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Carabidae assemblages in pine forests with different recreation regimes within and outside a megalopolis

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Abstract
The expansion of cities highlights the need for studies of the biodiversity on urban territories and factors affecting the structure and functioning of communities. In 2010–2011, we compared the abundance and diversity of carabid beetles in pine forests of natural origin within the Russian megalopolis Yekaterinburg and outside. To estimate the effects of recreation (R+: trampling, soil compaction, eutrophication) and other urbanization factors (U+: pollution, habitat fragmentation, adventive species), we selected 12 urban and non-urban forest sites with contrasting recreation regimes (U + R+, U + R−, U − R+, U − R−; three sites in each combination). We hypothesized that both urbanization and recreation decrease the abundance and diversity of carabids; the combination of two factors enhances negative effects. The total activity density of carabids and the abundances of all ecological groups increased in urban forests compared to non-urban ones. In urban forests, the Simpson dominance decreased, while Shannon diversity, total species richness, and mean number of species per site increased. The most abundant species in all forests were *Pterostichus oblongopunctatus*, *P. mannerheimii*, and *P. magus*, while *Carabus nemoralis* was abundant in urban forests only. Proportion (by the number of individuals) of forest species was lower and that of generalists and large-sized species higher in urban forests. High recreation load resulted in lower total abundance and diversity of ground beetles. Negative effect of recreation load on carabids leveled positive effect of urbanization: both abundance and diversity of ground beetles were lower at urban sites with intense recreational use compared to forest sites closed for townspeople.

Keywords Middle Urals · Urbanization · Recreation · Abundance · Diversity

Introduction

Urbanization is a complex social-ecological phenomenon with multiple closely bound ecological factors related to high concentrations of people and their activities within a limited area. The increase of urban areas is accompanied by air pollution, changes in the physicochemical properties of the soil, the microclimate, and the hydrological and hydrochemical regime of water bodies, the fragmentation or disappearance of natural habitats with the formation of new ones, and the introduction of adventive species. The transformation of natural habitats surrounded by urban territories changes the diversity and functioning of plant and animal communities (McKinney 2008; Jones and Leather 2012; Burkman and Gardiner 2014).

The effects of urbanization on carabid assemblages are studied rather well, and the responses of individual species to urbanization largely depend on their traits (Niemelä and Kotze 2009; Martinson and Raupp 2013). Several authors report lower abundance and species richness of carabids in urban parks compared to forests outside the cities, a higher dominance of a few species, mainly capable of flight, and a lower proportion of large-sized and flightless species (Niemelä and Kotze 2009). Green zones of cities are used by townsfolk for recreation; therefore the latter accompanies other anthropogenic factors affecting urban ecosystems. Recreation load affects carabid assemblages to varying degrees, depending on the level of ecosystem digression. The total abundance of carabid beetles can increase with recreation

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intensity (Grandchamp et al. 2000) or decrease with increased trampling (Babenko and Eremeeva 2007). The abundance of hygrophilic species decreases (Lehvävirta et al. 2006), while the number of open-habitat species increases at higher levels of recreation digression (Gryuntal and Butovskiy 1997). An extremely high recreation load results in a decreased proportion of forest mesophilic species and predators and an increased abundance of meadow species and generalists (Feoktistov 2000; Grandchamp et al. 2000). These studies of recreation effects were limited to forest areas of cities (Grandchamp et al. 2000; Feoktistov 2000; Lehvävirta et al. 2006; Babenko and Eremeeva 2007) or suburbs (Gryuntal and Butovskiy 1997). We are not aware of studies on recreation effects on carabids in non-urban forests. Therefore, it is unclear if recreation effects on carabid beetles coincide in cities and outside.

Studies of carabids in Yekaterinburg and vicinities started long ago. The main tasks were to reveal species composition and to estimate the relative abundances of species in different habitats (deciduous and coniferous forests, meadows, bogs, wastelands, lawns, and coasts of reservoirs) (Kozyrev 1991; Zinovyev 1996). The only study on ground-dwelling invertebrates in Yekaterinburg provided a comparative analysis of urban effects on the abundance and species diversity of most numerous and diverse upper taxa, including carabid beetles (Zolotarev and Belskaya 2015).

In this context, this study aimed at the description and analysis of urbanization and recreation effects on carabids of pine forests at the species, ecological group, and assemblage level, on the example of a large industrial city, Yekaterinburg (Russia, Sverdlovsk region). When comparing urban forests of a natural origin with non-urban ones, we tested the hypotheses that 1) the abundance and species diversity of carabids is lower in the city than outside; 2) urban assemblages of carabids are less even; 3) percentages in the total abundance of forest species, large-sized species decrease and those of generalist species increase in the city; 4) the abundance and species diversity of carabids decreases at high recreation loads.

Methods

Study area

The study was carried out in Yekaterinburg (Russia, 56°51′ N, 60°36′ E) and nearby forests in 2010–2011. This area is situated in the southern taiga subzone, in the southern part of the Sverdlovsk region, of which 65% are covered with forests. Land development started with the construction of a metallurgical factory in the beginning of the eighteenth century (Elagin 2012), and today, Yekaterinburg is a large industrial city covering an area of 498 km^2 and with more than 1.4 million inhabitants (data of 2010). It is one of the most heavily polluted cities of the Russian Federation (Sturman 2008). Basic air pollutants are dust particles, nitrogen dioxide, ammonia, and volatile organic compounds. Cars produce 86.6% of air emissions (163,100 t/year), and industrial enterprises and heat power plants produce 13.4% of the emissions (25,300 t/year). There are 15 forest parks within the city margins, covering a total area 12,400 ha (Bokachev et al. 2012).

For our study, we selected forest massifs of natural origin (Fig. 1) with a high stand basal area and an age ranging from 120 to 140 years, with 90–95% of pine (*Pinus sylvestris*) and 5–10% of birch (*Betula pubescens*) (Shavnin et al. 2010). The soils are typical and podzolized brown forest soils (burozems) with a slightly acid reaction (Smorkalov and Vorobeichik 2015). When estimating the effects of urbanization (U) and recreation (R) on carabids we distinguished low (−) and high (+) levels of these factors: non-urban vs. urban forests and areas of low vs. intense recreational use with trampled areas 0–5% and 11–39% respectively (Ermakov and Vorobeichik 2013). Each forest area had a unique combination of the factors. 1) The "South-West" forest park (U + R+), with an area ~ 0.4 km^2 (40 ha), is situated on the periphery of the city, 5.5 km from the center. It is surrounded by highways and residential areas and represents the recreation area of the townspeople. The trampled area is 11–16% of the total territory (Ermakov and Vorobeichik 2013). Until the mid- 1960s, this area was outside the city margins and bordered a peat-bog (Elagin 2012). 2) A fenced pine forest in the Botanical Garden of the Ural Branch of the Russian Academy of Sciences (U + R −), covering an area of 0.1 km^2 (10 ha), has been closed for townspeople over the last 50 years. The trampled area is 1–3% of the total territory. The Botanical Garden is situated near the "South-West" forest park. Evidently, these areas comprised a continuous forest until they were divided by the construction of a highway. 3) The vicinities of the Chusovskoye Lake (U–R+), a dense forest in the neighborhood of a holiday village, 20.4 km from the city. The trampled area is 32–39% of the total territory. 4) The vicinities of the Glukhoye Lake (U–R–), a little-visited dense forest, 17.6 km from the city. The trampled area is 0–5% of the total territory.

Our study areas had similar soil type, species composition and age of trees but differed in some characteristics of soil, understory and field layer. The soils of the urban forests had alkalified upper horizons, higher contents of nitrates and easily hydrolysable nitrogen compounds, and a thinner litter layer (Veselkin and Kaigorodova 2013). Urban forests differed from the non-urban ones by a denser understory of deciduous trees and shrubs (Appendix 1); adventive species (*Acer negundo*, *Amelanchier spicata*, *Malus baccata*) were abundant in the understory because of their use in urban landscaping. The development of the understory leads to considerable shading of the soil surface in the city with subsequent reduction of the field layer. The synanthropic nitrophils (*Glechoma hederacea*, *Urtica dioica*) dominated the field layer, which

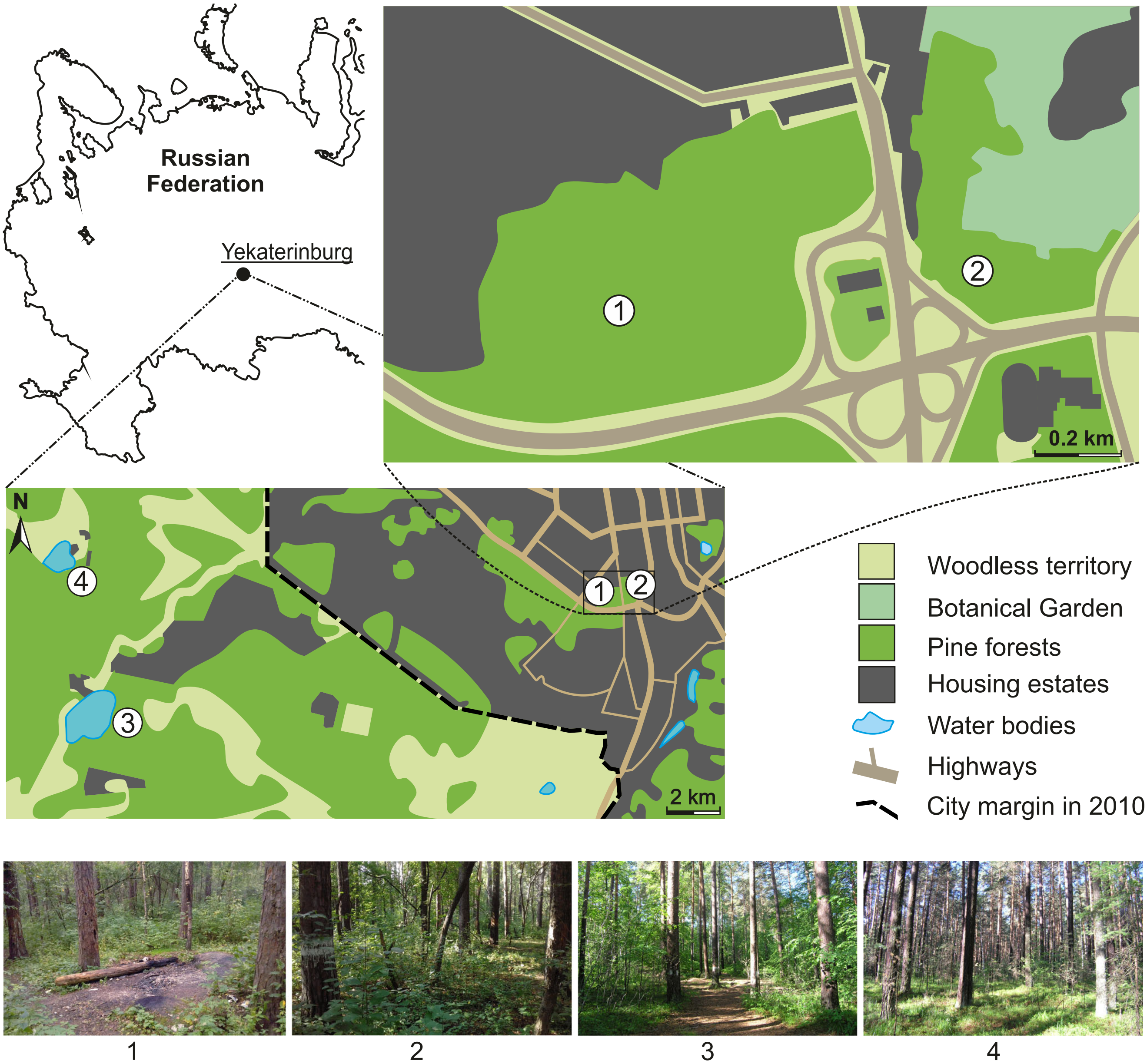

Fig. 1 Locations of the studied pine forest areas (circles) in Yekaterinburg and adjacent territories. 1 – South-West forest park, 2 – Botanical Garden, 3 – Chusovskoe Lake, 4 – Glukhoe Lake

was sparser because of strong shading. The non-urban forests had a more luxuriant field layer, dominated by *Calamagrostis arundinacea* and *Vaccinium myrtillus* (Zolotareva et al. 2012).

Counting method and species characteristics

Carabid beetles were sampled in 2010–2011 with pitfall traps (plastic jars 9 cm in diameter, filled with 3% acetic acid). To count species with spring-summer and summer-autumn activities, sampling was performed twice a season, at the beginning and at the end of summer, i.e. from 27th of May to 1st of June and from 19th to 26th of August in 2010; from 19th to 24th of May and from 19th to 24th of August in 2011. These are periods of high carabid activity, as shown by our earlier study (Belskaya and Zolotarev 2009). In each forest area, three sites were chosen randomly at distances 49–329 m between them (Appendix 2), with five traps per site placed in a line at a distance of 2–3 m from each other. Traps were located away from human trails, at places with undisturbed soil, in the same points for all samplings. At each sampling event, traps were exposed for 5 days.

For species identification, keys on imago (Kryzhanovskij 1965) and standard collections of the Museum of the Institute of Plant and Animal Ecology were used. Carabid taxonomy followed Kryzhanovskij et al. (1995). Ecological characteristics of species (feeding traits, habitat preference, and moisture preference) were extracted from the monograph on ground beetles of the Urals (Voronin 1999). In terms of feeding traits, we distinguished obligatory predators, “predators”, and mainly phytophagous species, “herbivores”. In terms of habitat preference, three groups were distinguished. The group “forest” included beetles inhabiting mainly forests, while the group “open habitat” included species of open habitats: meadows and fields. The group “generalists” included eurytopic species inhabiting both forest and open habitats. The species *Bembidion guttula*, with one specimen trapped near the Chusovskoye Lake, represented the “riparian” group. Regarding moisture preference, we distinguished hygrophilic, mesophilic, and xerophilic species. Data on body size of carabids were extracted from the “Key to Insects of the European USSR” (Kryzhanovskij 1965). According to the size classification of carabids (Sharova and Bulokhova 1995), we distinguished three size groups: 1) very small and small (body length 3–9 mm), 2) medium (9.1–11 mm), 3) large and very large (11.1–26 mm and larger).

Data processing

For each site and year, we determined the number of trapped individuals (N), species richness (S), Shannon diversity index $H = -\sum_i p_i \ln p_i$, and Simpson dominance index $D = \sum_i p_i^2$. Since the number of trapped individuals differed strongly between urban and non-urban forests, we calculated the number of species per minimal sample (S') by using the individual rarefaction procedure (Gotelli and Chao 2013). When analyzing ecological groups, we calculated the total and site-mean species richness both for the urban and non-urban forests and for areas with high and low recreation loads.

As a measure of carabid abundance, we used the activity density, i.e., the number of individuals in a jar trapped for 10 days (N'). This index was used because some traps were destroyed by the townspeople in 2011. Since the abundance of carabids differed significantly between the sampling periods, we calculated the activity density for each site as the sum of trapped beetles for each count period, divided by the actual number of traps in a given period. Subsequently, we summed the two values to obtain the estimate for the whole season. When testing the significance of differences in beetle abundance between years, load levels (U+ and U–, R+ and R–), species, and ecological groups, we used ANOVA (https://doi.org/10.5281/zenodo.293770). Data were transformed to approximate normality to comply with the parametric test assumptions. In some cases, we used ANOVA with heteroscedasticity-consistent standard errors (hc3 covariance matrix; Long and Ervin 2000). Pair-wise comparisons were performed with the Tukey’s HSD test. The analyses were carried out for the whole assemblage, for most abundant species and groups of species (> 5% of the total number of trapped beetles). Species were grouped by body size, habitat preference, and moisture preference. For the group of three species (*Pterostichus oblongopunctatus*, *Pterostichus mannerheimii*, and *Pterostichus magus*), which were recorded at all sites, we determined the effects of urbanization and recreation. For *Carabus nemoralis*, we determined only the effect of recreation within the city. When comparing the relative abundance of ecological groups in carabid assemblages, we used the χ^2 test with the Yeats correction.

Effects of the year and area on the diversity and composition of carabid assemblages were analyzed with General Linear Models and two-way ANOSIM (http://folk.uio.no/ohammer/past), with 10,000 permutations and the Bray-Curtis similarity index. For three indices (S', H, and D), models with normal distribution were chosen, and for S, the model with Poisson distribution was selected. Link function was logarithmic in all cases. Each site represented an experimental unit. The year had no effect on diversity indices ($p > 0.05$ in all cases) and on the composition of the assemblages ($R = 0.04$, $p = 0.33$). For this reason, in further analyses, data of the 2 years were combined for each site in order to increase the sample size and the validity of estimates. We analyzed the effects of urbanization and recreational use on the diversity indices of carabids with 2-way ANOVA. Further, we combined all sites with the same factor combination and evaluated the diversity profiles using Hill numbers (N_α):

$$N_0 = S, N_1 = \exp(H), N_2 = 1/D, N_\infty = 1/BP,$$

where BP is a proportion of individuals of the most abundant species (Hill 1973).

All calculations were performed using the R software (R Core Team 2017) with the additional package car (Fox and Weisberg 2010) and the web-interface ANOVA-Shiny (Mikryukov 2014), Statistica v10 software, and PAST, v 3.22 (Hammer et al. 2001).

Results

Species composition and abundance of carabids

Over the 2 years, 1400 individuals, belonging to 30 species, were trapped (Appendix 3). The most abundant were *P. oblongopunctatus* (38.8% of the total number of individuals), *P. mannerheimii* (17.9%), and *P. magus* (13.3%), which were caught at all sites. Less abundant species were *Carabus granulatus* (11 sites, 4.6%) and the exotic species *C. nemoralis*, which only inhabit urban territories in the Urals (six sites within the city, 8.9%). *P. oblongopunctatus* dominated the assemblage at all sites, followed by *C. nemoralis*, *P. mannerheimii*, and *P. magus* (the Botanical Garden and the South-West forest park), *C. granulatus*

(Glukhoye Lake), and *P. magus* (Chusovskoye Lake). Most beetles were predators (98.2% of the total number of individuals, all sites combined), and proportion of herbivores (*Amara similata*, *Curtonotus gebleri*, and *Harpalus latus*) equaled 1.8%. In terms of moisture preference, mesophilic species prevailed (19 species, 91% of all individuals). Hygrophilic (nine species, 6.9%) and xerophilic species (two species, 2.1%) were not numerous. Forest species (16 species, 80.1%) and generalists (nine species, 19.5%) prevailed in the assemblage, whereas species of open habitats were rare (four species, <1%). The percentages in the total abundance of large-sized (13 species) and medium- sized beetles (five species) were comparable (54.3% and 40.7% of all individuals, respectively). The proportion of small-sized beetles was low (12 species, 5%). The activity density of carabids in urban forests was higher than that in non-urban ones (Appendix 4, Table 1). This pattern was documented at the level of the whole assemblage and for all ecological groups. Nevertheless, this effect varied among the groups. The number of forest species in the pooled sample in Yekaterinburg was 3.2 times greater than outside, whereas the number of generalists was 5.6 times greater. Consequently, the proportion of generalists increased in the urban forests and that of forest species decreased ($\chi^2 = 9.544$, $p = 0.002$). The activity density of large-sized species increased more strongly compared to that of medium-sized species (4.3 and 2.7 times, respectively), resulting in a higher proportion of large-sized species in urban assemblages compared to non-urban ones ($\chi^2 = 13.713$, $p = 0.001$).

The effects of recreation load on the assemblage and all ecological groups were significant (Table 1). The interaction "urbanization" × "recreation" was also significant. The total activity density of carabids at urban sites with intense recreational use was lower than that in the non-recreational area in 2010 (Tukey's HSD-test, $p < 0.001$; Appendix 4). The activity density of forest species, large-sized species, hygro- and mesophilic species decreased significantly (Appendix 4). At the same time, the differences between non-urban forests with contrasting recreation regimes were non-significant both for the whole assemblage (2010: $p = 0.985$; 2011: $p = 0.811$) and for most trait groups (but in 2011 the activity density of generalists was higher at low level of recreation, $p = 0.024$). This pattern was constant throughout both years. Different species responded differently to anthropogenic impacts. The activity density of *P. mannerheimii* and *P. oblongopunctatus* was higher in urban forests, whereas that of *P. magus* was similar both within Yekaterinburg and outside (Fig. 2). The abundance of these species did not differ between forests with different recreation regimes either in the city or outside (Appendix 3). The activity densities of *P. oblongopunctatus*, *P. magus* (and *C. nemoralis* as well) in urban forests tended to decrease at high recreation load in both study years. The exclusion of this exotic species from the calculations did not change the results of the analysis of urbanization and recreation effects on ground beetle abundance.

Diversity

Shannon diversity (H) was higher and Simpson dominance (D) was lower within the city than outside (Table 2), indicating more diverse carabid assemblages in urban forests compared to non-urban ones. Species richness was also higher in urban forests. The total number of beetle species was 24 in the city and 19 outside, with site means of 13.2 ± 1.1 (SE) and 7.8 ± 1.1, respectively. For most ecological groups, species richness tended to increase in urban forests (Fig. 3). The forest species, hygrophilic, and xerophilic species showed significantly higher mean numbers of species per site in Yekaterinburg compared to outside.

Shannon diversity was lower and Simpson dominance higher in areas with intense recreational use, indicating less diverse assemblages in these forests. At the same time, the effect of recreation was significant only in urban forests (Table 2). The effect of recreation on species richness of carabids depended on the index of richness. Mean species numbers were comparable in forest areas with high (11.3 ± 1.6) and low (9.7 ± 1.6) recreation loads ($p = 0.31$). Recreation affected only the number of species per minimal sample (Table 3). However, differences were significant only between two areas, with higher values in the Botanical Garden (U + R–) compared to Chusovskoye Lake (U–R+) (Table 2). Recreation had no effect on the species richness of any ecological group.

Comparison of diversity profiles in urban forests revealed their divergence with an increase in the parameter α (Fig. 4). This indicates that the most abundant species determined differences among areas within the city. Outside the city, differences between areas with contrasting recreation loads were discernible at $\alpha < 2$, i.e., in the segment of the curve representing rare species.

Discussion

The current list of carabids of Yekaterinburg and adjacent areas includes 243 species (Voronin and Esyunin 2005). In the urban pine forests, we recorded 24 species in the sample of 1078 individuals. These values are comparable with earlier data (26 species, in a sample of 1192 individuals) obtained by continuous sampling (end of April – beginning of September) in four forest parks of Yekaterinburg (Zinovyev 1996). The number of species in non-urban forests in our study (19 species) was even higher than in similar pine forests of the southern taiga (10 species) (Zinovyev 2016). Therefore, we consider our sample to be sufficiently representative for the abundance and diversity analysis.

Table 1 The effects of year (2010 vs. 2011), urbanization (U, urban vs. non-urban), and recreation (R, high vs. low) on the activity density of carabids in pine forests of Yekaterinburg and adjacent territories

Subject	Source of variation	*df*	*F*	*p*
Whole assemblage	Year	1	4.9	0.041
	U	1	50.7	< 0.001
	R	1	72.9	< 0.001
	Year × U	1	0.5	0.472
	Year × R	1	1.0	0.336
	U × R	1	6.2	0.024
Dominant species (*Pterostichus oblongopunctatus*, *P. mannerheimii*, *P. magus*)	Species	2	51.3	< 0.001
	Year	1	5.7	0.021
	U	1	101.7	< 0.001
	R	1	0.1	0.805
	Species × Year	2	0.7	0.497
	Species × U	2	6.4	0.004
	Year × U	1	1.3	0.264
	Species × R	2	0.5	0.624
	Year × R	1	0.5	0.497
	U × R	1	10.4	0.002
Carabus nemoralis	Year	1	1.5	0.257
	R	1	1.4	0.270
	Year × R	1	1.2	0.299
Ecological groups by:				
Habitat preference (forest, generalist)	Group	1	114.6	< 0.001
	Year	1	2.9	0.099
	U	1	72.8	< 0.001
	R	1	18.5	< 0.001
	Group × Year	1	2.0	0.165
	Group × U	1	0.4	0.526
	Year × U	1	2.0	0.165
	Group × R	1	11.7	0.002
	Year × R	1	2.4	0.134
	U × R	1	3.1	0.090
Body size (small, medium, large)	Group	2	515.6	< 0.001
	Year	1	1.6	0.212
	U	1	124.4	< 0.001
	R	1	7.5	0.009
	Group × Year	2	0.7	0.516
	Group × U	2	5.0	0.011
	Year × U	1	0.9	0.344
	Group × R	2	1.5	0.239
	Year × R	1	1.4	0.246
	U × R	1	5.1	0.029
Moisture preference (hygrophilic, mesophilic)	Group	1	849.4	< 0.001
	Year	1	2.1	0.158
	U	1	62.8	< 0.001
	R	1	48.5	< 0.001
	Group × Year	1	3.1	0.090
	Group × U	1	0.3	0.592
	Year × U	1	2.0	0.163
	Group × R	1	8.7	0.006
	Year × R	1	1.9	0.181
	U × R	1	7.3	0.011

Interactions of 3 and 4 factors were insignificant and omitted

Effects of urbanization on the abundance of ground beetles

We expected that the total abundance of carabids decreases in urban areas. On the contrary, the activity density of beetles was significantly higher in urban forests compared to non-urban ones. This reaction is one of three possible responses to urbanization, although rarely reported (Niemelä and Kotze 2009; Jones and Leather 2012). Among eight studies of urbanization gradients in the framework of the GLOBENET project, this effect was found only in Canada. In the city of Edmonton, the number of carabid beetles in pitfalls was significantly higher than that outside the city (Niemelä et al. 2002). However, in this city, the abundance of beetles increased due to the presence of exotic species. In our study, the whole assemblage and all ecological groups showed higher abundances in urban forests compared to non-urban ones, even after the exclusion of *C. nemoralis*, which is a

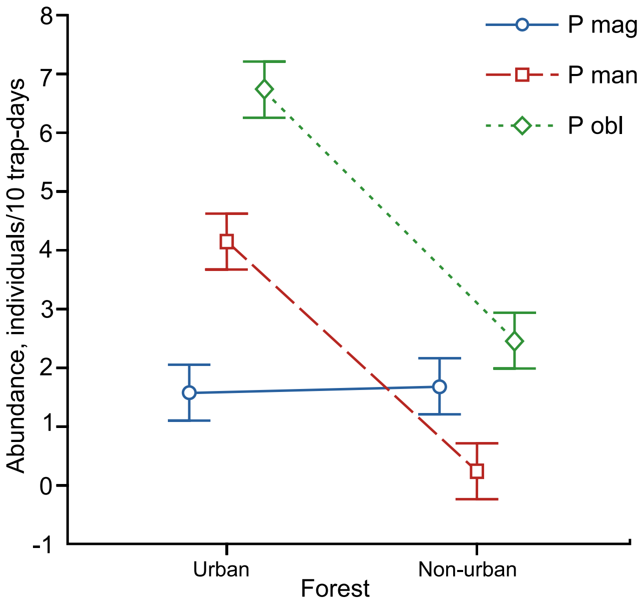

Fig. 2 Mean (± SE) abundance of the dominant species of Carabidae in the urban and non-urban forests ($n = 12$ sites in each of 2 years). Results of the ANOVA with Tukey's HSD test. Interaction «Species × Urbanization» is significant ($F = 6.4$, $p = 0.004$). Pmag = *Pterostichus magus*, Pman = *Pterostichus mannerheimii*, Pobl = *Pterostichus oblongopunctatus*

single (although highly numerous) exotic species in forest parks of Yekaterinburg. Higher activity density of carabids in urban forests of Yekaterinburg can be attributed to environmental change.

Many environmental factors shape carabid assemblages: the structure of the tree layer (forest type, canopy cover, mean height of trees, basal area), soil composition, soil moisture, litter layer thickness, cover of herbs (Niemelä et al. 1988; Luff et al. 1989; Walsh et al. 1993; Antvogel and Bonn 2001; Magura et al. 2008). Our study areas had similar basic characteristics: soil type (Smorkalov and Vorobeichik 2015) and structure of the tree layer (Shavnin et al. 2010), but

Table 2 Indices of diversity of carabids in pine forests of Yekaterinburg (U+) and adjacent territories (U–) at high (R+) and low (R–) recreation loads (combined data from 2 years)

Index	Factor combination			
	U + R+	U + R–	U–R+	U–R–
S	18	17	11	15
S′	6.03 ± 0.46	7.27 ± 0.13a	4.20 ± 0.3 a	6.57 ± 0.98
H	1.66 ± 0.08 a	1.99 ± 0.02 a	1.12 ± 0.03 a	1.50 ± 0.21
D	0.28 ± 0.02 a	0.18 ± 0.01 a	0.43 ± 0.02 a	0.35 ± 0.05

S – total number of species in pitfalls at three sites in a particular forest area, *S′* – number of species per minimal sample of 20 individuals (site mean ± SD); *H* – Shannon diversity, *D* – Simpson dominance (site mean ± SE). The same letters in the cells denote significant differences ($p < 0.05$) among forest areas (Tukey's HSD-test)

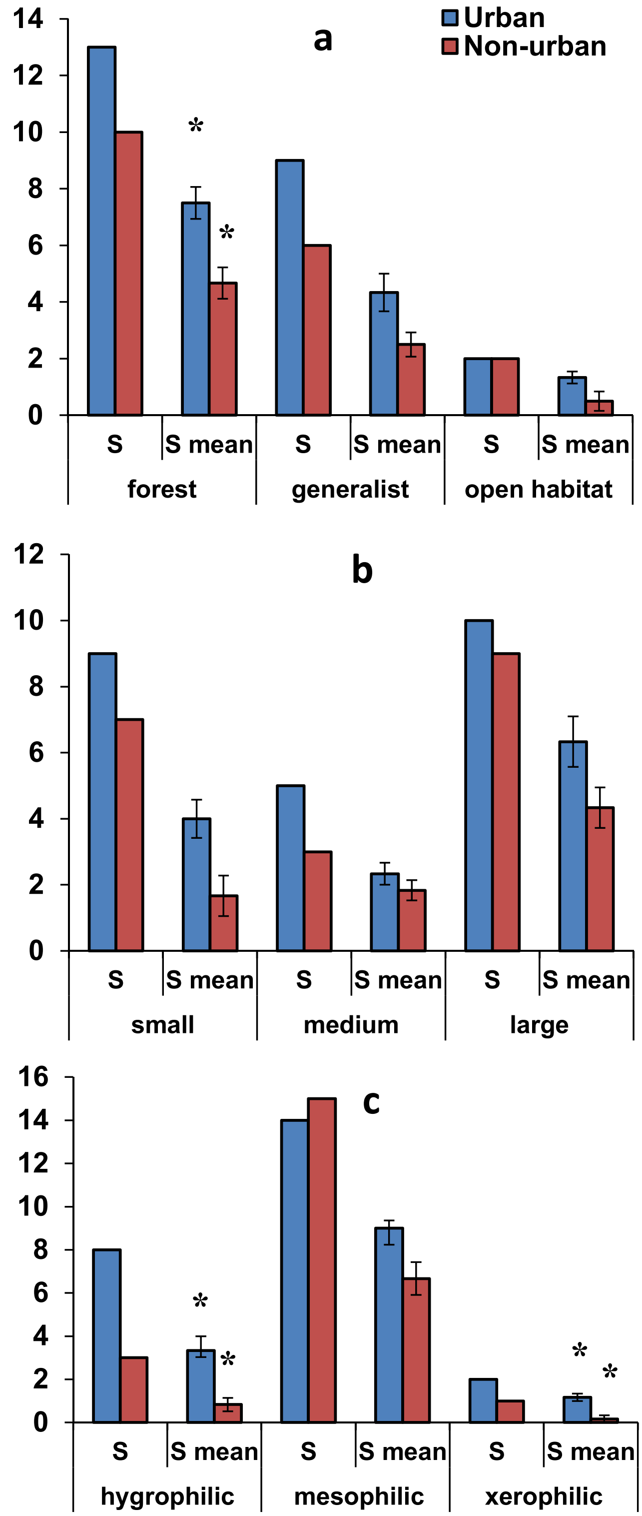

Fig. 3 Species richness of different ecological groups of Carabidae in urban and non-urban forests. Ecological groups by: a) habitat preference; b) body size; c) moisture preference. *S* is the total number of species; S_{mean} is the mean number of species per site (six sites in Yekaterinburg and six sites outside; combined data from 2 years). Bars denote standard errors. Results of the GLM with Poisson distribution and logarithmic link function. Asterisks indicate significant ($p < 0.05$) differences between areas

Table 3 Effects of urbanization (U, urban vs. non-urban) and recreation (R, high vs. low) on the diversity of carabids in pine forests of Yekaterinburg and adjacent territories (combined data from 2 years)

Index	Source of variation	*W*, *F*	*p*
*S**	U	8.2	0.004
	R	1.0	0.311
	U × R	0.4	0.546
S′	U	6.7	0.032
	R	7.2	0.028
	U × R	0.7	0.441
H	U	27.1	0.001
	R	12.0	0.009
	U × R	<0.1	0.867
D	U	27.6	0.001
	R	13.5	0.006
	U × R	0.1	0.817

*– Wald statistic is shown. In all cases df = 1

differed in some details which can affect beetle abundance. Urban soils differ from non-urban ones in having higher pH values (by 0.2–0.5 pH units), higher concentrations of nitrates and available nitrogen compounds (by 2–5 times), and thinner litter layer (by 1.5–1.7 times) (Veselkin and Kaigorodova 2013). It is known that litter thickness negatively correlates with the number of beetles in pitfalls (Guillemain et al. 1997). The thinner litter layer can partly explain higher abundance of beetles in urban forests. The potential effect of prey availability cannot be ignored as well. Laboratory experiments have shown that females receiving more food produce more eggs (Heessen 1980; Sota 1985; Van Dijk 1994). Poor diet can increase mortality of larvae because of cannibalism (Heessen and Brunsting 1981) and a high death-rate of imagoes during the winter diapause (Van Dijk 1994). The abundance of some

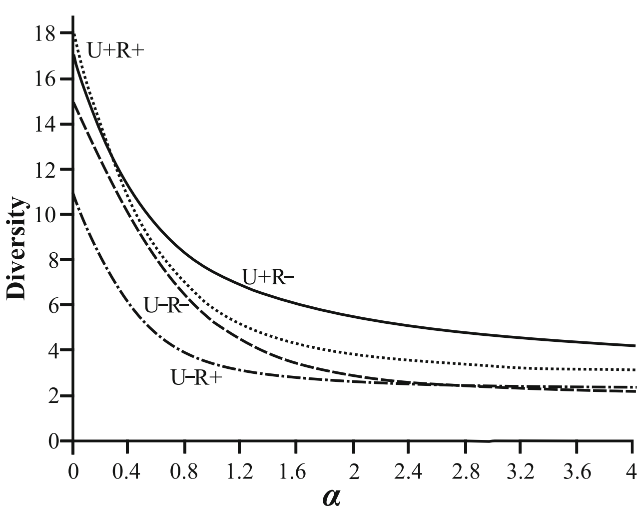

Fig. 4 Diversity profiles based on Hill numbers for assemblages of Carabidae in the urban (U+) and non-urban (U–) pine forests with high (R+) and low (R–) recreation loads. α = index of the Hill number

species correlates positively with the abundance of their prey (Loreau 1988; Guillemain et al. 1997; Koivula et al. 1999; Magura 2002). Since soil invertebrates are an important dietary component of ground beetles (Sergeeva and Gryuntal 1990; Sergeeva and Kryuchkova 1990; Gryuntal and Sergeeva 1994), it would be reasonable to expect large numbers of beetles at sites with a high abundance of soil invertebrates. Higher nitrogen content in urban soils is favorable for soil saprophages, particularly earthworms (Striganova 1980). As shown earlier, the densities of enchytraeids, molluscs, lithobiids, and acariform mites, comprising the main prey of carabids, as well as trophic activity of saprophages, were higher in the urban forests compared to non-urban areas (Ermakov and Vorobeichik 2013; Bergman et al. 2017). Therefore, higher activity density of carabids in urban forests can be attributed to better food supply.

Changes in the abundances of the most numerous species underlie reactions of the whole assemblage. The numbers of individuals of *P. oblongopunctatus* and *P. mannerheimii*, which combined accounted for 56% in the pooled sample, increased significantly in urban forests of Yekaterinburg. *P. oblongopunctatus* prefers habitats with dense vegetation in broadleaved forests of Europe (Magura 2002). In the middle taiga, its abundance is higher in small forest fragments and in moist habitats (Niemelä et al. 1988; Lehvävirta et al. 2006). We do not know whether these preferences apply also in the southern taiga of the Middle Urals, but *P. oblongopunctatus* was significantly more abundant in forest parks of Yekaterinburg with higher canopy cover (Appendix 1) compared to less shaded non-urban forests. In the Middle Urals, *P. mannerheimii* inhabits mixed and deciduous forests as well as willow and alder thickets along rivers (Voronin 1999). It seems that the presence of deciduous trees and shrubs in the understory of urban forests (Appendix 1) positively affects the abundance of this species.

Two species, *C. nemoralis* and *Platynus assimilis*, were recorded only within the city. *Carabus nemoralis*, which appeared in the territory of the city in the mid- 1950s (Kozyrev 1983, cited after Voronin 1999), is now one of the dominants in carabid assemblages of the forest-park zone. This eurytopic species (Thiele 1977) inhabits both forests and open habitats in Yekaterinburg (Zinovyev 1996; Zinovyev and Parkhachev 2017), as a result of which it was included in the group of generalists. Two main reasons can explain localization of this species only in urban territories in the Middle Urals. Firstly, too little time has passed since *C. nemoralis* intruded this area. Spreading along the roads, this species colonized human settlements first of all. Secondly, urban territories provide more favorable environment for this species. Additional studies are needed to specify factors determining high density of *C. nemoralis* in urban territories of the Middle Urals and its absence in the nearby boreal forests.

The hygrophilic species *P. assimilis* inhabits floodplain deciduous forests and wet meadows in the Urals (Voronin 1999). It lives in cities in shady and moist areas of parks, including lawns (Semenova 2008). Not surprisingly, most beetles of this species were caught in urban forests with higher shadiness, and presence of deciduous trees and shrubs in the understory compared to non-urban forests.

Contrary to our expectations, we did not document decreased activity density of any trait groups of carabids in urban forests compared to non-urban ones. In contrast, the abundance of all groups was higher in the city. At the same time, proportion of forest species was lower in urban forests than in non-urban forests (78% and 86% of all individuals respectively), and proportion of generalists was higher (20% and 12% of all individuals respectively). Proportion of large-sized species was higher in urban areas than outside (57% and 46% of all individuals respectively), which can be attributed to good food supply.

Effects of urbanization on the diversity of ground beetles

In this study, the carabid assemblages in urban forests retained features typical of assemblages of carabids in boreal forests. Namely, predatory mesophilic species with spring activity dominate.

The samples in Yekaterinburg showed more species and lower dominance compared to non-urban forests. As a rule, species richness reduced and dominance increased with increasing urbanization, although some studies showed no differences between urban and non-urban forests (Babenko and Eremeeva 2007; Niemelä and Kotze 2009; Aleksanov et al. 2010; Martinson and Raupp 2013). We neither detected a decreased number of forest species and large-sized species, which was documented in other cities (Sadler et al. 2006; Elek and Lövei 2007). The number of mesophilic species was comparable in our urban and non-urban forests. Also, the proportion of hygrophilic species was more than two times greater in the city (36%) than outside (17%), which may indicate higher moisture in urban forests. The forest species *Agonum fuliginosum*, *Loricera pilicornis, P. assimilis*, *Platynus mannerheimii*, which prefer wet habitats, were present in Yekaterinburg and absent outside. We suppose this is due to close proximity of our urban study areas to swampy meadows before the construction of housing estate.

The differences in the abundance and diversity of carabids between urban and non-urban forests are similar to the differences between conifer and deciduous or mixed forests in the Middle Urals. Carabid assemblages in deciduous or mixed forests have a higher diversity, a higher number of dominating species, and, consequently, a lower dominance. Beetles which are able to bury themselves in the forest litter (genus *Pterostichus*) and large beetles (genus *Carabus*) dwelling on the soil surface, are more abundant here (Voronin 1999). Such a habitat effect suggests that changes in ground beetle assemblages in Yekaterinburg are mainly associated with the transformation of vegetation in urban forests.

Many authors report adverse effects of urbanization on carabid assemblages including lower abundance and species richness, especially in forest-specialist species, in urban forests compared to suburban and rural forests (Ishitani et al. 2003; Venn et al. 2003; Magura et al. 2004; Sadler et al. 2006; Elek and Lövei 2007; Tóthmérész et al. 2011). However, some studies show differing results. For example, there was little difference in species richness across the gradient in Sofia. Morever, one forest stenotopic species was numerous at urban sites (Niemelä et al. 2002). Higher abundance and diversity of carabids, including forest group, in our study indicate positive effect of urbanization. We consider this as a result of indirect effects including change of soil properties (nitrogen-enrichment), modification of vegetation in lower forest stories, and better food supply for ground beetles.

Effects of recreation on ground beetle assemblages

The hypothesis on the negative effects of recreation load on the abundance of carabids was only partly supported. Within the city, the total abundance of carabids was significantly higher in the Botanical Garden than in the South-West forest park with intense recreational use. In non-urban forests, the effect of recreation was non-significant. This can be explained partly by the low number of people walking in non-urban forests in the end of spring – beginning of summer, with relatively cold and rainy weather and a high activity of ticks, and risk of tick transmitted diseases. Outside the city, the number of people using the forest for recreation peaks from the second half of summer until the middle of autumn, when most species of carabids are inactive. In the city, the active recreational use of forest parks starts after the snow thawing and continues until late autumn.

Adverse effect of recreation load on ground beetles was documented also in urban forests of Tomsk (Russia, Western Siberia). The abundance of carabids was lower in a forest park with intense recreational use compared to the nearby Botanical Garden with limited access for townspeople (Babenko and Eremeeva 2007). The authors attribute lower abundance of carabids in the park to worse conditions for beetle reproduction and decreased prey abundance due to soil compaction. At our study sites, trampling resulted in 1.2–1.5 times higher density of upper soil horizons, up to $0.95*10^3$–$1.10*10^3$ kg/m^3 (Veselkin and Kaigorodova 2013). At sites with intense recreational use, trophic activity (as a proxy for abundance) of soil saprophages (prey of carabids) was lower 1.1–1.3 times in the forest litter and 1.2–1.7 times in the humus layer (Bergman et al. 2017). However, the abundance of carabids can increase at high recreation load, as shown in urban forests of Helsinki. This was due to higher abundance of the opportunistic species *Pterostichus melanarius* at sites with high trampling (Grandchamp et al. 2000).

We did not observe replacement of dominant species at sites with high anthropogenic load. In our study, three of four dominating species tended to decrease their mean activity density in the South-West forest park with intense recreational use in both study years. Moreover, none of the species received a clear advantage in areas with high load. Differences between our results and those obtained in Helsinki may be explained by different levels of anthropogenic pressure. At our study sites used for recreation the trampled area was less and equaled 11%–16% in Yekaterinburg and 32–39% outside (Ermakov and Vorobeichik 2013), which is comparable to the intermediate level of disturbance in other studies (Lehvävirta et al. 2006).

The diversity of carabids was lower in recreational forests, as evidenced by a significantly lower Shannon index and higher dominance. At the same time, differences between recreation regimes were significant only in urban forests. We did not obtain strong evidences that recreation affects the species richness of carabids at the sites of pine forest under study. The standardized (using rarefaction) species richness of carabids decreased slightly at high recreation load. However, these differences were significant only between the Botanical Garden with a low number of visitors (U + R–) and the non-urban forest with intense recreational use (U–R+), which is most likely an effect of urbanization rather than recreation.

Conclusion

The comparison of carabid assemblages of pine forests of natural origin in Yekaterinburg and outside revealed significantly higher abundance and diversity, and lower dominance of ground beetles in urban forests. Almost all trait groups showed higher activity density: forest species and generalists; hygrophilic and mesophilic species; large-, medium-, and small-sized species. Forest species and mesophilic species dominated carabid assemblages at all sites. Proportion (by the number of individuals) of forest species was lower and proportion of generalists was higher in urban forests. Percentage of large-sized species was higher in Yekaterinburg than outside. Such changes in ground beetle assemblages in urban forests of Yekaterinburg can be attributed to modification of soil properties, vegetation of lower forest stories and better food supply.

Recreation load adversely affected carabid assemblages resulting in lower total abundance and diversity of ground beetles, likely due to soil compaction. Effect of recreation was significant only in urban forests. Both recreation and urbanization factors acted in opposite directions. Negative effect of recreation load on carabids leveled positive effect of urbanization: both abundance and diversity of ground beetles were lower at urban sites with intense recreational use compared to sites closed for townspeople.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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