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The Effect of Megalopolis Environment on the Feeding Activity of Soil Saprophages in Urban Forests

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Abstract—The feeding activity of soil saprophages was assessed by the bait-lamina test in pine forests of native origin within the city of Yekaterinburg and its suburbs in 2011–2013. Four areas, drastically different in terms of manifestation of two main factors—urbanization and recreation loads—were compared. The effect of urbanization on the feeding activity of soil saprophages was both positive and negative. Recreation loads, as a rule, adversely affected the feeding activity. Probable mechanisms responsible for the influence of a large city environment on the feeding activity of soil saprophages are discussed.

Keywords: urbanization, recreation loads, soil saprophages, feeding activity, forest litter, urban forests

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INTRODUCTION

Animal population of urban soils is a traditional object for soil zoology [10, 13, 14, 40]. However, habitat diversity in different cities and the deficiency of information on responses of many groups of soil invertebrates determine the necessity to continue accumulating data on the soil biota under urbanization. In most cases, researchers not separate consequences related to the impact of different stress factors on soil organisms in urban territories. The works on this aspect are few [7, 8, 17].

Usually, the effect of urbanization is considered as a rather uniform factor adversely affecting the soil biota. However, in industrial megalopolises, a complex of factors, differing not only in genesis, but also in their directions and results, act simultaneously. In first approximation, this complex can be divided into two components—urbanization *per se* (chemical, thermal, noise, and light pollution; changes in hydrothermal conditions, fragmentation of biotopes, invasion of alien species, etc.) and recreation loads (mechanical disturbance of the soil and plant covers, and eutrophication). Their strict partition is difficult enough, if it is possible at all, since recreation loads can be considered as one of the urbanization components. However, in suburb forests used by people for recreation, only this type of impact represents anthropogenic influence. Consequently, when comparing suburbs and urban areas with contrasting levels of recreation loads, one can try to separate the effects of the factors considered. The solution of this task comes actually to a scheme of the two-way ANOVA; such an approach was earlier implemented for soil macrofauna [7], mycorrhiza [3], herpetobionts [8], and soil respiration [17].

Feeding activity (FA) of soil saprophages is a parameter, which integrally characterizes their functioning. This characteristic is related not only to the abundance of invertebrates [27, 33, 34], but also to their physiological state [19, 28]. The FA is determined by the quality of substrate [31, 35, 42], morphology of the upper part of the soil profile [29, 39, 41], soil temperature and moisture [28], and soil chemistry [16, 23, 26]. Considering the informative value of these characteristics, it is interesting to assess the influence of urbanization and recreation loads on FA.

For estimating FA of soil saprophages, the bait-lamina test was proposed in the early 1990s [41]. The essence of this method is to evaluate the degree of consumption small fragments of artificial food baits by invertebrates during a relatively short-term period of exposure. In the recent decades, this method is actively used in soil ecology [25, 30], agronomy [38], and ecotoxicology [4, 5, 22–24, 37].

The aim of this work is to assess the influence of a large industrial city on the FA of soil saprophages, to determine the contribution of urbanization and recreation loads to its variability, and to reveal possible FA determinants. The following hypotheses are tested in this work: (1) the urbanization and recreation loads unidirectionally affect the FA of soil saprophages; (2) the influence of urbanization and recreation loads is negative; (3) the influence of urbanization and recreation loads is equal in different soil horizons (forest

Table 1. The characterization of the sample areas

Parameter	Sample area			
	U–R–	U–R–	U+R–	U+R+
Stand basal area relative to normal stand[a]	0.9–1.1	0.7–0.9	0.9–1	0.8–0.9
Standing volume, m^3/ha[a]	457–520	381–484	354–518	435–514
Area of road–path network, %[b]	0–5	32–39	1–3	11–16
Canopy cover, %[c]:				
shrub layer	0	0.5–20	75–80	80–85
arboreal layer	55–75	50–55	35–50	35–45
Projective cover, %[c]:				
moss layer	10–15	0.5–3	5–20	3–12.5
grass–dwarf shrub layer	70–85	60–70	20–45	35–50
Soil texture[d]	Loamy–sandy, sandy–loamy	Sandy–loamy, loamy	Loamy clayey	Sandy–loamy, loamy
Thickness, cm[d]:				
litter	1.2–1.8	1.2–1.7	0.8–0.9	0.8–1.1
humus-accumulative horizon	3.5–14.5	10.5–14.5	11.0	7.0–9.0
pH_{water}[e]:				
litter	5.2–5.4	5.0–5.5	5.5–5.9	5.5–5.9
humus-accumulative horizon	5.4–5.7	5.4–5.6	5.4–5.8	5.7–5.7
Content of $N_{hydrolyz}$, mg/100 g in[e]:				
litter	19.9–24.8	11.9–13.3	29.1–32.2	31.9–55.3
humus-accumulative horizon	5.3–6.9	3.3–4.4	5.2–6.0	5.8–8.1
Stocks in the 0–50-cm layer, mg/m^2[d]:				
Cu	7.5	9.2	11.4	6.5
Pb	4.2	5.4	5.1	5.0
Cd	0.1	0.2	0.1	0.1
Zn	10.3	11.8	9.5	8.2
Total abundance of saprophages, ind./m^2[f]:	325–443	336–468	593–1298	598–1060
Including earthworms	190–278	120–265	178–248	178–275
enchytraeids	0–50	5–98	85–563	160–483

Minimal and maximal values of the parameters for a sample area by the means per sample plot. Information sources: [a]—[21]; [b]—data supplied by O.V. Tolkach; [c]—[9]; [d]—data by S.Yu. Kaigorodova, [e]—[3], [f]—[7].

litter and humus-accumulative horizons), as well as in different years and seasons.

MATERIALS AND METHODS

The studies were conducted in the city of Yekaterinburg, the largest industrial center of the Middle Urals (the area is 50 thousand ha; the population is about 1.4 million). Yekaterinburg is referred to strongly polluted cities of Russia [20]. In 2010, atmospheric emissions amounted to nearly 190 thousand tons of pollutants (sulfur, carbon and nitrogen compounds; mineral dust, and heavy metals). Urban vehicles mostly (85%) contribute to the air pollution [20]. It is generally believed that the soils of Yekaterinburg are polluted with heavy metals. According to official data, in 2010, in the soils of the central district of this city, the maximal contents of copper, nickel, lead, chromium, zinc, cadmium, and manganese exceeded their background values by 58, 20, 18, 8, 6, and 3 times, respectively [6].

In the city and its suburbs, the following areas were chosen, where the factors of urbanization (U) and recreation loads (R) were active (+) or their influence was absent (–): (1) a forest area within the city, located in the arboretum of the Botanical Garden of the Ural Division of the Russian Academy of Sciences; it was closed for visitors for more than 50 years (U+R–); (2) the Yugo-Zapadnyi forest park, a recreation forest of Yekaterinburg, located close the arboretum; unlike the arboretum, citizens actively visit this park (U+R+); (3) a seldom visited forest near Lake Glukhoe, 10 km to the west of the city's boundary (U–R–); and (4) a frequently visited forest on the shore of Chukhovskoe Lake, 10 km to the west of the city's boundary (U–R+);

All these areas were occupied by native mature high-dense 120–140-year-old pine stands of quality

Table 2. Weather conditions in the time of measurements (mean ± standard error, accounting unit is a day)

Year	Series	Dates	Exposure duration, 24 h	Average daily air temperature, °C	Average daily amplitude of air temperature, °C	Total precipitation, mm*
2011	1	01–10.08	10	16.1 ± 0.9	8.6 ± 0.7	61.3
	2	11–22.08	11	17.4 ± 2.0	11.5 ± 1.0	2.8
	3	26.08–05.09	10	16.2 ± 1.3	10.1 ± 0.9	39.2
2012	1	05–15.06	10	18.7 ± 1.1	10.6 ± 1.5	112.1
	2	27.09–12.10	14	7.8 ± 0.9	7.2 ± 1.0	8.7
2013	1	14–23.05	9	10.7 ± 0.8	10.0 ± 1.3	17.0
	2	10–20.06	10	17.6 ± 1.3	11.8 ± 1.0	31.1
	3	15–26.07	11	18.7 ± 0.7	9.1 ± 0.9	32.7
	4	14–23.08	9	19.5 ± 0.6	11.8 ± 0.9	17.3

* —Total precipitation for an accounting series and three previous days.

classes II and III; the average height of trees was 25–30 m, the average diameter, 36–48 cm [21].

All the stands on sample areas are uniform in taxation characteristics (Table 1). Within the city, in the stands and in well-developed understory, the abundance of adventive species (negundo (*Acer negundo*), dwarf apple (*Malus baccata*), syringe (*Syringa vulgaria*), bird cherry (*Padus maackii*), June berry (*Amelanchier spicata*), cotoneaster (*Cotoneaster lucidus*)) was substantial. The ground vegetation layer was dominated by alehoof (*Glechoma hederasea*) and nettle (*Urtica dioica*) [9] that indirectly testifying to the high nitrogen content in the soils. Direct estimates of the easily hydrolyzable nitrogen concentrations confirmed this fact.

The development of the understory leads to a greater shadowing in the urban plots: the canopy cover of shrub and tree reached 75–85%, whereas in the suburb forests it was only 20%; therefore, lower abundance of the grass–shrub layer and higher soil moisture content were recorded. In the recreation areas, a network of roads and paths was formed occupying 40% of the total area.

The soil cover of the studied areas is represented by typical burozems (Cambisols (Humic)) and mid- and low-stony podzolized burozems (Skeletic Cambisols (Humic, Protospodic)) that are formed under good drainage. The bulk density of the humus horizons in the soils outside the network of roads and paths was equal (0.77–0.85 g/cm^3) in all the sample plots; under the influence of trampling, it increased by 1.2–1.5 times (0.95–1.10 g/cm^3), and the litter and humus horizons were often disturbed; on the slopes they were eroded. In the urban forests, even outside the road–path network, the thickness of the litter decreased by 1.5–1.8 times compared to that in the suburb ones [3].

In 2011–2013, the FA was measured several times for a season (Table 2). In 2011, three series of measurements were taken; in 2012 and 2013, two and four test series, respectively. In each sample area, three sample plots (25 × 25 m) were placed. Within the plot, five lines of laminas were arranged set at 1 m (five per line). The lines were located outside the road–path network, by the scheme of "envelope." Twenty-five bait-laminas were established in each sample plot. A total of 2700 bait-laminas were placed in 12 sample plots for three years.

A bait-lamina is a plastic lamina of 12 cm long with 16 holes (diameter is 5 mm) arranged every 5 mm. The holes were filled with bait—a moist paste presenting a mixture of nettle leaf powder with microcrystalline cellulose (3 : 7). It is known that earthworms and enchytraeids mainly consume such bait; collembolans and soil mites consume it much less [28, 36]. The laminas with bait were placed vertically in the litter and humus-accumulative horizons (a cut was made preliminarily by a sharp knife) so that the upper hole was at the depth of 0.5 cm from the litter surface. The exposure time was 9–11 days (only in the second series of 2012, it was 14 days). After the removal of the laminas out of the soil, they were examined using a binocular microscope. The degree of perforation of each hole (i.e. the degree of bait consumption by invertebrates) was evaluated according to the five-grade scale: 0—intact, 0.25—consumed 25%, 0.50—50%, 0.75—consumed 75%, 1—fully perforated. A total of measurements was 43200.

Since the publication of paper of von Törne [44], the degree of perforation of holes was usually evaluated according to the two-grade scale (0—the bait is intact, 1—the bait is perforated). The applying of the five-graded scale significantly increases the accuracy of estimating the FA and makes it more resistant to errors related to accidental damage of the bait. Furthermore, the scale expansion allows to evaluate not only the proportion of perforated holes (as in the original procedure), which is largely characterizes the spatial distribution of invertebrates, but also it enables one to estimate the rate of bait consumption per se, since the score is proportional to the volume of the substrate consumed.

Afterwards, FA was analyzed both along the entire lamina (total FA) and separately for two horizons—forest litter and humus—based on the values of their thickness in particular sample plots. In the suburb areas, the litter thickness was 1.2–1.8 cm (i.e. it corresponded to 3–4 upper holes); in the city, it was 0.8–1.1 cm (two holes); in all the cases, the underlying holes corresponded to the A1 horizon.

For the correlation of the FA with the abundance of soil saprophages, the data obtained in the sampling of the soil macrofauna in July, 2011 on the same sample plots were used (Table 1) [7].

Soil temperature was measured in 2013 using DS1921G F5 (Dallas Inc., USA) temperature loggers placed in the litter (one on each sample plot). The period of exposure was 135 days (12.06–25.10), the interval of measurements was 2 h, and the discrete interval was 0.1ºC. Unfortunately, three loggers from the U+R+ sample area were lost, so it was impossible to evaluate the effect of recreation loads on temperature. Based on the temperature data obtained, the following parameters were calculated: average daily temperature (12 readings), average daytime temperature for the period from 08 to 22 o'clock (8 readings), average night temperature from 24 to 06 o'clock (4 readings), diurnal amplitude (difference between the maximal and minimal temperatures for 24 h), daily variability (the mean square deviation for 24 h, 12 reading).

The soil moisture was measured in 2013 (at the beginning and end of the bait-lamina exposure, strictly in points of their location) using a field electronic HH2 analyzer with a ThetaProbe ML2 detector (Delta-T, Great Britain). The moisture (vol %) was determined in the 0- to 5-cm layer including the litter and A1 horizon.

The weather conditions (air temperature and precipitation) were characterized by the data from the Yekaterinburg meteorological station on www.rp5.ru (Table 2).

The statistical analyses were performed with Statistica 6.0 and R 2.11.0 software. The significance of the influence of the factors and their interaction was estimated by multi-way ANOVA with a correction for heteroscedasticity by the Huber–White method (algorithm hc3). The multiple comparisons were made by the Tukey test.

RESULTS

Feeding activity of soil saprophages. A very high variability of FA was revealed within individual laminas (Fig. 1). In all series at all the sample plots, laminas with both intact baits and completely consumed ones were revealed. The average values of FA per a sample plot significantly differed between the areas, series, and soil horizons (Fig. 2).

The results of the three-way ANOVA testify to unequal effects of urbanization, recreation loads and season on FA in different years. Thus, in 2011 and 2013, all three factors significantly affected the total FA, but in 2012, the influence of urbanization was insignificant (Table 3). Urbanization adversely affected the total FA in summer decreasing its value by 1.5–1.8 times in 2011, by 1.9 times in 2012, and by 1.2–1.5 times in 2013. However, it had a positive effect on the total FA in autumn increasing it by 1.1 times in 2011 and by 1.5 times in 2012 (Fig. 2). The influence of recreation loads on the total FA was negative in all the cases: in the recreation areas, it was lower by 1.1–1.2 (2011), 1.3–1.5 (2012), and by 1.2–1.5 times (2013) (Fig. 2).

As the urban and suburb plots differed in the litter thickness (Table 1), the "genetic horizon" factor was included into the analysis of variance as an additional one. The interactions "urbanization × genetic horizon" are significant in all the cases: $F(1; 48) = 12.8; p < 0.001$ (2011); $F(1; 32) = 9.6; p < 0.001$ (2012); $F(1; 64) = 26.8$; $p < 0.010$ (2013). This confirmed the necessity to consider FA separately in different soil horizons.

The influence of urbanization on FA in the litter related to the year and series was both positive (FA was greater by 1.1–2.1 times) and negative (FA was less by 1.4 times). In the humus-accumulative horizon, the effect of urbanization was also positive (by 1.1–1.4 times), or negative (by1.2–2.2 times) depending on the year and series (Fig. 2). It is worthy to note that in different soil horizons, the direction of influence of urbanization on FA determined in the same series did not always coincide.

Recreation loads, as a rule, led to a decrease in FA by 1.1–1.3 times (litter) and 1.2–1.7 times (A1), but in the autumn of 2011 and 2012, FA in the litter in both recreation and nonrecreation areas was similar.

A relative contribution of the considered factors to the FA variation is convenient to represent with the help of the variance decomposition into its components (Fig. 3). The contributions of the factors differed by years and genetic horizons. Thus, the contribution of the "season" factor to the FA variability in the forest litter changed from 0.1% (2013) to 54.4% (2011), in the humus–accumulative horizon, from 5.2% (2013) to 59.2% (2011). The contribution of recreation loads and urbanization also strongly varied between years: in the litter—0–59.0 and 0–5.8%, respectively, in the humus–accumulative horizon—6.6–36.7 and 4.3–25.3%, respectively (Fig. 4).

Abundance of soil saprophages. Based on the data [7], the total abundance of invertebrates was 1.1–2.7 times higher in the urban soils as compared to that in the suburb areas; the number of saprophages, representing about 50% of the total abundance of invertebrates, was 1.3–4.0 times greater. In all the cases, this fact was related to the greater number of enchytraeids, for which the moister and rich in nitrogen urban soils are more suitable (Table 1). The abundance of earth-

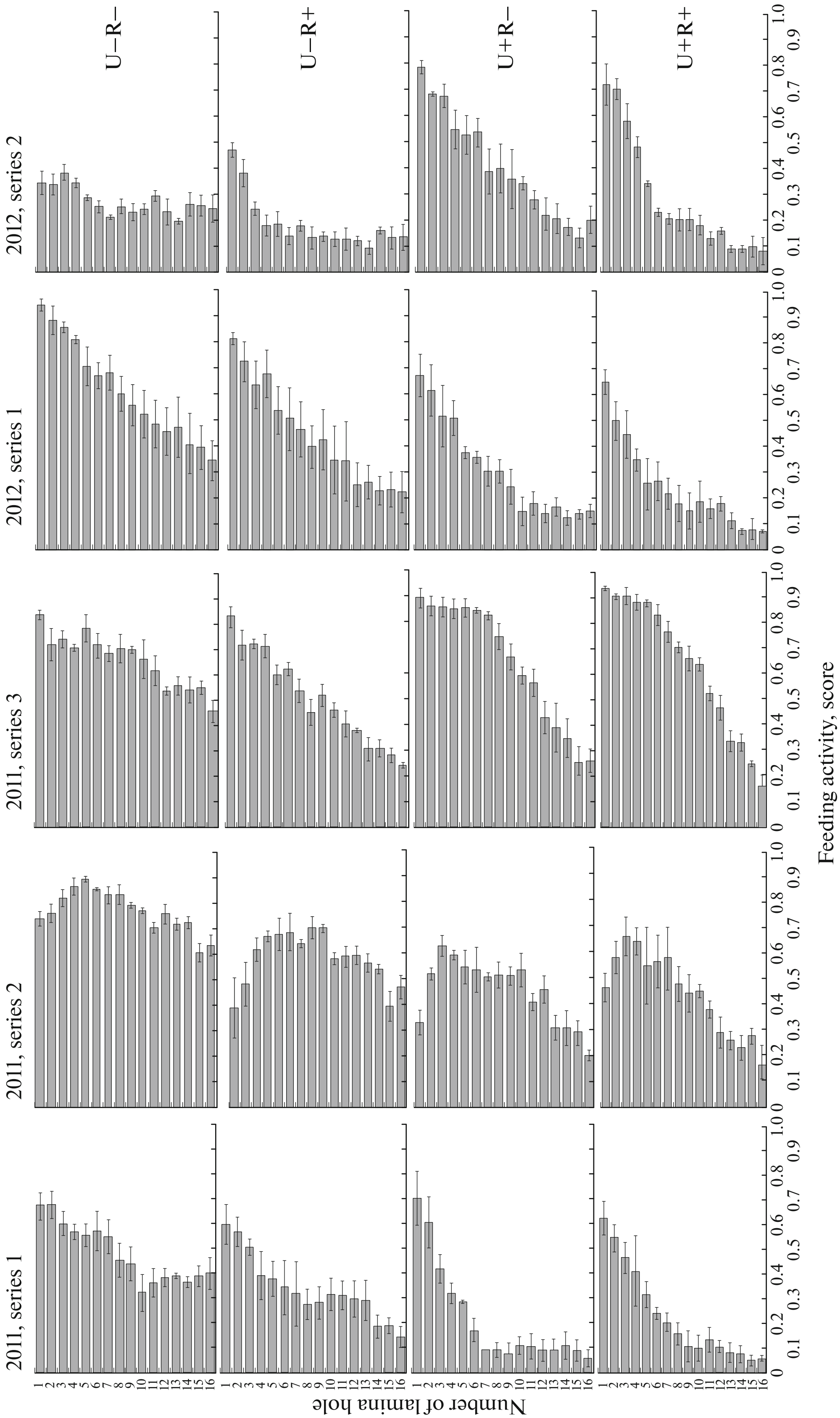

Fig. 1. The vertical distribution of soil saprophages' FA by years, areas, and series. Horizontal lines—standard error ($n = 3$). The accounting unit is a sample plot.

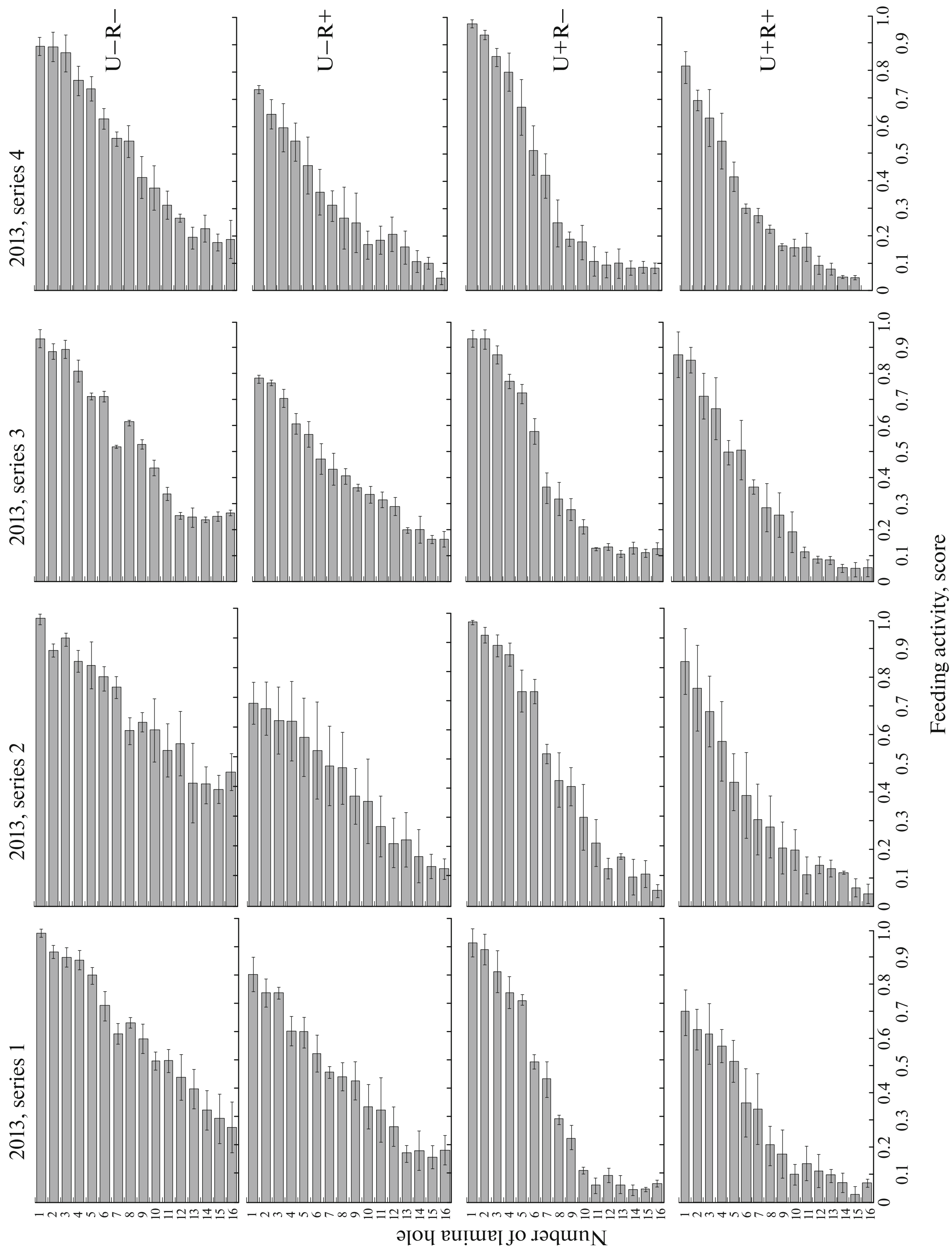
2013, series 1
2013, series 2
2013, series 3
2013, series 4
U−R−
U−R+
U+R−
U+R+
Number of lamina hole
Feeding activity, score

Fig. 1. (Contd.)

Table 3. The results of the three-way ANOVA for differences in the feeding activity between series, grades of urbanization and recreation loads

Source of variation	*df*	Total FA		FA in the A1 horizon		FA in litter	
		F	*p*	*F*	*p*	*F*	*p*
2011							
Series (S)	2	100.7	<0.001	110.9	<0.001	40.2	<0.001
Recreation (S)	1	20.0	<0.001	21.2	<0.001	0.2	0.694
Urbanization (U)	1	42.0	<0.001	40.2	<0.001	9.8	0.005
S × R	2	0.3	0.719	0.4	0.661	0.8	0.465
S × U	2	25.1	<0.001	25.5	<0.001	21.6	<0.001
R × U	1	21.7	<0.001	21.0	<0.001	5.0	0.034
S × R × U	2	0.1	0.942	0.1	0.880	2.9	0.076
2012							
Series (S)	1	4.5	0.050	1.5	0.243	62.1	<0.001
Recreation (R)	1	21.0	<0.001	30.5	<0.001	1.5	0.245
Urbanization (U)	1	2.1	0.165	2.2	0.155	52.8	<0.001
S × R	1	0.01	0.909	0.2	0.690	2.4	0.140
S × U	1	20.0	<0.001	12.2	0.003	41.8	<0.001
R × U	1	0.005	0.946	0.001	0.991	0.1	0.837
S × R × U	1	0.8	0.376	0.7	0.414	0.4	0.541
2013							
Series (S)	3	4.4	0.011	3.3	0.033	0.2	0.888
Recreation (R)	1	58.3	<0.001	28.0	<0.001	47.6	<0.001
Urbanization (U)	1	44.9	<0.001	25.0	<0.001	6.0	0.020
S × R	3	0.6	0.604	0.6	0.611	0.4	0.784
S × U	3	1.5	0.244	1.4	0.262	0.8	0.483
R × U	1	2.0	0.163	1.7	0.196	0.2	0.690
S × R × U	3	0.1	0.982	0.2	0.923	0.5	0.670

F—Fisher criterion, *p*—significance level, *df*—degrees of freedom for a factor. The accounting unit is a sample plot.

worms in the soils of the studied areas did not differ, but in the urban soils, their shift to the deeper horizons was observed due to a decrease in the litter thickness. The stronger influence of urbanization, as compared to recreation loads, on the abundance of soil saprophages was found [7]. Similar results were obtained for herpetobionts in the same areas [8].

Soil temperature. The influence of urbanization on the average daily and average daytime temperatures was statistically insignificant $F(1;12) = 0.4–0.6$, $p = 0.45–0.52$). At the same time, the average night temperature was higher in the city than in the suburbs, whereas the diurnal amplitude and the daily variability of the temperature was lower (Fig. 4) (all differences were significant, $F(1; 12) = 8.6–14.8$; $p < 0.01$). The differences in each of the studied parameters between the series were significant ($p < 0.05$).

Soil moisture. Only the driest sample area at Glukhoe Lake (U–R–) differed in the volumetric soil moisture content from the rest ones (Fig. 5). In this area, the variation of soil moisture between the series was low (15.6–16.7%), whereas in other areas, the soil moisture was much higher (by 1.3–1.4 times) in the first half of the summer than in the second one. Since the volume soil moisture was not estimated separately for the litter and humus-accumulative horizon, and the litter was rather thick there, the moisture values for the sample area at Glukhoe Lake turned out lower than for the others.

DISCUSSION

The comparison of our results on FA of soil saprophages with the data of other authors was difficult due to differences in the methods for its measurement (different duration of exposure, bait composition, metric for perforation, etc.). Nevertheless, the FA values in the suburb area without recreation (0.26–0.78), despite the difference in measurement scale, were similar to the values obtained by other authors. Thus, in the hornbeam–willow forests of Tula region, the FA was 0.61

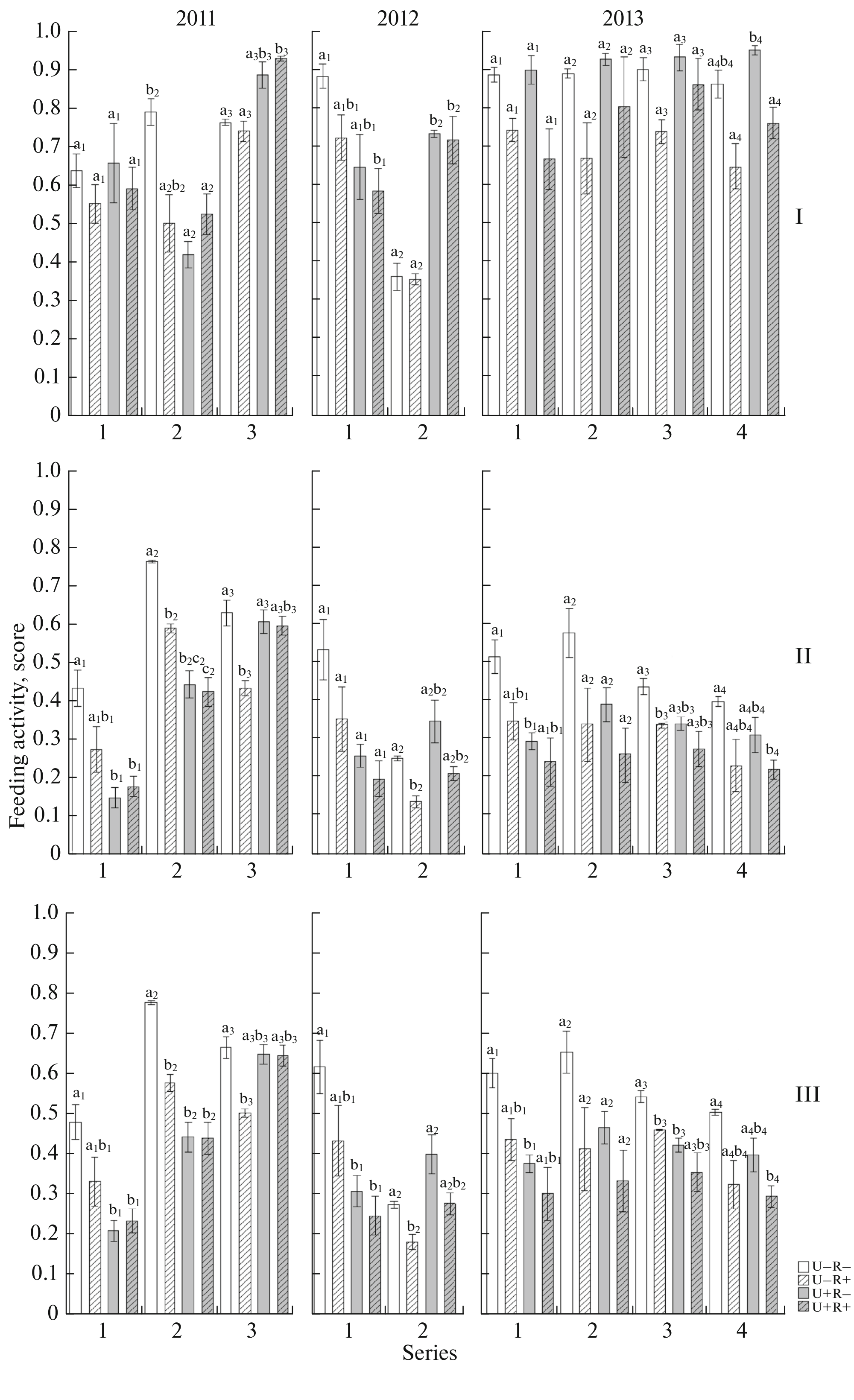

Fig. 2. The FA of soil saprophages in litter (I), humus-accumulative horizon (II) and total FA (III) in areas contrasting in the levels of urbanization and recreation loads. Vertical bar is standard error ($n = 3$). Means differing from each other within a series (Tukey test, $p < 0.05$) are marked by different letters (the lower index is number of series). The accounting unit is a sample plot.

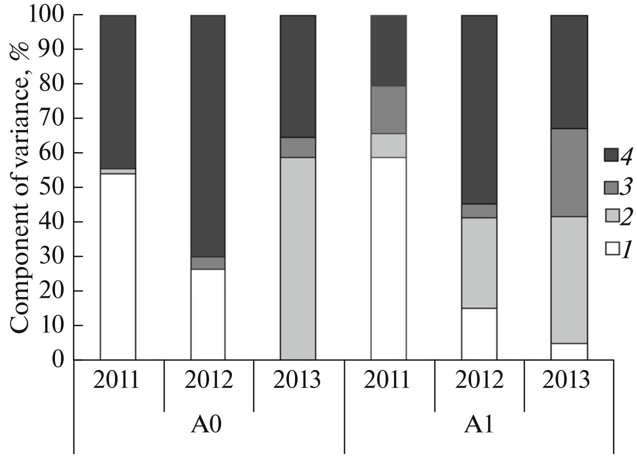

Fig. 3. Variance components of saprophages' FA in the AO and A1 soil horizons in different years related to differences in *1*—series, *2*—recreation loads grades, *3*—urbanization grades, *4*—residual variance. The accounting unit is a sample plot.

[5]; in the spruce forests of Kaluga region, 0.65 [29]; and in the pine plantations of Siberia, 0.67 [2]. The revealed trend of decreasing FA with depth is rather typical; it was noted many times earlier [4, 29, 39, 42].

The FA values in the urban plots were greater (0.18–0.69) than those obtained for urban territories by other authors. In the strongly transformed urban soils of northwestern England, FA was only 0.01–0.12 for 7 days of exposure [32]. In the recreation plots, FA was also higher (0.16–0.67) than that obtained in the areas with the strongly anthropogenically disturbed soil cover (0.10–0.32) [1].

Basing on our results, we have to reject all three testable hypotheses. It turned out that the impact of urbanization and recreation loads on FA can be manifested, firstly, in different directions, secondly, it is not always negative and, thirdly, varies between years, seasons and horizons. This pattern testifies to the absence of one strongly affecting factor and require particular consideration.

Different ecological factors forming a complex effect of urbanization can affect differently the abundance of soil saprophages and their FA. Among the positive effects of urbanization are the following. First, the greater nitrogen content in urban soil; nitrogen is the main element limiting the development of earthworms. It is well known that growth rate and fertility of earthworms increase drastically when they live in the substrate rich in nitrogen [19]. Second, thermal pollution in cities extends the period when the soil warms up to the temperature above 10°C—the temperature, at which the FA of saprophages substantially increases [28]. In addition, in cities, at the end of

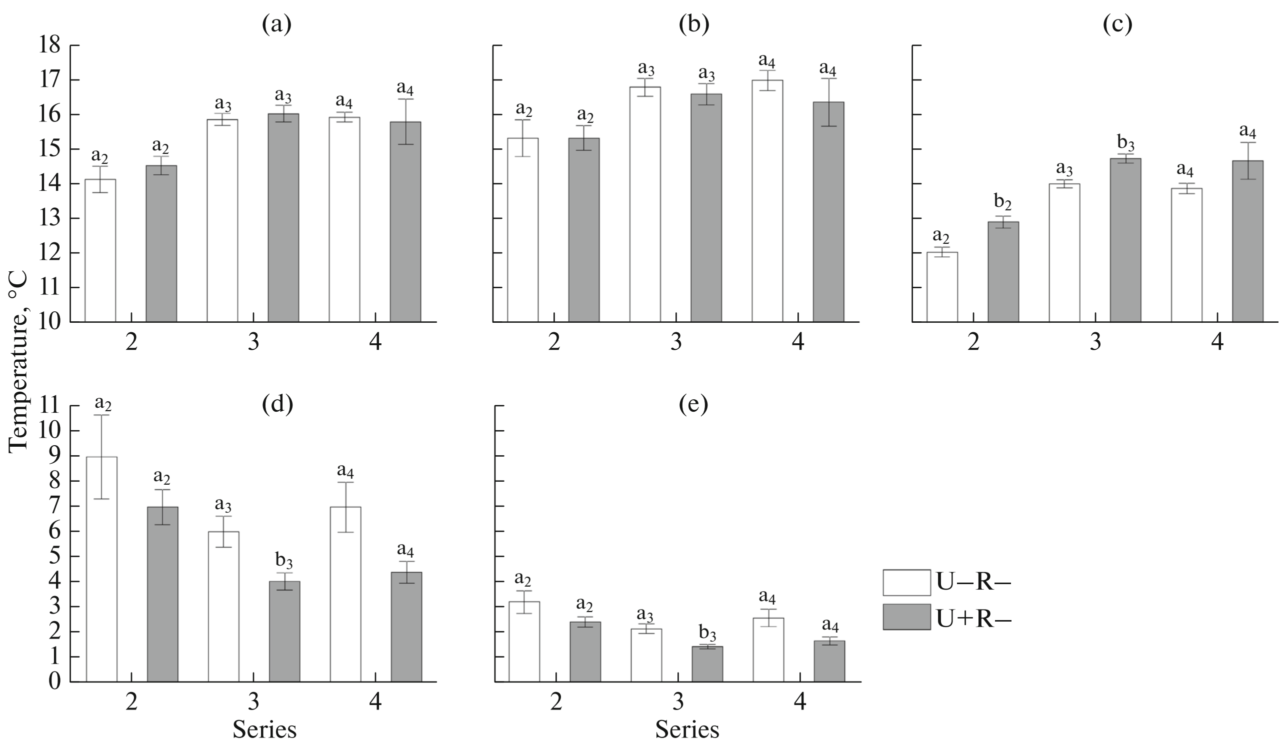

Fig. 4. Changes in the (a) average daily temperature, (b) average daytime temperature, (c) average night temperature, (d) daily temperature amplitude, and (e) variability of the daily temperature in urban and suburb areas based on counting series of 2013. Error bars are standard errors (n = 3). Values significantly differing between each other within a series (Mann–Whitney test, $p < 0.05$) are marked by different letters (the lower index is number of series).The accounting unit is a sample plot.

growing periods, a peak of organic matter input to the soil occurs later [11] and is reflected in the dynamics of saprophages abundance and, consequence, in their FA [12, 18]. Third, the smoothed temperature fluctuations within the 24-h period observed in urban territories also promote an increase in FA [43].

In contrast to expected, the content of heavy metals in the soils of the suburb and urban areas was found to be similar (Table. 1). This fact is contradictory to the official materials on the metal pollution of Yekaterinburg soils [6]. Most probably, this is related to the fact that the official data are referred to central districts of the city and its open areas (lawns), while our data were obtained in peripheral urban forests. The similarity in the metal content among the plots enables to suggest that the adverse influence of urbanization on FA is determined by some other factors rather than by the toxic effects of pollutants on soil biota. First of all, the litter in urban forests, being very thin, is not able to keep microclimate conditions optimal for invertebrates [13, 42]. The soils of urban areas, due to natural reasons, are somewhat more dense (Table 1), which may restrict vertical movements of soil invertebrates and their FA [29, 42].

The influence of recreation loads on the soil is mainly determined by trampling and contamination of its upper layer with a great amount of domestic waste (plastic, glass, and metal), which limits the space for life of soil invertebrates [29]. In addition, garbage increases soil water permeability and decreases it water-holding capacity, which disturbs the normal water regime and, as a consequence, inhibits the activity of the soil biota [15]. The influence of recreation loads is different; it is weaker in cities and stronger in suburbs reflecting the proportion of the areas with different recreation loads. Recreation loads affects FA in the humus-accumulative horizons to the greatest extent irrespectively of season, whereas its adverse impact in the litter is observed only in summer, when the intensity of recreation is maximal.

The role of the season factor in the explanation of FA variation differed between the years (Fig. 4). In 2011 and 2012, its role was more significant due to a wider range of precipitation within the growing periods, and in 2012, due to the wider range of the average diurnal temperature (Table 2). In 2013, temperature and precipitation ranges were narrower (Table 2, Figs. 3 and 5), thus the seasonal variability of FA was weakly pronounced.

Basing on our estimates of soil macrofauna abundance [7] in the urban areas differing from the suburb ones by the higher number of saprophages (primarily, of enchytraeids), one should also expect higher values of FA. The positive relationship between FA and abundance of soil saprophages is quite regular [27, 45], although it is not always revealed [29, 39], as in our case.

The absence of a unidirectional impact of urbanization on the abundance of saprophages and their FA can be explained by some reasons: (1) vertical redistribution of invertebrates in the urban plots from the thin litter to the underlying soil horizons; (2) probable differences in food preferences and rations of saprophages in different plots. The bait used (a mixture of nettle and cellulose) may be less attractive for invertebrates in the urban plots, where nettle occurs more often than outside the city. At last, the participation of other pedobionts, microarthropods in particular, in addition to earthworms and enchytraeids is possible in the consumption of the bait, but they were not counted in manual sorting of soil monoliths.

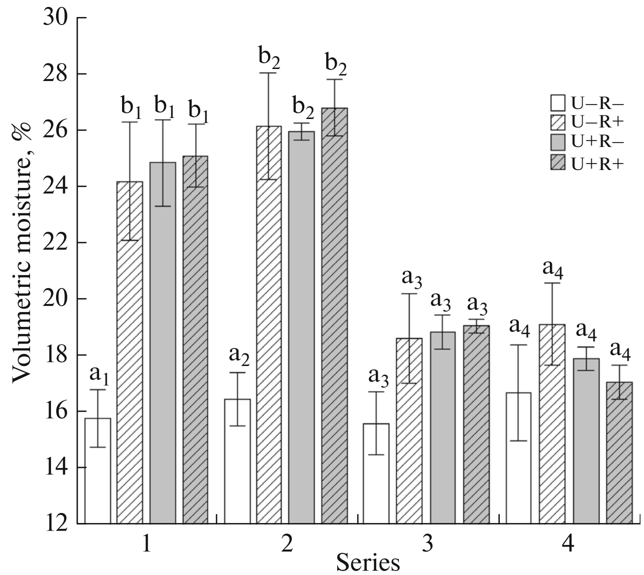

Fig. 5. The volumetric moisture of the upper (0–5 cm) soil layer in urban and suburb areas. Error bars are standard errors ($n = 3$). Values significantly differing between each other within a series (Tukey test, $p < 0.05$) are marked by different letters (the lower index is number of series). The accounting unit is a sample plot.

It is worthy to note that the bait-lamina test used in our work has certain limitations. The main limitation is that it does not allow correctly estimate the rate of bait consumption when rate approaching the upper limit of the scale (FA cannot be more than 1). The duration of exposure in our work was more often adequate to the rates of bait consumption. However, in some cases, the difference between the high and low FA values could be underestimated.

CONCLUSIONS

The hypothesis of negative and unidirectional effects of urbanization and recreation loads on the FA of soil saprophages and the hypothesis of their similar manifestation in different years, seasons, and in different soil horizons have not been confirmed. The influence of urbanization on the FA could be both positive and negative, whereas recreation loads reduced it. The action of the considered factors differed between years, seasons, and soil horizons.

The factor of urbanization, being complex in nature, includes not only elements of adverse influence on the soil biota, but also the favorable ones—an elevated nitrogen content in the soil, mitigated fluctuations in temperature within days, and a longer period of biological activity. The adverse effect of urbanization on the FA of saprophages was not directly related to the toxic pollution of the soils; it was specified by the transformation of upper soil horizons. Thin litter of urban forests is not able to support the optimal microclimate regime, and the heavier soil texture limits the movements of animals.

The reduction of the FA in the plots with strong recreation loads is associated with the compaction of the soils and disintegration of the forest litter under the influence of trampling, pollution with weakly decomposable domestic waste, which limits the living space of soil invertebrates and disturbs the water regime of the sites.

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