences of urban pressure. Klausnitzer (1987: table 57) summarizes the Warsaw results on urban and suburban areas.

A much-neglected aspect in urban ant studies is the dependence on ants of a huge number of symbiotic (*sensu lato*, including scavengers, parasites, parasitoids and predators) insects, crustaceans and other arthropods (*see* table 13–1 in Hölldobler & Wilson 1990). As many symbionts of ants are host-specific, impoverishment of urban ant faunas will evidently cause gross reduction in the diversity of their symbionts. In Fennoscandia, the *Formica rufa*-group wood ants belong to the common and abundant species, but are among the first ones to suffer from urbanization. Because many local and rare myrmecophilous arthropods are entirely dependent on wood ants as hosts (Collingwood 1979), extinctions of wood ants will lead to a loss of a large and highly diverse specialist fauna.

Homogenization of urban faunas

Urbanization as a major cause of biotic homogenization has recently become one of the central themes in urban studies. By definition, biotic homogenization means increasing similarity of species assemblages among areas (McKinney 2006). In urban studies, the definition posits biotic homogenization into the context of urban pressure instead of cities as a whole. Species adapted to heavy urban pressure tend to become top-abundant species over vast urban areas and dominate especially in city centres, whereas differences among cities are more predominant in suburban and fringe urban habitats (for general homogenization *see* McKinney 2006; for birds *see* Clergeau *et al.* 2006).

Our comparison of ant faunas of many European cities (Table 4) seems to support the above generalization by pinpointing a few top-abundant species over most of the cities, *L. niger* being the leading homogenizer. It is, however, a matter of further empirical studies to decide how strong this possible homogenization is. Top-abundant species common among cities tend to be common and abundant also in the environs of the city with plenty of suitable habitats available. Along with the change in regionally common and abundant ant species also the city top-dominants change. We disagree with opinions reducing the problem to global statements without considering biogeography and regional differences. For example Savard *et al.* (2000) maintain that the structure, functions and constraints of urban ecosystems are quite similar worldwide, and Clergeau *et al.* (2006) suggest that in general the ecological structures are similar in different biogeographical areas. These statements may hold at a higher level of generalization, but in the context of homogenization of urban faunas and floras certainly not, as shown above on a northern and central European scale.

Indeed, along an urban gradient from northern Finland to Warsaw, the turnover of ant faunas along the gradient was faster among cities than among regions around the cities (Vepsäläinen & Pisarski 1982b). Moreover, several species, especially thermophilic ones, are substantially more abundant in cities than in their environs. Not all of such species are common to the cities of northern and central Europe, but are dependent on available source populations. For example *Solenopsis fugax*, a successful Mediterranean-element species of the city centres of Warsaw (Pisarski & Czechowski 1978) and Vienna (Schlick-Steiner & Steiner 1999), is practically unable ever to colonize Helsinki without a drastic climatic change. A shift from northern and central European cities to more southern arid areas is even more likely to discourage broad-scale generalizations. Although cities of more northern latitudes may favour thermo- and xerophilous species, in warmer and drier regions cities may (because of being moister and cooler than their environs), on the contrary, favour species which live in cooler and moister habitats than do most of the regional species (Pisarski & Vepsäläinen 1987).

The above examples on different aspects of homogenization demonstrate that the issue is not simple. Clearly, empirical studies with special attention to the scale of studies and comparisons are needed. The results may be substantially different on α, β and γ scales (e.g., Willig *et al.* 2003), as should be evident already from the urban ant literature used by us in comparing similarities and differences among cities.

Conclusions

Traditionally, cities have been regarded as human-induced, non-natural islands isolated by a hostile "sea." This paradigm has led to a plethora of studies on various fragmented landscapes, including some on cities (e.g., Faeth & Kane 1978), where the main aim has been to relate species richness to habitat "island" size by curve-fitting (*see* Haila 2002). As any habitat patch within a mosaic of other patches, cities and their habitats poorly fit into the metaphor of an island isolated by extensive ocean waters. Rather, studies on much less isolated natural islands (e.g., those in the Baltic Sea) can be useful while studying fragmented habitats (Vepsäläinen & Pisarski 1982a, Haila 1990), including those of cities (Vepsäläinen & Pisarski 1982b, and this study).

Instead of being hostile "seas", rural landscapes are source areas for many if not most urban organisms. Cities with their impoverished and, for many species, often low-quality habitats rather serve as sinks. In our study area, species were mainly drawn from the pool of common and abundant species in the environs of the city; this seems to be a general finding in many urban studies on various taxa (*see* discussion above). Here, the size and quality of the habitat patch are crucial denominators for the success of any species — size and quality naturally to be considered relative to the ecology of the species.

Finally, urban studies often look for indicator species of urban pressure or habitat degradation (e.g., McFrederick & LeBuhn 2006). We suggest, however, that it may be more fruitful to search for measures how to improve the biodiversity of cities. It is easy to estimate the urban pressure of city centres by naked eye, but it is ecologically more challenging to find out how to increase the habitat diversity in order to obtain representative rural species to the city (for suggested measures *see* Mabelis 2005). Success in such an endeavour would not only improve the function of urban ecosystems by turning urban sink habitats toward more self-sustaining ones. For many inhabitants of large cities, this approach would also mean an improvement of the quality of their own lives.

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Appendix. Environmental variables categorised into five classes: 1 = sparse coverage or a few items, 5 = dense coverage or many items (*see* Material and methods for category cutpoints). Habitat = habitat patch with replicate number: ru = ruderal field, ro = rocks, ve = roadside verges, me = meadows, ya = yards and residential areas, pa = parks, de = mixed deciduous forests, co = coniferous forests, al = allotment gardens, mi = mixed habitats. Environmental variables: Closure = canopy closure, Vegcover = field-layer coverage of vascular plants, Stumps = tree stumps, Sticks = sticks, Stones = stones.

Habitat	Closure	Vegcover	Stumps	Sticks	Stones
ru1	1	1	1	1	1
ru2	2	2	1	2	2
ro1	2	2	3	2	2
ro2	2	3	3	3	3
ro3	3	3	2	2	3
ro4	2	3	2	2	3
ro5	3	3	3	3	4
ve1	1	2	1	1	2
ve2	1	2	1	1	2
ve3	1	2	1	1	2
ve4	1	3	1	1	2
me1	2	2	2	2	3
me2	2	3	2	2	2
me3	2	3	2	3	3
ya1	2	3	2	1	2
ya2	2	3	2	1	2
ya3	2	3	2	1	4
ya4	2	3	2	1	2
ya5	3	3	3	1	4
pa1	1	2	1	1	2
pa2	1	2	1	1	2
pa3	2	2	2	2	2
pa4	2	3	2	2	3
de1	5	4	3	3	3
de2	4	3	3	3	3
de3	3	3	4	3	3
de4	4	4	4	2	3
co1	5	4	4	2	3
co2	4	3	3	3	3
co3	4	3	4	3	3
co4	4	4	3	2	3
al1	3	3	4	2	5
al2	3	3	4	2	5
mi1	2	2	3	4	3
mi2	3	3	3	4	2
mi3	3	3	3	4	3