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Comparative analysis of the population structure of *Crematogaster subdentata* and *Lasius neglectus* in the primary and secondary ranges (Hymenoptera: Formicidae)

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Abstract
The population structure of *Crematogaster subdentata* Mayr, 1877 in the primary (native) (Uzbekistan) and secondary ranges (Crimea, Rostov-on-Don) is analyzed. The data obtained indicate an uncommon behavior for invasive ants – the formation of supercolonies in the primary range (the size of the foraging area is about 600 m^2) in the urban territory. Nesting in houses and in trunks of old trees occurs both in the zone of invasion and in the primary range. The data of the distribution of the second invasive species in the same regions – *Lasius neglectus* Van Loon et al., 1990 are provided. Comparison of the population structure (ratio of the mono- and polycalic colonies, presence of the supercolonies and their sizes), parameters of the colonies (average number of the nests and forage trees per colony) showed the advantage of *Crematogaster subdentata* over *Lasius neglectus*, which is gradually crowded out by the first species in the places of contact.

Keywords: Ants, invasion, monocaly, polycaly, supercolonies, pests, interspecific relations.

Introduction

The study of invasive ant species is one of the relevant areas in modern myrmecological research. Invasive species have been accidentally introduced outside their native ranges and have a negative, often very significant, effect on both native fauna and natural ecosystems as a whole (Holway et al. 2002). Some invasive ant species in the shortest possible time after the start of invasion can create populations with high density of colonies that cooperate with each other, and displace not only local ant species, but also other invertebrates (Cremer et al. 2006).

There are known now more than 200 ant species introduced into new habitats (Suarez et al. 2010), but not all of them are able to form supercolonies (or secondary federations, according to the terminology of Zakharov 1991). One of the dangerous pest ant species in Europe is *Linepithema humile* (Mayr, 1868). Some its populations in Southern Europe stretch continuously for hundreds of kilometers along sea coasts (Giraud et al. 2002), and its spread can be very high, up to 150 m annually (Suarez et al. 2001). In invaded territories native ant species might be often completely crowded out, and only workers of invasive species are found on food baits, as shown, for the example, for *Wasmannia auropunctata* (Roger, 1863) (Breton et al. 2005).

Although most of the invasive species inhabit the tropical and subtropical regions, some of them, e.g. *Myrmica rubra* (Linnaeus, 1758), became an essential pest in the temperate zone of the North America (Wetterer & Radchenko 2011).

Two invasive ant species, *Lasius neglectus* Van Loon, Boomsma et Andrásfalvy, 1990 and *Crematogaster subdentata* Mayr, 1877, are found in natural and anthropogenic habitats in Ukraine and Russia: (Radchenko et al. 2012; Stukalyuk 2015, 2018; Stukalyuk & Radchenko 2018; Stukalyuk & Netsvetov 2018).

Lasius neglectus was described from Budapest in 1990, and now its range covers Central and Southern

Europe, the Caucasus, Crimea, southern regions of the European part of Russia, Asia Minor, Iran, Israel, Kyrgyzstan and Uzbekistan, and found also in Kyiv (Seifert 2000; Schultz & Seifert 2005; Schultz et al. 2006; Espadaler et al. 2007; Czechowski et al. 2012; Radchenko et al. 2012; Artokhin et al. 2013; Radchenko 2016; Stukalyuk 2018; Stukalyuk & Radchenko 2018). It was assumed till now that *L. neglectus* could arise in Asia Minor (Seifert 2000; Cremer et al. 2008; Ugelvig et al. 2008; Stukalyuk & Radchenko 2018), but very recently we provided evidences that the native range of *L. neglectus* is the Central Asia (Stukalyuk et al. 2020).

Crematogaster subdentata almost certainly originated in the Middle Asia. It was described from Turkmenistan and Uzbekistan, and its native range covers, besides the Middle Asia and southern Kazakhstan, eastern Anatolia, southern Transcaucasia, Iran, Afghanistan, western China and Tibet (Dlussky et al. 1989; Arakelyan 1994; Radchenko 2016).

In the secondary range *C. subdentata* was found in the parks of Kherson and Nikolaev, as well as in the Saki district of Crimea (Stukalyuk 2015) and in Rostov-on-Don (Radchenko 2016). According to our data (Stukalyuk 2015; Stukalyuk & Netsvetov 2018), *C. subdentata* here has biological and behavioral features characteristic for invasive ant species: small size of workers, polycalic colonies, which able to unite into supercolonies that occupy big areas, tolerance of workers from different colonies to each other and aggressiveness towards other ant species (Holway et al. 2002; Ness & Bronstein 2004).

Within the native range in the city of Tashkent, *C. subdentata* is also capable to form supercolonies (Akhmedov 2015), what distinguishes this species from other invasive ants. Particularly, *Lasius neglectus* does not form big colonies and supercolonies in the native range (Stukalyuk et al. 2020). Furthermore, at least in Eurasia, *C. subdentata* is the only known invasive arboreal species.

Below the data on coexisting of *C. subdentata* and *L. neglectus* on the same territory, on the size and structure of their colonies and populations are given for the first time, and their interspecific relations are observed.

The aim of this work is to compare the population structure of *C. subdentata* and *L. neglectus* in the primary and secondary ranges.

Objectives of the study are: a) assess the state of populations of both species in the same habitats; b) compare average characteristics of *C. subdentata* and *L. neglectus* colonies (number of nests, number of trees visited by workers, character of their activity on the foraging trails) and interactions between each other, as well as with the native ant species; c) assess the ecological potential of these species (the number of species of trees visited, the impact on the assemblages structure of the native ant species, the traits of colonization of various habitats).

Material and Methods

Study area

The studies were conducted in 2013 and 2017 in the Crimea (Saki district), Kyiv, Rostov-on-Don and Rostov Region, Tashkent and the Kyzylkum desert. In the Crimea and Rostov-on-Don both species are invasive, but in Uzbekistan they are native ones. The supercolony of *Crematogaster subdentata* and one *Lasius neglectus* colony was found in Saki district; in the rest of Crimea *L. neglectus* is widespread throughout the anthropogenically changed habitats. *C. subdentata* is absent in Kyiv, and *L. neglectus* is an invasive species here.

Collecting of ants and forage area mapping.

Collecting of ants and investigation of the nest density of *C. subdentata* and *L. neglectus* was carried out according standard methods (Dlussky 1965 a, b). The mapping of the forage areas of *C. subdentata* and *L. neglectus* was carried out according Dlussky (1965 b) and Zakharov & Goryunov (2009). Location of the main and auxiliary nests and the structural elements of the foraging area (the trails, visited trees with aphids' colonies) were applied on graph papers. We considered as one subunit of the supercolony an isolated polycalic colony, which connected with other subunit by communication. We found seven isolated supercolonies of *C. subdentata* in Uzbekistan and 10 ones in Rostov-on-Don and Bataisk (Rostov Prov.) (by five ones on each city), as well as the same amount of supercolonies of *L. neglectus* here. 30 polycalic colonies of *C. subdentata* were counted in Crimea (vil. Mihailovka, Saki Distr.). Route counting of the number of nests in trees and buildings (for *C. subdentata*), or nests in the ground, usually at the base of trees (*L. neglectus*), were carried out within the territory of each subunit. Counts within groups of trees were carried out in a strip of 10 m each, from the beginning of the territory of the foraging territory to its end (where ants forage on trees). Each route accounting was carried out parallel to the previous one, from the beginning of the territory to its end, at a distance of 10 m. The geographical coordinates of supercolonies were obtained using the Google Maps service, the boundaries of the subunits were outlined, and the area of the foraging territories. The number of nests was calculated based on the number of counting routes and the total length of them.

Detailed mapping of the foraging area

The detail mapping of one *Lasius neglectus* colony and three *Crematogaster subdentata* colonies was carried out in Rostov-on-Don. During mapping the foraging areas of *C. subdentata* 88 trees and shrubs of 19 species, and 20 trees of 3 species for this of *L. neglectus* where inspected. Six *C. subdentata* colonies were investigated in Tashkent, and four colonies – in the Kyzylkum desert. When mapping the foraging areas of *C. subdentata* in Tashkent,

500 trees and shrubs of 13 species were examined, and 100 trees and shrubs of 12 species were investigated for *L. neglectus*. Eleven colonies of *L. neglectus* were found in Kyiv in 2018, and 39 trees of 4 species were examined. The native ant species found together with *L. neglectus* and *C. subdentata* were registered. The general distribution of both invasive species in the cities was taken into account by the route method; the number of nests and/or level of the colony organization were counted every 100 m of the route in a 10 m wide strip.

The following parameters were also taken into account: a) the average number of nests per colony as a parameter, potentially reflecting its size; b) the average number of visited and protected trees as a parameter that reflects, in addition to size, expansiveness in the development of resources. Trees and shrubs visited by ants were determined to species or at least to the generic level.

For statistical data processing the Origin 8.0 program was used. The reliability of differences between the signs was checked using a t-test, with $p < 0.05$. The text and the tables show the values of attributes (mean ± standard error of mean).

Results

Habitats of Lasius neglectus *and* Crematogaster subdentata *and biological characteristics of these species in different regions.*

C. subdentata occupies varies habitats in Crimea: coastal canebrake, gardens, tree plantations, very often inhabits wooden houses, beams in stone houses and economic extensions, etc. It organizes foraging trails both on the ground, on above-ground sections of pipelines and on tree branches. *C. subdentata* also colonizes cane beds, where it builds fodder nests in the cavities of its stems, but it avoids xerophytic steppe places. The total size of the foraging territory of one supercolony of *C. subdentata* here was 270 ha. The same of the 111 investigated colonies of *L. neglectus* vary from 50 m^2 (monocalic colony) to 2 ha in two supercolonies in Evpatoria and Sudak (Crimea).

In Rostov-on-Don, *C. subdentata* lives mainly in private houses and in old low-rise buildings, although sometimes it has been found on the lower floors of relatively new high-rise buildings. In warm seasons *C. subdentata* workers forage mostly on trees around houses, and only at the end of winter they are foraging in indoor habitats. It distributes in Rostov-on-Don and Bataisk almost all over the cities, and superculonies are interrupted only by the streets, water ponds and tree strips more than 200 m length without houses.

In contrary, *L. neglectus* is distributed here more fragmentarily; large areas of continuous distribution of more than 300 m in length were found in nearby forest belts, in landfills, in places of dumping of construction waste, in parks and gardens.

Secondary nests outside of heated premises probably survive in the winter not every year, therefore they are located only in inhabited localities not further than 200 m from heated buildings. Colonies of *C. subdentata* are highly polygynous and populous: they may contain more than hundred queens and up to hundreds of thousands to millions workers. They build nests in dead, but yet dry, solid, not rotten wood, under the bark of trees (especially in poplar and willow), sometimes in heat insulation foam, in wood under tarpaper, and in other places, in particular, near hydro- and thermal insulation. Many nests are located in fairly solid materials and there is difficult to access them for detail investigation of its population. Activity and intensity of its workers on foraging trails are very high, comparable to those of *Lasius fuliginosus* (Latreille, 1798).

C. subdentata is most likely distributed during transportation of wood and garbage, containing its colonies. The economic and epidemiological significance of *C. subdentata* is little studied, in premises it is probably similar to those of *Monomorium pharaonis* (Linnaeus, 1758), and is aggravated by the possibility of outdoor foraging and by the larger number of workers.

In Kyzylkum desert, *C. subdentata* inhabits mainly sandy massifs with saxaul (*Haloxylon* sp.) and juzgun (*Calligonum* sp.) vegetation and builds nests in soil near the roots of saxaul. Its colonies are monogynous and monocalic, containing up to 1000 workers. The foraging area is limited to saxaul tree, near which the colony lives, where workers tend aphids or coccids and collecting various small invertebrates on trees, and they were found very rarely on the ground surface. Aphids were also found on the saxaul roots in September-October, probably ants transported them here.

It seems that *C. subdentata* lives in optimal conditions in Tashkent. Its main nesting sites here are old private adobe or wooden houses (96% of nests found), and only 4% of the nests were found in modern concrete buildings. Besides, one nest of *C. subdentata* was found in the garage among lumber. In other cities of Uzbekistan (Khiva, Urgench) large populations of *C. subdentata* were also found.

So, in cities *C. subdentata* is able to form systems of polycalic colonies and supercolonies (or secondary federations, by the terminology of Zakharov 1991). Polycalic colonies include one large central nest and smaller auxiliary nests connected with central one by trails. Queen and brood are present both in the central and in the auxiliary nests. The exchange of queens between auxiliary nests within the federation was observed several times. Marikovsky (1979) has noted that several queens could be found in the nest of *C. subdentata* in natural conditions, but in Tashkent were found huge populations of *C. subdentata*, incomparable by the nest density, number of workers and queens and population structure with those in natural habitats.

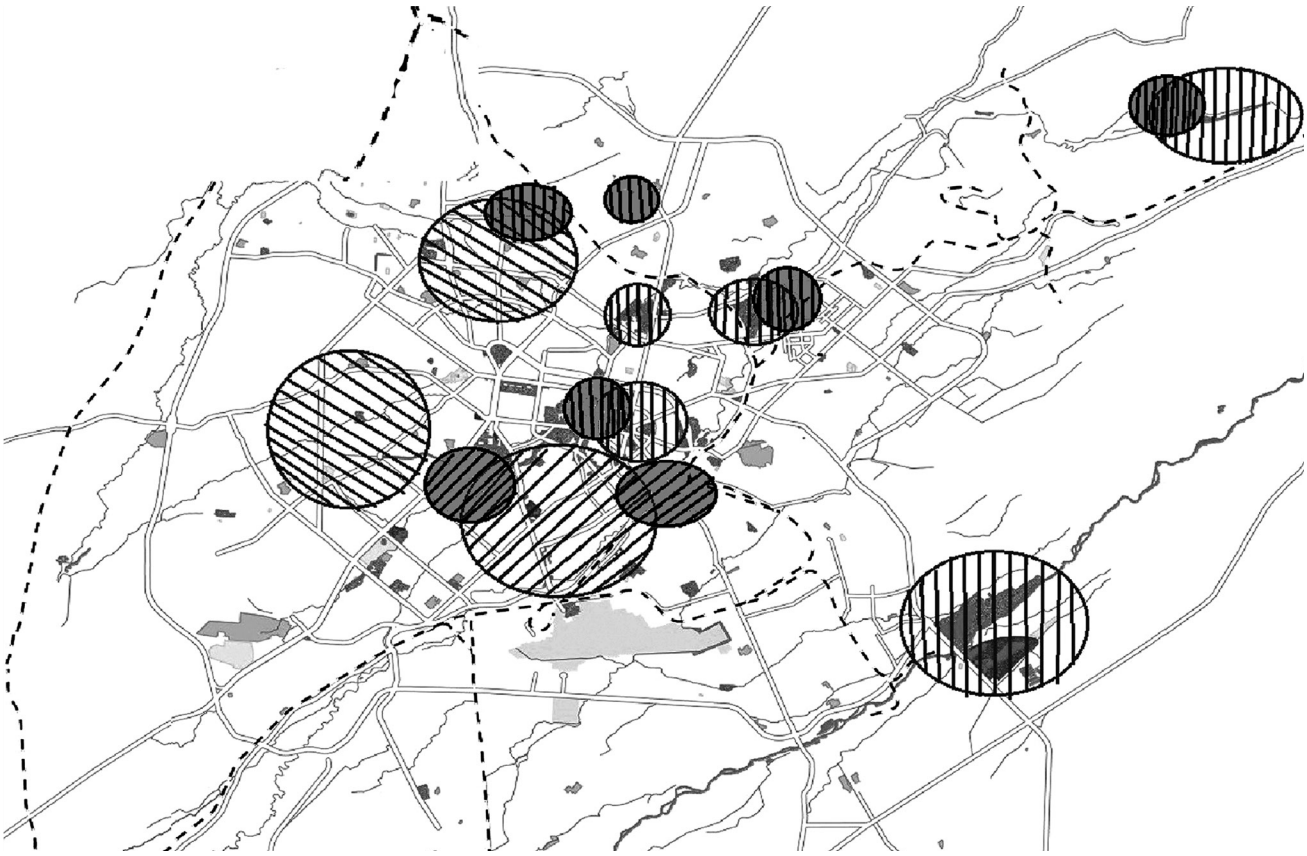

Fig. 1 – Distribution of *Crematogaster subdentata* and *Lasius neglectus* in Tashkent *C. subdentata*, polycalic colonies, *C. subdentata*, monocalic colonies, *L. neglectus*, > 20 nests per 100 m, *L. neglectus*, 10-20 nests per 100 m, *L. neglectus*, < 10 nests per 100 m.

Another characteristic feature of *C. subdentata* in Tashkent was presence of large number of winged gynes in their nests in spring, while males were completely absent. It is interesting to notice that nuptial flight of these ants in natural habitats occurs in September.

The supercolonies of *C. subdentata* may occupy all wooden parts of houses and buildings of various sizes, ranging from 50 m^2 to more than 100 m^2. The territory around houses an average size of 600 m^2 becomes a foraging area, where workers actively tend and spread aphids on each growing here tree.

C. subdentata successfully competes with *L. neglectus* in common foraging areas, sometimes completely displacing the latter species into surrounding areas. It can be argued that *C. subdentata* has no competitors among other species of ants of its size class [*L. neglectus*, *Tapinoma erraticum* (Latreille, 1798)] in the anthropogenic environments.

Workers of *C. subdentata* do not interrupt their activity in the winter in sheltered and heated premises. In general, they cause great inconvenience to people, destroying houses and damaging food sources, not telling about tending and protection of aphids on fruit trees.

Lasius neglectus is characteristic dweller of urbanized areas throughout the central and southern parts of Crimea, and was found outside the human settlements only in Kanakskaya gully in the vicinity of Privetnoe village. The dispersal of this species is most likely due to human activity, and it is accidentally imported into new habitats together with introduced plants. This explains its distribution mainly in parks and squares of cities and towns. All *L. neglectus* polycalic colonies were found in Evpatoria and Sudak in public gardens and parks not further than 100–300 m from the sea coast, and monocalic colonies, as a rule, are associated with single trees and were occurred up to 2–3 km from the coast.

This invasive species was found in Kyiv in 2017 year on the territory of the Mir Hotel (Goloseevsky district), and in summer of 2018 we discovered *L. neglectus* population in the city center, on Pushkinskaya and Proreznaya streets. Eleven polycalic colonies live here, workers visit trees planted in the holes, as well as trees in two adjacent squares.

The colonies of *L. neglectus* in Rostov-on-Don contain from 10 to several hundred queens (15 nests were excavated). Nests are built in the ground, often under stones, and near houses – in greenhouses and pots with indoor plants, but they occur rarely in premises; nests were found very often in places of accumulation of construction debris.

This species has significant potential for dispersion to the semi-natural habitats, because it successfully hibernates

and is generally weakly depends on humans. Currently, it is common or even widespread in disturbed habitats, e.g. in the forest belts along railways. Its dispersal probably occurs with the transporting of soil and building materials containing colonies. Some myrmecophylous arthropods are very common in *L. neglectus* nests, e.g. *Atelura formicaria* Heyden, 1855 and *Myrmecophilus acervorum* Panzer, 1799, ant-cleptobiont *Solenopsis fugax* (Latreille, 1798) was also found. *L. neglectus* coexists for a long time in semi-natural habitats with other ant species, except for *Lasius niger* (Linnaeus, 1758) and *Lasius alienus* (Foerster, 1850), particularly with ants of other size classes or trophic preferences, such as *Formica sanguinea* Latreille, 1798 or *Messor structor* (Latreille, 1798).

In Tashkent, *Lasius neglectus* usually meets locally and does not form large colonies, although the density of nests might be quite high, up to 20 nests per 100 m of route. There were no visible connection between the individual nests, as well as the no exchanges of workers, food, queens, brood, and there are no trails between nests. We also did not find any underground tunnels to neighboring nests during excavation of 20 nests. At the same time, there were not less than 10 queens per colony.

Table 1 – I – monocalic colony (1 nest), II – colony with simple polycaly (from 2 nests, but only 1 central one), III – true polycalic colony (from 2 to 5 central nests), IV – supercolony (up to 5 nests).

Region	Type of colony	*L. neglectus*	*C. subdentata*
Crimea	I	49.5	40.0
	II	16.2	30.0
	III	22.5	20.0
	IV	11.8	10.0
Kyiv	I	0	-
	II	0	-
	III	30.0	-
	IV	70.0	-
Tashkent	I	100	16.8
	II	0	16.6
	III	0	16.6
	IV	0	50.0
Kyzylkum desert	I	-	75.0
	II	-	25.0
	III	-	0
	IV	-	0
Rostov-on-Don	I	0	0
	II	30.0	30.0
	III	40.0	30.0
	IV	30.0	40.0

This species inhabits in Tashkent more humid and shady places: parks, tree plantations, the botanical garden, and orchards near private houses. Ants often build nests in trees and wood remnants, actively expanding the paths of xylophagous insects, and are also found in houses, even in ferroconcrete ones (the latter is not characteristic of *Crematogaster subdentata*). Workers abruptly reduce activity outside of the nests in summer in time of high temperatures, and virtually stop foraging. Nests of *L. neglectus* in the vicinity of the city were found in the dry grassland, but workers were not active outside till dusk. It is interesting to notice that workers of *L. neglectus* in Tashkent not only tend aphids, but are active predators and are aggressive towards other ant species, attacking them regardless of the size of their workers, and tightly clinging to their antennae and legs. The myrmecophilous cricket *Myrmecophilus acervorum* and bristletails, *Atelura* sp., were found in nests of *L. neglectus*

The structure of the foraging territories of Crematogaster subdentata *and* Lasius neglectus.

Both these species in their habitats are capable for effective development of the territory. They have large colonies and a protected foraging area, what is inherent in dominant and invasive ant species.

At the same time, colonies size of these species, as well as the ratio of colonies with different levels of social organization, may vary in different regions (Table 1). Thus, about half of *L. neglectus* colonies in Crimea, are small and monocalic.

In contrary, monocalic colonies were not found in Kyiv, and there are only polycalic colonies and supercolonies. Populations of *L. neglectus* in this city appeared recently, most probably not earlier that in 2014-2015, and they are in a state of active expansion now. Formation of large polycalic colonies and supercolonies is one of the conditions for the successful expansion of invasive ant species.

Invasion of *Lasius neglectus* started in Crimea no less than 40 years ago (Stukalyuk & Radchenko 2018), its expansion probably started to subside and monocalic colonies of this species prevail now. All *L. neglectus* colonies are monocalic in Tashkent. When *L. neglectus* started invised Tashkent from natural habitats, the most suitable for it sites were, probably, already occupied by *Crematogaster subdentata* (Fig. 1), what prevented growth of colonies of the first species.

Distribution of *L. neglectus* colonies In Rostov-on-Don is opposite to that in Crimea and is similar to Kyiv: there are no monocalic colonies, and number of polycalic colonies and supercolonies are roughly equally distributed among themselves (Table 1, Fig. 2).

Perhaps expansion of *L. neglectus* in Rostov-on-Don started later than in Crimea, but earlier than in Kyiv, therefore large colonies prevail. In Kyiv this species was found only in two places, whereas in Rostov it widespread not only in the territory of the city, but also in the Rostov Region. The invasion of *L. neglectus* probably started at 2012.

In Crimea number of monocalic colonies of *C. subdentata* predominates, but they located on the periphery of the supercolonies. With time, they likely will be included to the supercolony, what may indicate the expansive state of *C. subdentata* population in this territory. At the same time, location of the population is still compact – the supercolony occupies an area of about 270 hectares.

C. subdentata in Rostov-on-Don and Rostov Region is one of the mass species and forms here large polycalic colonies and supercolonies (Table 1). Apparently, *C. subdentata* appeared in Rostov-on-Don earlier than in Crimea: it was found in Rostov-on-Don in 1980s, but in Crimea – at the beginning of 2000s (Radchenko, unpublished data).

The similar population structure of *C. subdentata* is typical also for Tashkent, where polycalic colonies and supercolonies also predominate, while in natural habitats in the Kyzylkum desert this species, as a rule, forms small, monocalic colonies (Table 1). Thus, habitats strongly influenced by an anthropogenic pressure both in primary and secondary areas, are more suitable for *C. subdentata* than

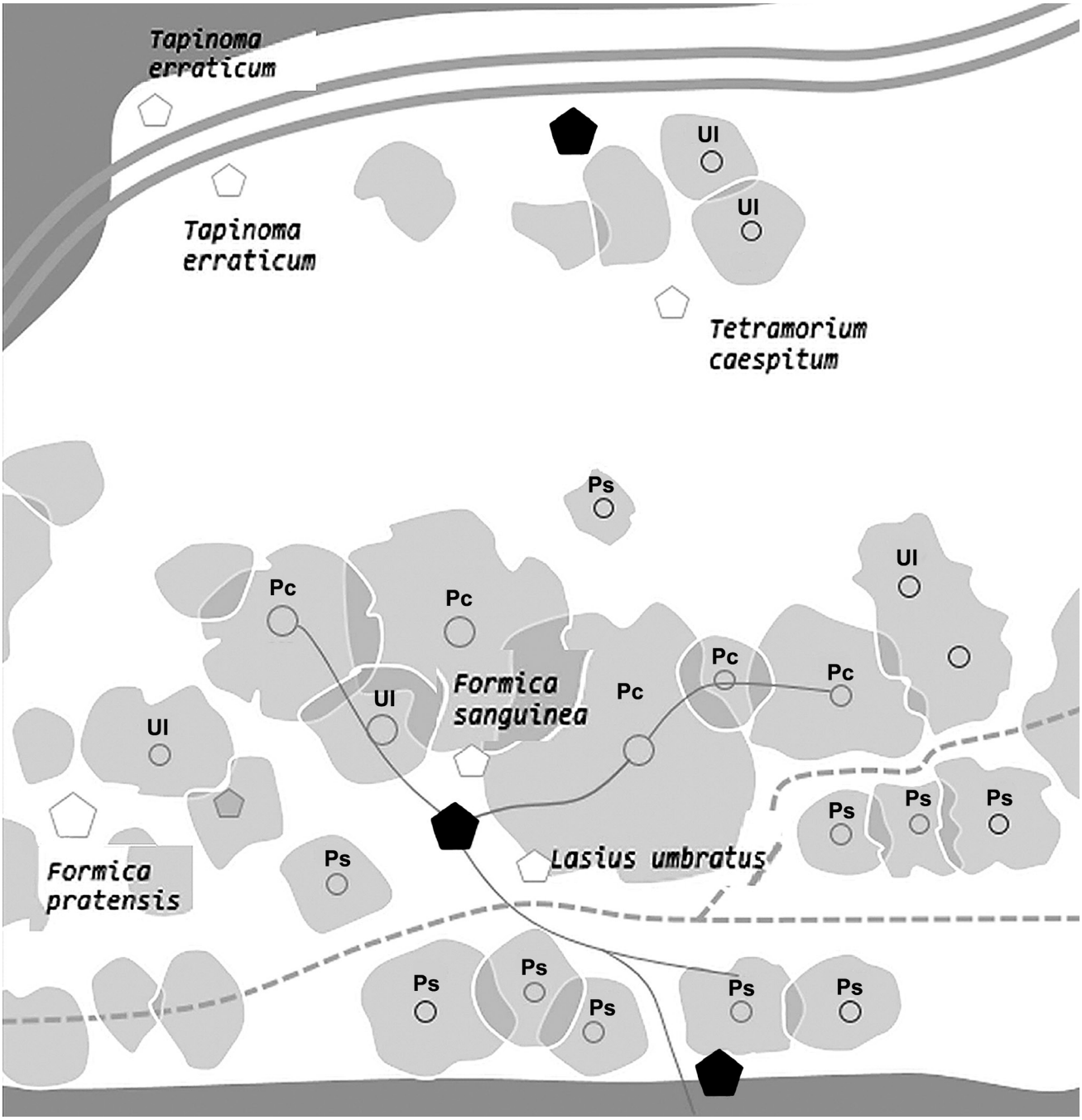

Fig. 2 – Scheme of the foraging areas of *Lasius neglectus* in Rostov-on-Don ⬟ nests of *Lasius neglectus* with brood and queens; ⬠ nests of other ant species; trees: Pc – *Prunus cerasus*, Ps – *Prunus spinosa*, Ul – *Ulmus* sp.

Table 2 – The average number of nests and foraging trees per colony of *C. subdentata* and *L. neglectus* in different regions.

Region	*L. neglectus*		*C. subdentata*	
	average number of nests per colony	average number of visited trees per colony	average number of nests per colony	average number of visited trees per colony
Crimea	2.7 ±0.3	2.0 ±0.2	1.7±0.1	5.1±0.8
Kyiv	8.2±1.4	2.3±0.2	-	-
Rostov-on-Don	1.8±0.8	3.8±2.7	12.0±2.0	44.0±34.0
Tashkent	1.0±0	1.0±0	13.8±9.1	22.4±13.5
Kyzylkum desert	-	-	1.2±0.2	1.0±0

Table 3 – The average activity of workers on the trails in native dominant species and invasive ant species (n / 2 min).

Ant species		Activity on trails
N	*Crematogaster schmidti*	27.9±1.0
N	*Formica pratensis*	46.5±3.8
I	*Crematogaster subdentata*	187.7±23.7
I	*Lasius neglectus*	50.5±2.5

natural ones. Unlike *L. neglectus*, *C. subdentata* forms large, usually polycalic colonies in all anthropogenic habitats in both the primary and secondary range (Figs 3, 4).

The maximum nests number per colony of *L. neglectus* is in Kyiv, where its population is in a state of expansion. So, in Kyiv, there are 4.0 times more nests per colony than in Rostov-on-Don, and 3.5 times more than in Crimea (Table 2, $p < 0.05$).

At the same time, the average number of trees with colonies of aphids per *L. neglectus* colony is approximately the same in all locations except for Tashkent, where it is 2-3 times less ($p < 0.05$). This may be caused by the size of colony – all *L. neglectus* colonies in Tashkent are monocalic.

A greater variation of this parameter is noted for *C. subdentata*. In Crimea and in the Kyzylkum desert indicators of the number of nests and trees per colony are minimal, but if in Crimea a large number of examined monocalic colonies "shifted" the average indicators downward, in the Kyzylkum practically all colonies of this species are really monocalic.

Majority of *C. subdentata* colonies in Rostov-on-Don and Tashkent are polycalic and 6.0-7.0 times bigger by the number of nests ($p < 0.05$), and these species have 4.0-8.0 times larger foraging areas by the number of controlled and visited trees ($p < 0.05$). In general, populations here stabilized its borders and occupy all suitable habitats.

It is also worth to notice that on average *C. subdentata* has 2.0 times more nests per colony for all locations than *L. neglectus*, and 8.5 times more controlled foraging trees. The size of the colony can also be indicated by number of workers on the trails (Table 3). Thus, in native dominant species having a protected foraging area, activity of foragers is 3.0-6.0 times less than that of *C. subdentata* ($p < 0.05$). *C. subdentata* has an average 3.5 times more workers on the trails than *L. neglectus* ($p < 0.05$) what indicates larger size of its colonies.

Attendance of plants by invasive ants Lasius neglectus *and* Crematogaster subdentata *in different regions*

In Crimea, *L. neglectus* predominantly visits introduced species of trees, as well as some local plants – *Pinus nigra pallasiana* (Lamb.) Holmboe, 1914, *Ulmus laevis* Pallas, 1784 and others (Fig. 5 d). In Rostov-on-Don, *L. neglectus* prefers to visit deciduous trees, as well as introduced species, such as glades (*Ailanthus* sp.) and others (Fig. 5 e). In Tashkent, *L. neglectus* is more common on Oriental sycamore, poplar, elm, fruit trees (Fig. 5 f).

Similar preferences are in *C. subdentata*. In Crimea, it visits mainly cultivated plant species – mulberry, walnut, plum (Fig. 5 a), and among wild plants prefers willow. In particular, *C. subdentata* visited colonies of aphids (*Chaitophorus salicti* Schrank, 1801) on willow and coccid (*Pseudochermes fraxini* Kaltenbach, 1860) in ash tree. In Rostov-on-Don, *C. subdentata* visits both introduced species (*Ailanthus altissima* (Mill.) Swingle, 1916., *Gleditsia triacanthos* Linnaeus, 1753) and wild-growing trees (poplar, linden) (Fig. 5 b). Foragers visit primarily colonies of Homoptera, extrafloral nectaries (for example, on *Campsis radicans* (Linnaeus) Seem ex Bureau, 1867, *Catalpa* sp., *Ailanthus altissima*) and trash plots. Some species of aphids visited by *C. subdentata* are: on walnut it is *Panaphis juglandis* Goeze, 1788, on plum – *Myzus persicae* Sulzer, 1776. In Tashkent, *C. subdentata* prefers to visit fruit trees, poplar, walnut, mulberry, and less commonly – introduced tree species (Fig. 5 c), but it was not found on conifers, oriental sycamore, *Catalpa*, and also on apricot.

Interactions of Lasius neglectus *and* Crematogaster subdentata *with native ant species in different regions.*

Crimea. We found here 16 ant species in the habitats of *C. subdentata*: *Messor structor*, *Formica glauca* Ruzsky, 1896, *Tetramorium caespitum* (Linnaeus, 1758), *Myrmica specioides* Bondroit, 1918, *Myrmica rubra*, *Myrmica bergi*

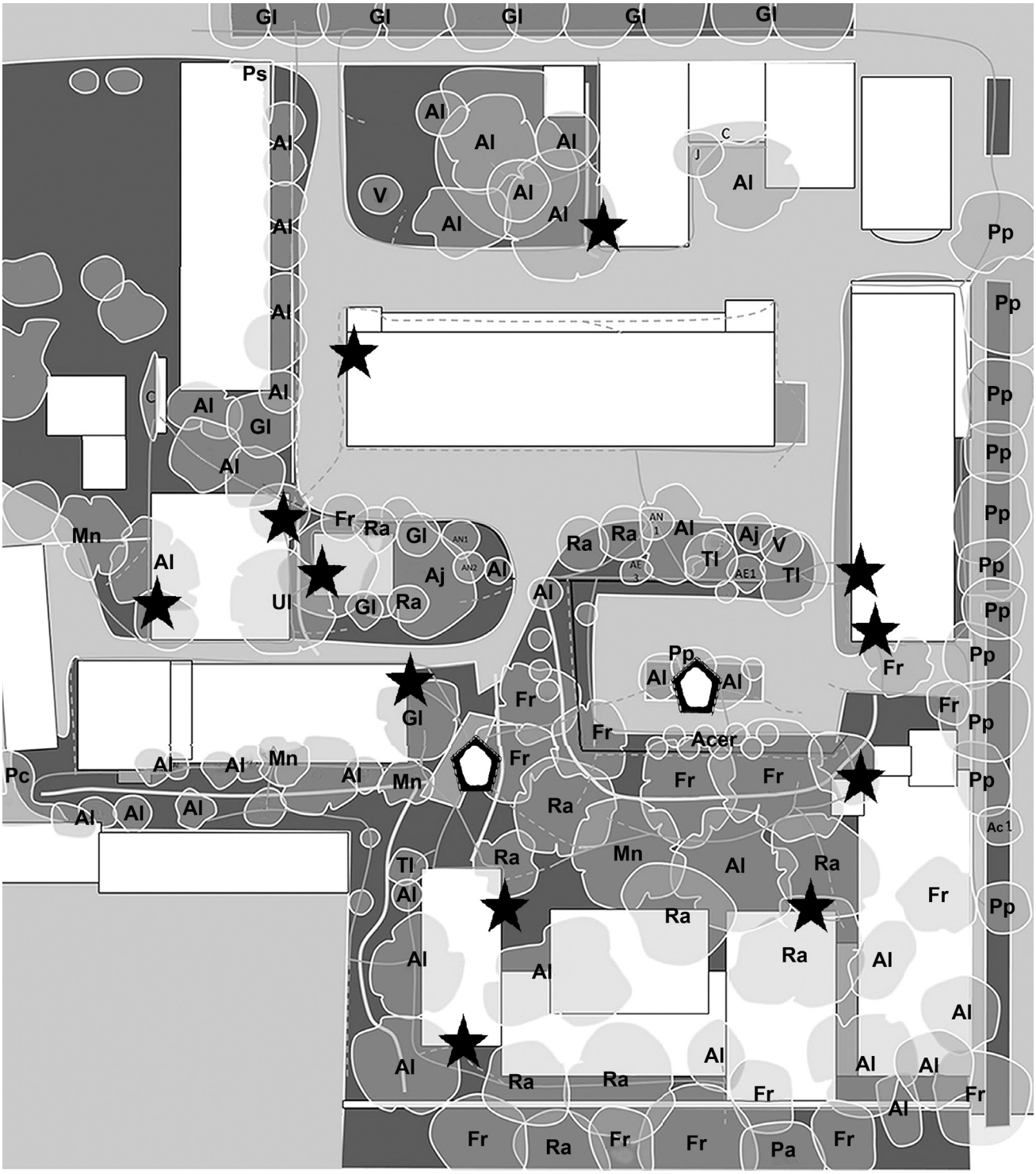

Fig. 3 – Scheme of the foraging areas of *Crematogaster subdentata in Rostov-on-Don* ⬠ *large accessible nests of C. subdentata* in buildings and outside; ★ inaccessible nests of *C. subdentata* in buildings; trees: Ac – *Acer* sp., Ae – *Aesculus hippocastanum*, Aj – *Albizia julibrissin*, Al – *Ailanthus altissima*, An – *Acer negundo*, C – *Campsis radicans*, Fr – *Fraxinus* sp., Gl – *Gleditsia triacanta*, J – *Juglans regia*, Mn – *Morus nigra*, Pa – *Prunus americana,* Pc – *Prunus cerasus*, Pp – *Populus niger*, Ps – *Prunus spinosa*, Ra – *Robinia pseudoacacia*, Tl – *Tilia* sp., Ul – *Ulmus* sp., V – *Viburnum* sp.

Ruzsky, 1902, *Cardiocondyla stambuloffi* Forel, 1892, *Plagiolepis pallescens* Forel, 1899, *Solenopsis fugax*, *Cataglyphis aenescens* (Nylander, 1849), *Camponotus piceus* (Leach, 1825), *Camponotus fallax* (Nylander, 1856), *Camponotus aethiops* (Latreille, 1798), *Lasius paralienus* Seifert, 1992, *Strongylognathus christophi* Emery, 1889, *Tapinoma eraticum*. *C. subdentata* does not have a significant negative impact on the species richness of other ants compared to the

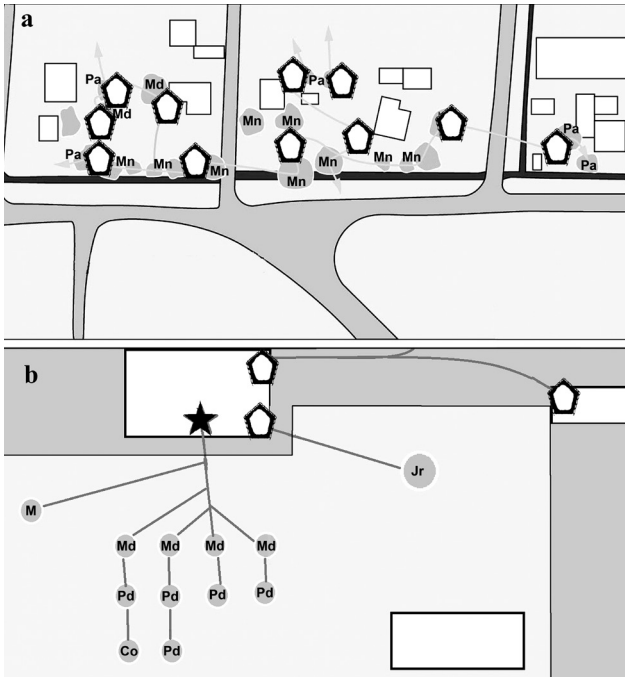

Fig. 4 – Scheme of the foraging areas of *Crematogaster subdentata* in Crimea (A) and Tashkent (B) ⬠ large accessible nests of *C. subdentata* in buildings and outside; ★ inaccessible nests of *C. subdentata* in buildings; trees: Co – *Cydonia oblonga*, Jr – *Juglans regia*, M – *Morus* sp., Md – *Malus domestica*, Mn – *Morus nigra*, Pa – *Prunus americana*, Pd – *Prunus domestica*.

local dominant *M. bergi*. The interaction of *M. bergi* and *C. subdentata* colonies occurs at the different levels of social organization: supercolony of *C. subdentata* and polycalic colonies of *M. bergi*. Conflicting colonies have different sizes, differing by several orders of magnitude. With the long-term interaction between supercolony of *C. subdentata* and polycalic colonies of *M. bergi*, the latter were degraded, nests of *M. bergi* was separated from each other, and foraging areas of this species clearly decreased in size. When the boundaries of the supercolony of *C. subdentata* and the populations of *M. bergi* came into contact, permanent conflicts started first on the periphery and gradually shifting to the center. To stop the advancement of the borders of a supercolony of an invasive species can only be done by a similar social structure of a native species.

Tashkent. *Cataglyphis aenescens*, *Messor laboriosus* Santschi, 1927, *Pheidole koshewnikovi* Ruzsky, 1905, *Plagiolepis* spp., *Formica glauca*, various species of the genus *Tetramorium* Mayr, 1855, *Tapinoma erraticum* and *Camponotus lameerei* Emery, 1898 inhabits the same territories as *Crematogaster subdentata*. Interactions with *Ph. koshewnikovi* have not been studied, but in relation with other species *C. subdentata* acts as a clear dominant or ignores their presence at all. This is due to significant differences of ecological niches in different species (Dlussky 1981).

At the same time, *Crematogaster subdentata* and *Lasius neglectus* are noticeably interacted. In the common territories, they have strictly separated foraging areas, and both species were found extremely rarely on the same tree. If this occurs, there are directly conflicted, which usually ended in favor of *C. subdentata*, or in favor of the party with the numerical advantage of foragers. In general, *C. subdentata* can displace *L. neglectus* to the periphery of the territory.

Crimea. We recorded 10 ant species together with *L. neglectus* on the same tree trunks: *Camponotus fallax*, *Camponotus aethiops*, *Camponotus truncatus* (Spinola, 1808), *Camponotus piceus*, *Camponotus lateralis* (Olivier, 1792), *Dolichoderus quadripunctatus* (Linnaeus, 1771), *Formica cunicularia* Latreille, 1798, *Formica glauca*, *Plagiolepis pallescens* and *Crematogaster schmidti* Mayr, 1853. *Tetramorium caespitum* and *Tapinoma erraticum* were also found on the foraging territory of *Lasius neglectus*, but on a soil surface only. It is characteristic that in the Crimea *L. neglectus* does not oust native ant species. Apparently, the resources (such as sugary production of aphid colonies) on trees visited by it are sufficient for all species, although *L. neglectus* may play a dominant role in their consumption. In the case of monocalic colonies, this can also be explained by the small size of the colony, when it is impossible to control visits of aphids by other ant species. Ants from polycalic colonies usually form one or two trails on a tree trunk and workers walking rarely outside of them. Native species, except for *Crematogaster schmidti*, climb the trunks singly and do not form trails. But at the same time foraging areas of large colonies *C. schmidti* and *L. neglectus* do not overlap.

In **Rostov-on-Don**, in seminatural environments *Lasius neglectus* colonies may coexist for a long time in same territory with other species of ants (except for *Lasius niger* and *Lasius alienus*), especially with ants of other size classes or foraging preferences, e.g. with *Formica sanguinea* and *Messor structor*. Herpetobiont *Tetramorium caespitum* and occasionally arboreal *Dolichoderus quadripunctatus* inhabit same places as *Crematogaster subdentata*.

We recorded partial overlapping of foraging territories of *C. subdentata* and *L. neglectus* only twice. In both cases *L. neglectus* occupies plots with minimal dynamic density of workers of *C. subdentata*, and its colonies are small. Most probably, it penetrated to this territory with the planting of young trees in parks. Moreover, *L. neglectus* tends root aphis here, but *C. subdentata* actively forages on trees.

Comparison of the size of the foraging areas and the number of nests in the supercolonies of Lasius neglectus and Crematogaster subdentata in the invasion zone and in the natural habitats.

The size of colonies of *C. subdentata* is Crimea is the smallest (in average 6.5 ± 1.1 nests per one subunite is the supercolony) compare to Tashkent (303.7 ± 55.5 nests) and Rostov-on-Don (271.8 ± 103.2 nests) (Fig. 6 a). This can be explained by the fact that the invasion in Crimea started in the early 2000s (Stukalyuk 2015) and in Rostov-on-Don much earlier – in the 1980s. During this time,

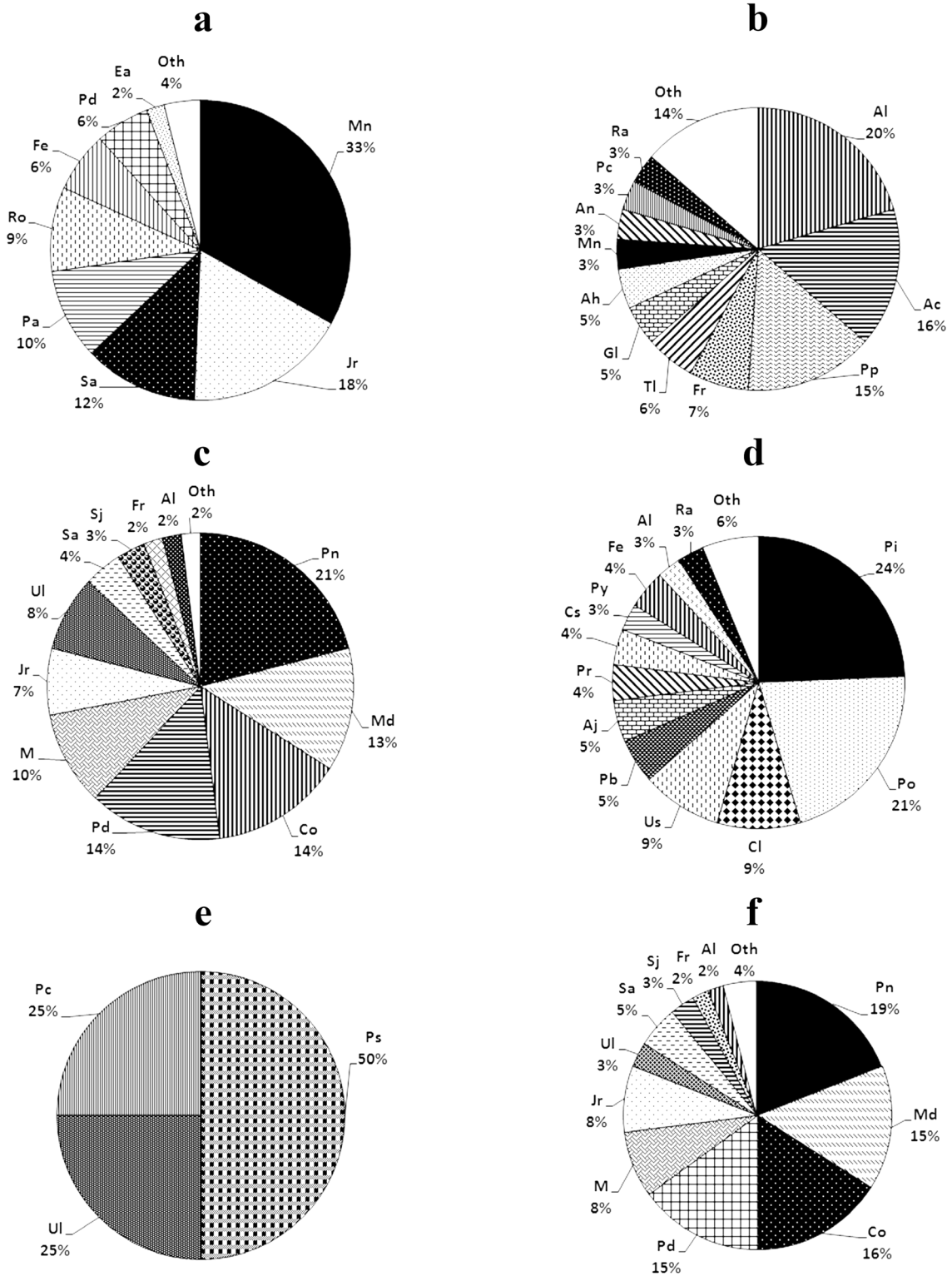

Fig. 5 – Relation of tree and shrub species visited by *Crematogaster subdentata* (a, Crimea, b, Rostov-on-Don, c, Tashkent) and *Lasius neglectus* (d, – Crimea, e, – Rostov-on-Don, f, – Tashkent). Trees: Ac – *Acer* sp., Ah – *Aesculus hippocastanum*, Aj – *Albizia julibrissin*, Al – *Ailanthus altissima*, An – *Acer negundo*, Cl – *Cedrus libani*, Co – *Cydonia oblonga*, Cs – *Cupressus sempervirens*, Ea – *Elaeagnus angustifolia*, Fe – *Fraxinus excelsior*, Fr – *Fraxinus* sp., Gl – *Gleditsia triacanta*, Jr – *Juglans regia*, M – *Morus* sp., Md – *Malus domestica*, Mn – *Morus nigra*, Pa – *Prunus americana,* Pb - *Pinus brutia*, Pc – *Prunus cerasus*, Pd – *Prunus domestica*, Pi – *Pinus pallasiana*, Pp – *Populus niger*, Po – *Populus alba*, Pr – *Prunus cerasifera*, Ps – *Prunus spinosa*, Py - *Populus pyramidalis*, Ra – *Robinia pseudoacacia*, Sa – *Salix* sp., Sj – *Styphnolobium japonicum*, Tl – *Tilia* sp., Ul – *Ulmus* sp., Us – *Ulmus laevis*.

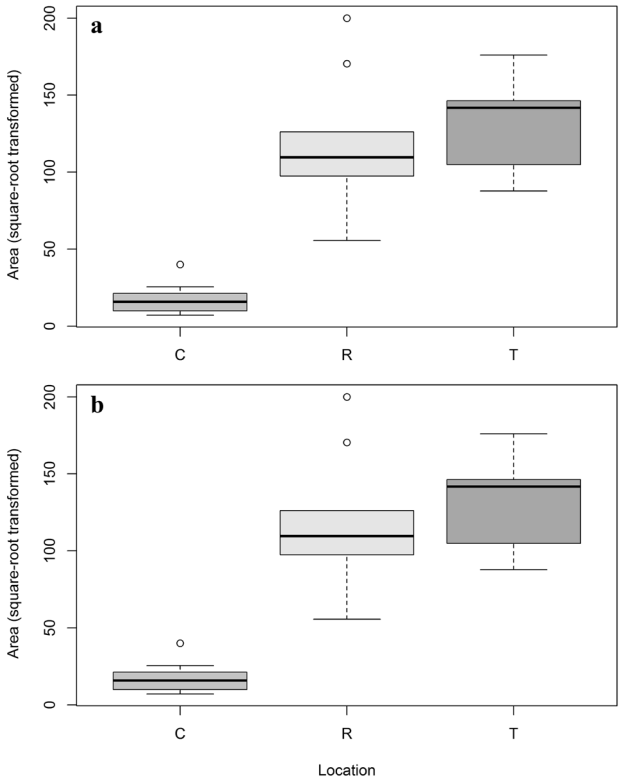

Fig. 6 – Average values of the average size of the foraging areas of *Crematogaster subdentata* (a) and *Lasius neglectus* (b) in the primary and secondary ranges. C – Crimea, T – Tashkent, R – Rostov-on-Don.

supercolonies of this species reached their maximum size, occupying virtually the entire urban agglomeration of Rostov-on-Don and Bataisk. In Tashkent, *C. subdentata* is a native species that has settled throughout the city for hundreds of years.

On the other hand, invasion of *L. neglectus* in Crimea started a quite long time ago, at least from the 1970s (Stukalyuk & Radchenko 2018), and during this time supercolonies have already degraded, and the largest polycalic colonies have no more than 25-30 nests and do not occupy territories of more than 2 ha (Fig. 6 b). On average, one colony of *L. neglectus* in Crimea accounts for 2.0 ± 0.2 nests.

The invasion of *L. neglectus* In Rostov-on-Don started more recently, in 2012, and supercolonies of this species exist here and contain in average 22.9 ± 5.2 nests per one subunit in the supercolony. In Tashkent, *L. neglectus* is a native species (Stukalyuk et al. 2020), it does not form large colonies (1.2 ± 0.1 nests per one colony). A pairwise comparison of the average areas occupied by the two species confirmed the obvious advantage of *C. subdentata* over *L. neglectus* in Crimea (Fig. 7 a), Rostov-on-Don (Fig. 7 b) and Tashkent (Fig. 7 c).

Therefore, during the period accessible for analysis (from the 1980s) *C. subdentata* proved to be more stable compared to *L. neglectus*, capable of forming stable supercolonies that retain their sizes for decades.

Discussion

The level of aggressiveness of ants is primarily determined by the dynamic density of workers on foraging areas, what in turn depends on the size of the colony (Zakharov 2015). Consequently, workers of *Lasius neglectus* from large polycalic colonies are more aggressive and competitive in direct contacts with native ant species with lower levels of social organization. Becoming the main consumers of carbohydrate resources (aphid's honey dew) in specific habitats, workers of *L. neglectus* from the polycalic colonies reduce availability of the resources for other species, ultimately displacing them and depleting species richness. For example, in Budapest, in the territory of the supercolony of *L. neglectus*, 10 species of ants were found, but in the control plots – 17 (Nagy et al. 2009). At the same time, at the initial stage of invasion, there is no complete crowding out of native ant species, as shown for the monocalic *L. neglectus* colony in Kyiv (Stukalyuk 2018). Polycalic *L. neglectus* colonies in Crimea cover areas up to 2 hectares with no more than 20 visited trees in the foraging area. This is significantly less than in the Mediterranean region and in the Central Europe, where the area of the supercolonies of this species can reach 3,600 hectares (Czechowska & Czechowski 2003; Espadaler et al. 2007). In many localities of Crimea we noted a high proportion of monocalic colonies. Unlike many regions of the Central and Southern Europe, in Crimea *L. neglectus* does not have a significant impact on the native species richness. Probably, the resources (honey dew) on shared trees are sufficient for all species of ants, although *L. neglectus* may play a dominant role in their consumption. For monocalic colonies, this can also be explained by the small size of the colony, what does not allow control tree visits by other ant species. *L. neglectus* foragers from polycalic colonies, as a rule, form 1 or 2 trails on the trunk and are rarely found outside them. Local species, except for *Crematogaster schmidti*, climb alone along the trunks without forming trails and the territories of the foraging areas of large *C. schmidti* and *L. neglectus* colonies do not overlap.

The body size of *Crematogaster subdentata* is one and a half times smaller the body size of the local dominant *Myrmica bergi*. McGlynn (1999) compared body sizes of 78 invasive ant species from 26 genera with those of native species belonging to the same genus. In 22 genera, native species were larger than invasive ants. Moreover, using the example of *Wassmania auropunctata*, the author showed that workers from the secondary range were smaller than those from native habitats. Colony size and the size of workers are interconnected: big colonies produce small workers, but in large numbers (Oster & Wilson 1978).

Most of the characteristics and effects on biota of *C. subdentata* in the new habitat can be attributed to the

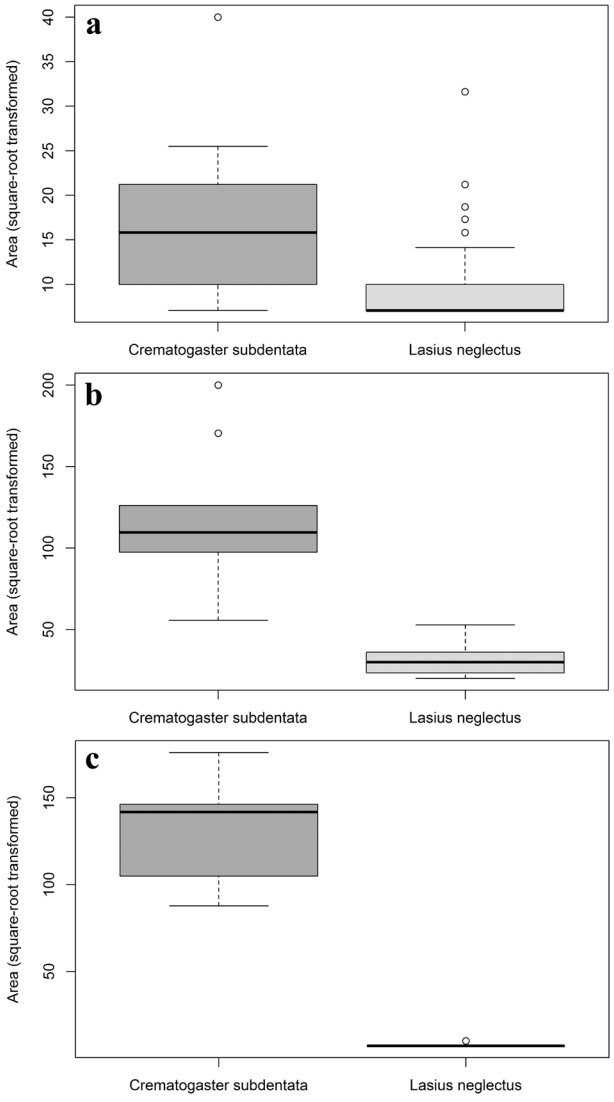

Fig. 7 – Comparison of the sizes of foraging areas of polycalic colonies and supercolonies of *Crematogaster subdentata* and *Lasius neglectus* in the primary and secondary ranges: a, Crimea, b, – Rostov-on-Don, c, Tashkent.

category of "candidates" for invasive species, where the authors have already placed *L. neglectus* (Holway et al. 2002). Among these characteristics are the following:

- small sized and monomorphic workers. Small sizes are characteristic for all the most successful invasive ant species (no more than 5 mm), some of which have monomorphic workers – *Wassmania auropunctata*, *Linepithema humile*, *Anoplolepis gracilipes* (F. Smith, 1857);
- omnivorous: *C. subdentata* feeds the corpses of small vertebrates and invertebrates. In addition, it is an active trophobiont, using not only honey dew, but also aphids and other homopterans, and is able to store dry aphids and even San Jose scale (*Quadraspidiotus perniciosus* Comstock, 1869) in Middle Asia (Folkina 1978; Dlussky 1981; Dlussky et al. 1990) for an unfavorable period;
- the presence of polygyny and polycaly, and in some cases – supercolonies in new habitats. For the Crimean population of *C. subdentata*, such structures are characteristic in the zone of high density of colonies. There is no data on similar structures in the native habitats of Central Asia, but polycalic colonies and supercolonies of this species prevail in Tashkent;
- displacement of native ant species. This effect is clearly not pronounced for *C. subdentata*, it can affect only arboreal species or, in the cultural phytocenoses of the steppe Crimea, species visiting trees. Competition of native ant species with *C. subdentata* is mainly for resources or for habitats. In the conditions of deficiency of nesting sites, the local arboreal or territorial species might be completely supplanted.

In other regions, where invasive ant species is herpetobiont, the opposite situation is observed. Despite the aggressive behavior of invasive *L. neglectus* (herpetobiont), some species, such as the arboreal *Crematogaster scutellaris* (Olivier, 1792) and stratobiont *Temnothorax lichtensteini* (Bondroit, 1918) did not change their dynamic density and activity. The cause is spatial separation of species (Paris 2007).

In some cases the foraging territories of supercolonies of two invasive species, for example, *Tapinoma magnum* Mayr, 1861 and *Lasius neglectus* in Slovenia (Bračko 2019) are close to each other, but do not overlapped, since both species prefer somewhat different habitats. Our data showed that the territories of supercolonies of two invasive species can partly overlap, but only if one of them is low in numbers.

Both *C. subdentata* and *L. neglectus* have high invasive potential, but that of *C. subdentata* seems higher if compared to *L. neglectus*. Both species have many common features: a) polygyny; b) polycalic colonies; c) the foraging area is protected from other dominant species; d) a high level of aggressiveness to other species; e) active trophobiosis with homopterans; e) round-the-clock activity; g) ability to effectively develop anthropogenically modified territories.

The following facts speak in favor of the advantage of *C. subdentata*:

a) *C. subdentata* is an arboreal species and uses various substrates for nesting – wood, polystyrene, roofing felt, walls of houses (as a rule, private ones), and can also build nests in the ground. *L. neglectus* is a herpetobiont that depends on the availability of free land, which is not always available in urban environments;
b) *C. subdentata* is capable for accumulating food resources, e.g. dry invertebrate remnants;
c) *C. subdentata* has an organization by the type of secondary federation (supercolony), while *L. neglectus* has primary federation. The differences between these systems are that there are no exchanges by workers, broods and queens between neighboring nests (poly-

calic colonies) in the primary federation, but this is present in the secondary federation. Such exchanges make it possible to disperse more quickly, as well as found new nests or restore weak ones;

d) the nuptial flight is unknown for *L. neglectu*s in the secondary area (se also Stukalyuk et al. 2020) therefore, the rate of dispersion of this species is low (up to 200 m per year), and it spreads mainly by humans with transportation with plants or soil. In contrary, the nuptial flight is a typical phenomenon for *C. subdentata*, and fertilized gynes may found their nests far from the maternal colony, that can merge subsequently;

e) the genus *Crematogaster* Lund, 1831 is characterized by the unique morphological features compared to all other Myrmicinae ants: its postpetiole articulates on the dorsal surface of the first gastral segment. This structure is believed to be closely connected with defense and hunting behaviors. The sting in *Crematogaster* species is well developed, but with a blunt, spatulate tip that is unsuitable for pricking (Buren 1959; Kugler 1978), and the venom is applied topically by wiping on a victim instead of injecting it inside the body (Buren 1959; Longino 1993). By holding its gaster raised up and even somewhat forward, over its head, a worker can attack prey or enemies in a 360° radius. Moreover, workers of *Crematogaster* bite quite painfully. This behavior gives them significant advantages in direct conflicts with competing species, including *Lasius neglectus*.

Finally, it is necessary to emphasize the high probability of further invasion of *Crematogaster subdentata* in the countries of the Southern, and possibly the Central Europe, what may lead to unpredictable changes in the composition and structure of native assemblages of ants, as well as cause significant economic damage.

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