

# Common Shrew (*Sorex araneus*, Eulipotyphla) Population and the Food Supply of Its Habitats in Ecologically Contrasting Environments

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**Abstract**—Studies in the fir–spruce forests of the Middle Urals, in habitats with varying degrees of transformation by natural disasters (windfalls and fires), have shown that the abundance and dynamics of invertebrate communities determine the food supply of shrew habitats, one of the most important microhabitat characteristics. The indicator of food supply reflects the state of the foraging base of the common shrew and is a stable biotopic characteristic, the stability of which is maintained due to the redistribution of the abundance of different taxonomic groups of soil mesofauna in the course of their long-term dynamics. The abundance of the common shrew was not related to the food supply of the habitats of the current year, but depended on the food supply of the previous year, and this dependence was most pronounced in strongly disturbed habitats.

**Keywords:** *Sorex araneus*, ecologically contrasting habitats, windfall, fire, microhabitat characteristics, food supply, soil mesofauna

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The common shrew (*Sorex araneus* L., 1758) is one of the most widespread species of shrews in the world. Representatives of the genus *Sorex* have the highest metabolic rate among terrestrial mammals, which explains the functioning of shrews, which is close to the limit of physiological capabilities [1, 2]. Due to their wide distribution, abundance, incredible voracity and 24-hour activity, shrews are important components of taiga ecosystems. In regulating the abundance of invertebrates, their role is a mosaically acting factor, but at a high abundance, shrews can reduce the biomass of prey [3]. Moving in the forest litter, shrews promote the mixing of its components in the upper soil horizons, which accelerates the germination of seeds of trees and shrubs. In many natural foci of tick-borne encephalitis, along with rodents, they are the main hosts for the larvae of ixodid ticks and top the list of animals that can regularly maintain the circulation of the virus [4–6].

The vital activity of animals in nature is carried out in habitats with a certain range of environmental conditions and, accordingly, resources in which the species is able to survive and reproduce. As specific periods of life of small mammals pass in small areas, the microhabitats is the “mediator” between the population and the external environment, the characteristics of which reflect the protective and forage conditions of

the animals [7]. It is known that the choice of habitats by shrews is primarily determined by their feeding capacity, which affects the numerical distribution of individuals and can be estimated from the values of the total number or biomass of invertebrates [3, 8]. Consequently, the index of food supply in the habitats of shrews is equivalent to the total abundance of soil-litter invertebrates and is an important biotopic characteristic determined by complex processes in communities of various taxonomic and numerical composition.

The diet of the common shrew has been studied quite fully, its food range is much wider and more varied in comparison with other species of the genus, and the diet can vary depending on the season, weather, and habitat [3, 9, 10]. It does not have a rigid attachment to certain food objects, switching in different years from one object to another, depending on how often they are found in habitats [11]. The diet of the species is based on numerous and accessible species of large soil-litter invertebrates. In August–September, its diet is dominated by earthworms (Lumbricidae), spiders (Aranei), harvestmen (Opiliones), both adults and larvae of various coleopterans (Coleoptera), among which ground beetles (Carabidae) predominate, they also eat rove beetles (Staphylinidae) and click beetles (Elateridae), consume a huge number of

diptera larvae (Diptera), as well as terrestrial mollusks (Gastropoda) [11–15]. Conversely, in winter, when preferable objects such as earthworms are difficult to access, shrews can consume less profitable and less acceptable prey, such as diplopods (Diplopoda) [14].

Despite the interest in studying the dependence of the numerical distribution of shrews on the abundance of their potential prey [3], such data are scarce and sometimes ambiguous, which is explained by the use of different methods. The absolute methods of counting the abundance of shrews and invertebrates show the presence of a close positive correlation in the biotopes with the most favorable foraging base in undisturbed natural conditions [3, 16]. In habitats disturbed by natural catastrophic events (windfalls and fire), the relationship between the number of shrews and the abundance of invertebrates may not be obvious due to the transformation of habitat conditions, which leads to disturbances in the structure of the population of small insectivores: a redistribution of species in terms of numbers, a change in share participation and a change in dominance [17–22]. In communities of soil–litter invertebrates, which are closely dependent on a number of plant and soil parameters, in habitats with varying degrees of pyrogenic impact, the abundance and species diversity of most taxa change, and the ratio of dominant groups is disrupted. The soil mesofauna of pyrogenic territories is influenced not only by the strength of the fire, the structure of vegetation and soil, but also by the composition of the undisturbed communities of invertebrates surrounding the damaged areas [23–28].

Currently, the few works devoted to the study of small insectivorous animals living in windfall-pyrogenic biotopes, contain no information on the nature of the dependence of the shrew population on the parameters of their habitat environment. The main goal of our work is to study the relationship between the abundance of the common shrew and the abundance of soil–litter invertebrates in ecologically contrasting biotopic conditions, reflecting the food supply of its habitats. We assumed that the indicator of food supply, which is determined by complex processes in numerous and taxonomically diverse communities of invertebrates, is a long-term stable characteristic of the state of the food supply for *S. araneus* in biotopes with varying degrees of disturbance by natural catastrophic factors and is reflected in the abundance of this species. We studied the chronographic and biotopic variability of microhabitat parameters, analyzed the dynamics of the abundance of the common shrew, assessed its relationship with microhabitat characteristics in ecologically contrasting habitats, investigated the dynamics and variability of the abundance of soil mesofauna, as well as the contribution of individual taxonomic groups to the communities of the compared biotopes. The new data obtained can be useful for studying the biota's resistance to the consequences of natural extreme events, a significant increase in

which (especially forest fires) has been observed in recent decades [29].

## MATERIAL AND METHODS

The material for the study (shrews and invertebrates) was collected in forest biocenoses of the low-mountainous part of the Middle Urals on the territory of the Visimskii Reserve (57°19'–57°3' N and 59°20'–59°50' E) in Sverdlovsk oblast, where the common shrew is widespread and is the most abundant species in the population of shrews [30].

The ecological contrast of the environmental conditions of animal habitats in the studied protected area is caused by a significant transformation of forest biogeocenoses under the influence of a powerful windfall in 1995 and two subsequent extensive fires in 1998 and 2010. Based on a comparative analysis of microhabitat characteristics, three contrasting biotopes were selected: undisturbed (I), slightly disturbed (II), and severely disturbed (III). Biotope I is a plot of a fir–spruce tall herb–fern primary forest that was not disturbed by the windfall and fires, biotope II is a plot of a birch reed grass–forb forest, partially disturbed by the windfall and one fire, and biotope III is a plot disturbed by the windfall and two fires, originally it included a large-fern and linden types of primary and conditionally primary fir–spruce forests. At present, biotope III is a windfall-pyrogenic biocenosis, the plant communities of which are at different stages of post-catastrophic restorative successions. All the studied biotopes are located in the near-summit parts of low mountains: biotope I is located on the flat near-summit part of the slope of the Malyi Sutuk Mountain (560 m above sea level), and biotopes II and III are located on the near-summit part of the gentle slope of the Lipovyi Sutuk Mountain (495 m above sea level).

In June 1998, the spread of the fire was facilitated by a large amount of combustible material formed over the vast windfall area. The fire stretched out in a strip 1 to 1.5 km wide and 10 km long, its total area was about 1610 hectares. In August 2010, in the northeastern part of the Visimskii Reserve, the fire spread over an area of 1,800 hectares, and various plantations fell into its zone, mainly from undergrowth formed in areas of continuous windfall. The influence of the two fires on forest biogeocenoses was different: the second fire was weaker, it was mosaic, spots with green mosses remained, and the fire passed quickly through the areas with the growth of reed grass that dominated this biotope, destroying in many places only the already drying grass stand. In 2010, on the territory of the old fire (1998), there was a lot of dry grass, unburned trunks and fallen dead wood (its share was 14%). The second fire, unlike the first, did not affect all previously burnt areas, or the intensity of combustion on them was insignificant [31, 32]. As a result of the complex impact of natural catastrophic factors, forest phy-

**Table 1.** Weather conditions in the area of the Visim reserve according to the Visim meteorological station (average values of air temperature and the amount of precipitation for May–August)

Parameter	Year							Average (1987–2018)
	2012	2013	2014	2015	2016	2017	2018	
Air temperature, °C	15.8	14.6	13.5	13.4	16.0	12.9	10.7	14.1
Amount of precipitation, mm	222.9	251.8	345.4	511.0	194.5	378.6	397.3	309.0
Hydrothermal coefficient	2.64	3.60	5.63	8.18	2.34	6.87	6.33	4.4

tocenoses were transformed into windfall-purogenic plant communities [33].

The relative number (abundance) of the shrew population, expressed as the number of individuals per 100 trap-days, was estimated using the standard trap-line method. Shrews were captured in biotope III from 1998 (the year of the first fire) to 2019, and in biotopes I and II, from 2013 to 2019, as the survey lines were laid three years after the second fire. In each of the three studied biotopes, 50 wire traps were set up simultaneously at a distance of 5–10 m from each other annually at the end of August—the first half of September, the exposure time was 5 days. Around each trap, in an area of 10 m<sup>2</sup>, a quantitative description of the parameters of the microhabitats of small mammals was carried out on the basis of the method proposed by O.A. Lukyanov and G. Bujalska [7].

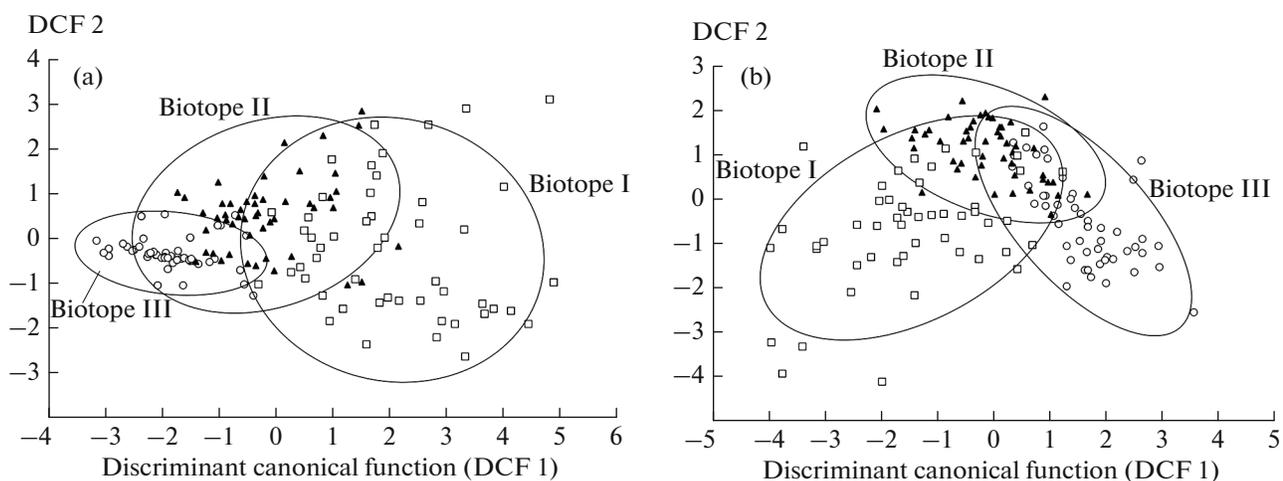
Descriptions on sites around 150 traps were carried out in August 2013, and repeated at the same time in 2017 according to seven microhabitat characteristics: area of coverage (m<sup>2</sup>) of plots with moss (*MC*), herbaceous vegetation (*HC*), shrubs (*CS*), abundance (specimens) of undergrowth of tree species (*AU*), cross-sectional area (m<sup>2</sup>) of trunks of living trees (*TC*), dry trees and stumps (*SC*), coverage area (m<sup>2</sup>) of deadwood (*LC*). A total of 300 descriptions were carried out. The index of food supply for the habitats of the common shrew was assessed by the total abundance of large soil-litter invertebrates larger than 2 mm (soil mesofauna) caught in biotopes I and II in 2013–2017, and in biotope III in 1998–2017 by direct method of counting: digging soil samples and manually sorting it on the spot [34].

At the end of August – the first half of September, 50 samples of 15 x 15 x 20 cm were analyzed on each test plot, the selected invertebrates were fixed in 70% alcohol. The total abundance of soil mesofauna was measured, as well as the abundance of supraspecific taxa (family rank and higher) (specimens/m<sup>2</sup>). The inclusion of individual taxonomic groups in the analysis is justified by the necessity to assess their contribution to the total abundance of the compared invertebrate communities. The following taxa were taken into account: earthworms (*Lumbricidae*), enchytraeids (*Enchytraeidae*), spiders (*Aranei*), harvestmen (*Opiliones*), stone centipedes (*Lithobiidae*), soil centipedes (*Geophilidae*), diplopods (*Diplopoda*), hemipterans

(*Hemiptera*), ground beetles (*Carabidae*), rove beetles (*Staphylinidae*), click beetles (*Elateridae*), lepidopterans (*Lepidoptera*), hymenopterans (*Hymenoptera*), dipterans (*Diptera*), and gastropods (*Gastropoda*). Other *Coleoptera* include soldier beetles (*Cantharidae*), weevils (*Curculionidae*), leaf beetles (*Chrysomelidae*), round fungus beetles (*Leiodidae*), pill beetles (*Byrrhidae*), silken fungus beetles (*Cryptophagidae*), sap beetles (*Nitidulidae*) bark beetles (*Scolytidae*), and earth-boring dung beetles (*Geotrupidae*), other invertebrates included all other taxa not listed. The material was collected in the second half of August, because the population of shrews is most numerous in late summer and early fall, and the composition of communities of soil-litter invertebrates, characterized by seasonal variability, is the most stable [3, 9].

To study the effect of weather conditions on the population of shrews and the abundance of invertebrates, we used data from the Visim weather station. Selyaninov's hydrothermal coefficient (HTC) was calculated as the ratio of the amount of precipitation on days when the air temperature was above +10°C, multiplied by 10, to the sum of the differences between the average daily temperature and +10°C for this period. To characterize the year as “wet” or “dry”, the HTC values were compared with its average annual value (Table 1).

Statistical processing of the collected material was performed using the Statistica 6.0 software package. The study of the relationship between the abundance of the common shrew and the total abundance of invertebrates, the abundance of individual taxonomic groups of soil mesofauna and HTC values was carried out using the Pearson linear correlation coefficient (*r*), having previously performed the logarithm procedure for the values, the distribution of which deviates from the normal. The correlation between the abundance of shrews and the total abundance of invertebrates was taken into account only for the coinciding years of counts: in biotopes I and II, in 2013–2017, and in biotope III, in 1998–2017. The relationship between the abundance of shrews and the abundance of their potential food items was assessed in the current and previous seasons, as the abundance of soil mesofauna in the previous year reflects the food reserves of the winter period, and the abundance of invertebrates in the current year characterizes the actual stocks of shrews. To reveal the differences between biotopes in



**Fig. 1.** Microhabitat characteristics of the common shrew (by 7 quantitative indicators) in biotopes I – III in (a) 2013 and (b) 2017 (ellipses show 95% confidence regions).

terms of the complex of microhabitat characteristics and the taxonomic composition of soil mesofauna, discriminant canonical analysis was used. The relationship between the abundance of the common shrew and weather conditions and microhabitat characteristics was assessed using regression analysis. The level of chronographic and biotopic variability of the total abundance of invertebrates, the abundance of individual taxa, as well as microhabitat parameters of shrews was studied using two-way analysis of variance.

## RESULTS AND DISCUSSION

**Microhabitat conditions of the common shrew.** In the three compared biotopes, the microhabitats significantly differed in six parameters: the area of coverage of microplots with moss ( $F = 63.79, p < 0.001$ ), herbaceous vegetation ( $F = 19.37, p < 0.001$ ), shrubs ( $F = 56.42, p < 0.001$ ), abundance of undergrowth ( $F = 4.39, p < 0.05$ ), sectional area of trunks of living trees ( $F = 41.80, p < 0.001$ ), dead wood and stumps ( $F = 16.02, p < 0.001$ ). There were no biotopic differences in the area covered by deadwood ( $F = 0.61, p > 0.05$ ); its values did not differ in different years either ( $F = 2.87, p > 0.05$ ). The area of coverage of microplots with herbaceous vegetation and the abundance of undergrowth were characterized by high chronographic variability ( $F = 19.01, p < 0.001$  and  $F = 51.28, p < 0.001$ , respectively). Microhabitat characteristics associated with the area covered by shrubs ( $F = 0.02, p > 0.05$ ), the cross-sectional area of the trunks of living trees ( $F = 1.59, p > 0.05$ ), dry trees and stumps ( $F = 0.29, p > 0.05$ ) did not have significant interannual differences. Discriminant analysis of microhabitat variables showed highly significant differences between the three biotopes according to descriptions in 2013 and 2017 (Wilkes  $\Lambda = 0.26, F = 13.38, p < 0.001$  and Wilkes  $\Lambda = 0.16, F = 19.85, p < 0.001$ , respec-

tively). The maximum differences in microhabitat characteristics were observed between strongly disturbed biotope III and undisturbed biotope I (Figs. 1a, 1b). The greatest contribution to the discrimination of the microenvironment of the three habitats was made by the variables assessing the area covered by moss, herbaceous vegetation, and shrubs, as well as the cross-sectional area of the trunks of living trees.

Analysis of variability of characteristics showed that the microenvironment in undisturbed and weakly disturbed biotopes is less variable than in highly disturbed ones; in these habitats, the smallest interannual range is characterized by the largest number of variables (Table 2). In biotope III, the least variable was the area of herbaceous cover ( $HC$ ), the interannual range of values of which was the lowest in comparison with biotopes I and II. In general, in biotope III, microhabitat characteristics had the highest values of the coefficients of variation, which indicates the heterogeneity of environmental conditions caused by the complex impact of natural catastrophic factors. This biotope proved to be more heterogeneous in terms of the coverage of areas with moss ( $MC$ ), trunks of dry trees and stumps ( $SC$ ), as well as the cross-sectional area of trunks of living trees ( $TC$ ). The variable  $LC$ , the area covered with lying dead wood, was characterized by the minimum variability and a similar range of interannual variability in all biotopes (Table 2). Similarly high values of the coefficients of variation in the years of descriptions and a relatively low interannual range of variability in the compared biotopes were characteristic of  $SC$ , the area covered by trunks of dry trees and stumps. The revealed biotopic differences in microhabitat characteristics made it possible to consider the environment of the compared habitats as ecologically contrasting.

**Influence of weather conditions and microenvironmental factors on the population dynamics of the common shrew.** In the long-term dynamics of the abundance of the common shrew in the three compared biotopes in 2013–2019, two years stand out: 2014, the year of maximum values, and 2018, the year of deep depression (Fig. 2). A significant increase in the number of shrews in 2014 compared to the previous year in biotopes I, II, and III (two-, five-, and threefold, respectively) may be explained by the prevailing favorable conditions for the warm and humid summer season of 2013 with an even distribution of precipitation (Table 1). As it is known that the abundance of shrews in the current year is positively influenced by favorable weather conditions of the previous season [35], it can be assumed that a deep depression in the abundance of the common shrew in all compared biotopes in 2018 is a consequence of unfavorable weather conditions not only in the previous 2017, the spring-summer season was waterlogged, and the amount of precipitation exceeded the average annual, but also the previous seasons: waterlogged 2015 and dry 2016 (Table 1). At the same time, the observed high level of abundance of the common shrew in 2019, which was preceded by the wet and cool summer season of 2018, cannot be unambiguously explained by the influence of weather factors. According to data, the frequency of changes in the species abundance does not always coincide with the frequency of changes in weather conditions [35]. In general, the level the common shrew abundance values in the period 2013–2019 proved to be higher in a strongly disturbed biotope compared to biotopes I and II (Fig. 2). Earlier, we showed [18] that the increase in the abundance of *S. araneus* in burned-out areas is explained by the peculiarities of its more successful recovery in comparison with other species of the genus, which indicates the favorable conditions for the habitation of the species during the postpyrogenic recovery of forest biocenoses.

Analyzing the dependence of the common shrew on the environmental conditions of its habitats, we found a relationship between its abundance and the largest number of microhabitat parameters in a heavily disturbed biotope as compared to biotopes I and II. Thus, in 2015 and 2017, at a low level of population in biotope III, a direct dependence of the abundance of shrews on the area of coverage of microsections with moss ( $\beta = 0.66, p < 0.001$ ), shrubs ( $\beta = 0.30, p < 0.05$ ), and dead wood ( $\beta = 0.34, p < 0.05$ ) was noted. A connection with the latter characteristic was also revealed at a high level of abundance of the species in 2019 ( $\beta = 0.39, p < 0.01$ ). This indicates the numerical predominance of the common shrew at any level of its abundance in disturbed areas with improved protective conditions and confirms the fact that the most littered habitats are preferred by the animals [3]. In a weakly disturbed biotope, the dependence of the species abundance on microenvironmental characteristics was not found; in the undisturbed habitat, a relationship

**Table 2.** Microhabitat characteristics of biotopes with varying degrees of disturbance

Parameter	2013			2017			<i>R</i>
	$\bar{X}$	<i>s</i>	<i>CV</i>	$\bar{X}$	<i>s</i>	<i>CV</i>	
<b>Biotope I</b>							
<i>MC</i>	3.29	2.17	66	2.17	1.79	83	1.2
<i>HC</i>	7.15	1.85	26	5.16	2.11	41	1.6
<i>CS</i>	1.33	1.24	93	1.27	1.32	104	1.1
<i>AU</i>	4.66	5.40	116	4.66	5.07	109	1.1
<i>TC</i>	0.081	0.084	104	0.07	0.08	120	1.1
<i>SC</i>	0.05	0.09	165	0.05	0.06	131	1.3
<i>LC</i>	0.66	0.47	71	0.78	0.62	79	1.1
<b>Biotope II</b>							
<i>MC</i>	1.26	1.69	134	0.71	0.92	130	1.0
<i>HC</i>	5.71	2.35	41	3.22	1.92	60	1.5
<i>CS</i>	0.24	0.43	179	0.13	0.26	200	1.1
<i>AU</i>	4.92	3.82	78	6.74	4.62	69	1.1
<i>TC</i>	0.08	0.07	88	0.06	0.04	67	1.3
<i>SC</i>	0.02	0.04	200	0.03	0.05	167	1.2
<i>LC</i>	0.69	0.47	68	0.94	0.67	71	1.0
<b>Biotope III</b>							
<i>MC</i>	0.89	1.31	147	0.02	0.08	400	2.7
<i>HC</i>	5.47	2.27	41	6.68	2.45	37	1.1
<i>CS</i>	0.21	0.39	186	0.43	0.51	119	1.6
<i>AU</i>	1.10	2.41	219	12.78	9.01	71	3.1
<i>TC</i>	0.004	0.012	250	0.007	0.011	143	1.7
<i>SC</i>	0.004	0.018	500	0.01	0.04	400	1.3
<i>LC</i>	0.77	0.65	84	0.75	0.66	88	1.0

$\bar{X}$  is the mean value, *s* is standard deviation, *CV* is the coefficient of variation (ratio of standard deviation to the mean value of a trait), *R* is the range of variability (ratio of interannual values of variation coefficient).

was found with only one parameter: in 2016, with a low population size, individuals prevailed in areas with a larger area of coverage of microsites with moss ( $\beta = 0.38, p < 0.05$ ).

**Dynamics of the abundance of soil mesofauna.** The communities of the studied biotopes are based on the most numerous taxa, typical representatives of the soil-litter layer of forest territories of the taiga zone: rove beetles, stone centipedes, spiders, enchytraeids, earthworms and ground beetles. In different years, the share of their contribution to the communities of the compared biotopes ranged from 10.1 to 30.5%. These taxa define the differences between biotopes. The greatest contribution to their discrimination in all years (except for 2016) is made by earthworms: the values of the Wilkes' lambda (Wilkes  $\Lambda$ ) in these years are equal to 0.49–0.59 ( $p < 0.001$ ). Significant for the observation period (2013–2017), except for 2017, was

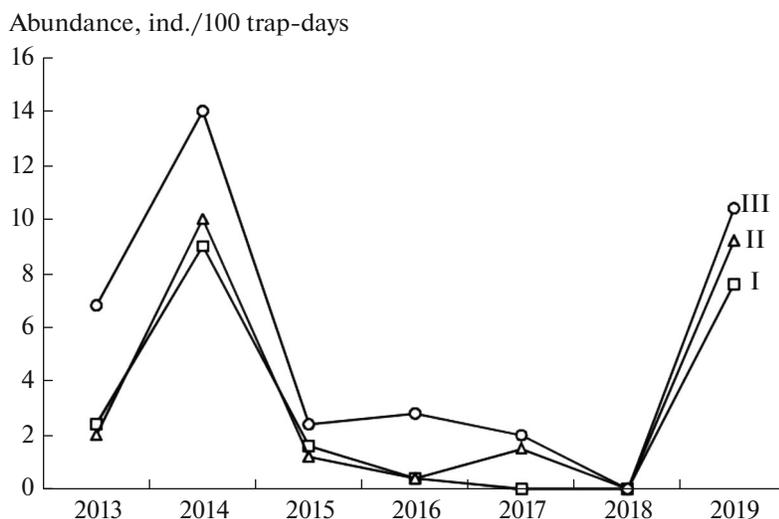


Fig. 2. Long-term change in the abundance of the common shrew in biotopes with varying degrees of disturbance.

the contribution of ground beetles: Wilkes  $\Lambda = 0.45$ – $0.56$  ( $p < 0.001$ ). Along with earthworms in 2013, 2014 and 2017, the differences in the composition of communities between biotopes were introduced by enchytraeids (Wilkes  $\Lambda = 0.48, 0.53, 0.57$ ;  $F = 3.49, 13.77, 13.13$ ;  $p < 0.05, p < 0.05$  and  $p < 0.001$ , respectively), and in 2015 and 2016, by rove beetles (Wilkes  $\Lambda = 0.59, 0.49$ ;  $F = 5.30, 3.61$  at  $p < 0.05$ , respectively).

Differences in the share of taxa in communities in different years are due to their ecological characteristics, which are manifested in changing environmental conditions. It is known that air temperature and precipitation have an indirect impact on soil-litter invertebrates, affecting the state of the litter and soil cover. In biotope I, with a well-defined layer of coniferous litter and herbaceous plants, as compared to biotopes II and III, where the litter horizon is weakly expressed, rove beetles were abundant. For this group, as well as for stone centipedes and spiders, the most favorable weather conditions were in 2013 with moderate temperature and precipitation in the summer season (Table 1): they were numerous in all biotopes (Table 3). The weather conditions of this year proved to be favorable for enchytraeids and ground beetles in the highly disturbed biotope, in which their abundance was high (Table 3). For ground beetles, as well as for other representatives of soil mesofauna, the temperature on the soil surface and the level of precipitation are considered the most important factors, and the meteorological parameters of the previous year affect the level of the number of ground beetles to a greater extent than the current one [36]. In biotopes I and II, representatives of this group were few in number; a negative relationship between their abundance and HTC was found ( $r = -0.63$  and  $-0.78$ , respectively). Note that the multispecies group of ground beetles, not only in 2013, but also in other years of observations, was character-

ized by a significantly high level of abundance in the strongly disturbed biotope.

The results of studies of the influence of the pyrogenic factor on ground beetles are contradictory. Some authors point to an increase in the number of this group in biocenoses after a fire by 2–3 times [28]; according to our data [24], their abundance decreases, which is explained by the specifics of the counting methods. The method of soil traps revealed an increase in the species diversity of the population of ground beetles in a burned-out area and a decrease in their total number: a decrease in the number of typical forest species simultaneously with an increase in forest-meadow, meadow and field species, an increase in the proportion of hygrophils, the total specific abundance of mixophytophages and litter borehole strato-bionts [24]. Changes in the ecological structure of the multispecies population of ground beetles are explained by the prevailing conditions on burned-out areas, where, under the influence of the pyrogenic factor, the litter supply is destroyed or sharply reduced, the upper soil layer is compacted, humidity decreases, the microclimate of the soil-litter ground layer shifts towards a more xerothermal one with less stable temperature conditions and humidity. Under these conditions, the existence of organisms becomes the most extreme, the rate of recovery of the number of different groups differs, which also significantly depends on the intensity of the impact of fires [26, 28, 37].

In the wettest year for the period under study, 2015, characterized by the maximum HTC value (Table 1), the highest abundance values are characteristic of the hygrophilic group of earthworms in the strongly disturbed biotope (Table 3). These oligochaetes have a long-term development cycle, which requires stable moisture [25]. This is confirmed by the high positive values of the correlation coefficient of their abundance

**Table 3.** Abundance (mean value  $\pm$  standard error) of the main groups of soil-litter invertebrates in biotopes I–III, specimens/m<sup>2</sup>

Taxon	2013	2014	2015	2016	2017
<b>Biotope I</b>					
Lumbricidae	27.8 $\pm$ 5.4	16.4 $\pm$ 3.5	38.9 $\pm$ 7.8	12.2 $\pm$ 5.3	30.0 $\pm$ 6.0
Enchytraeidae	7.8 $\pm$ 4.2	4.7 $\pm$ 2.2	34.4 $\pm$ 11.8	8.9 $\pm$ 7.8	4.4 $\pm$ 2.1
Aranei	65.6 $\pm$ 7.1	22.2 $\pm$ 4.9	24.4 $\pm$ 6.1	53.3 $\pm$ 10.3	23.3 $\pm$ 5.2
Opiliones	–	1.2 $\pm$ 1.0	4.4 $\pm$ 2.6	4.4 $\pm$ 2.1	2.2 $\pm$ 1.5
Lithobiidae	87.8 $\pm$ 9.1	59.7 $\pm$ 10.6	40.0 $\pm$ 7.4	81.1 $\pm$ 13.1	33.3 $\pm$ 6.9
Geophilidae	27.8 $\pm$ 6.5	14.0 $\pm$ 4.1	14.4 $\pm$ 4.3	7.8 $\pm$ 3.9	15.6 $\pm$ 6.1
Diplopoda	3.3 $\pm$ 1.8	1.2 $\pm$ 1.0	2.2 $\pm$ 1.5	2.2 $\pm$ 1.9	1.1 $\pm$ 0.9
Hemiptera (im + l)	3.3 $\pm$ 1.8	8.19 $\pm$ 4.1	1.1 $\pm$ 0.9	2.2 $\pm$ 1.5	1.1 $\pm$ 0.9
Carabidae (im + l)	3.3 $\pm$ 1.8	8.2 $\pm$ 2.8	6.7 $\pm$ 2.5	1.1 $\pm$ 0.9	4.4 $\pm$ 2.6
Staphylinidae (im + l)	110.0 $\pm$ 14.3	66.7 $\pm$ 12.5	65.6 $\pm$ 13.9	70.0 $\pm$ 11.4	38.9 $\pm$ 8.8
Elateridae (im + l + p)	2.2 $\pm$ 1.5	1.2 $\pm$ 1.0	4.4 $\pm$ 2.1	2.2 $\pm$ 1.5	7.8 $\pm$ 3.1
Other Coleoptera (im + l + p)	11.1 $\pm$ 3.5	8.2 $\pm$ 2.8	8.9 $\pm$ 3.2	13.3 $\pm$ 5.1	31.1 $\pm$ 10.9
Lepidoptera (l + p)	2.2 $\pm$ 1.5	–	1.1 $\pm$ 0.9	2.2 $\pm$ 1.5	5.6 $\pm$ 2.3
Hymenoptera, Symphyta (l + p)	11.1 $\pm$ 3.4	1.2 $\pm$ 1.0	3.3 $\pm$ 1.8	2.2 $\pm$ 1.5	–
Diptera (l + p)	18.9 $\pm$ 5.0	16.4 $\pm$ 7.7	41.1 $\pm$ 6.8	10.0 $\pm$ 4.3	17.8 $\pm$ 4.4
Gastropoda	1.1 $\pm$ 0.9	11.7 $\pm$ 4.0	8.9 $\pm$ 3.3	6.7 $\pm$ 3.0	2.2 $\pm$ 1.5
Other invertebrates	12.2 $\pm$ 3.8	15.2 $\pm$ 3.4	3.3 $\pm$ 2.4	4.4 $\pm$ 2.1	8.9 $\pm$ 3.2
Total abundance	395.6 $\pm$ 27.7	233.9 $\pm$ 24.2	298.9 $\pm$ 34.2	284.4 $\pm$ 23.0	227.8 $\pm$ 28.9
<b>Biotope II</b>					
Lumbricidae	51.1 $\pm$ 10.9	54.4 $\pm$ 6.7	36.7 $\pm$ 6.9	13.3 $\pm$ 4.8	74.4 $\pm$ 10.0
Enchytraeidae	10.0 $\pm$ 3.7	3.3 $\pm$ 1.9	16.7 $\pm$ 4.4	2.2 $\pm$ 1.6	7.8 $\pm$ 3.9
Aranei	62.2 $\pm$ 12.0	17.8 $\pm$ 5.0	22.2 $\pm$ 5.0	50.0 $\pm$ 8.9	31.1 $\pm$ 6.8
Opiliones	1.1 $\pm$ 0.9	5.6 $\pm$ 2.8	1.1 $\pm$ 0.9	3.3 $\pm$ 2.5	4.4 $\pm$ 2.1
Lithobiidae	76.7 $\pm$ 8.9	68.9 $\pm$ 9.4	31.1 $\pm$ 7.2	45.6 $\pm$ 7.5	54.4 $\pm$ 9.6
Geophilidae	21.1 $\pm$ 4.8	22.2 $\pm$ 6.0	16.7 $\pm$ 4.7	15.6 $\pm$ 3.7	38.9 $\pm$ 7.3
Diplopoda	26.7 $\pm$ 8.5	11.1 $\pm$ 5.2	12.2 $\pm$ 5.5	21.1 $\pm$ 5.3	5.6 $\pm$ 2.8
Hemiptera (im + l)	20.0 $\pm$ 7.5	15.6 $\pm$ 4.9	3.3 $\pm$ 1.9	12.2 $\pm$ 3.2	11.1 $\pm$ 3.5
Carabidae (im + l)	11.1 $\pm$ 3.5	7.8 $\pm$ 4.2	4.4 $\pm$ 2.1	6.7 $\pm$ 2.5	6.7 $\pm$ 3.0
Staphylinidae (im + l)	90.0 $\pm$ 12.0	40.0 $\pm$ 7.4	14.4 $\pm$ 4.6	50.0 $\pm$ 8.1	44.4 $\pm$ 6.4
Elateridae (im + l + p)	12.2 $\pm$ 3.9	16.7 $\pm$ 4.4	11.1 $\pm$ 3.8	7.8 $\pm$ 2.7	41.1 $\pm$ 6.4
Other Coleoptera (im + l + p)	15.6 $\pm$ 5.4	6.7 $\pm$ 2.5	5.6 $\pm$ 2.4	10.0 $\pm$ 3.4	7.8 $\pm$ 3.5
Lepidoptera (l + p)	3.3 $\pm$ 1.9	1.1 $\pm$ 0.9	–	–	1.1 $\pm$ 0.9
Hymenoptera, Symphyta (l + p)	4.4 $\pm$ 2.1	–	2.2 $\pm$ 1.8	1.1 $\pm$ 0.9	5.6 $\pm$ 2.4
Diptera (l + p)	33.3 $\pm$ 5.9	18.9 $\pm$ 5.0	15.6 $\pm$ 4.7	7.8 $\pm$ 3.1	26.7 $\pm$ 5.2
Gastropoda	7.8 $\pm$ 3.1	7.8 $\pm$ 3.1	14.4 $\pm$ 4.0	10.0 $\pm$ 3.4	14.4 $\pm$ 5.8
Other invertebrates	14.4 $\pm$ 4.9	6.7 $\pm$ 2.5	10.0 $\pm$ 3.4	5.6 $\pm$ 2.4	12.2 $\pm$ 4.8
Total abundance	461.1 $\pm$ 41.6	304.4 $\pm$ 22.6	217.8 $\pm$ 23.8	262.2 $\pm$ 20.3	387.8 $\pm$ 32.8
<b>Biotope III</b>					
Lumbricidae	35.6 $\pm$ 6.6	39.8 $\pm$ 8.4	80.0 $\pm$ 11.7	15.6 $\pm$ 3.8	51.1 $\pm$ 8.9
Enchytraeidae	41.1 $\pm$ 9.2	36.3 $\pm$ 7.3	14.4 $\pm$ 7.0	1.1 $\pm$ 0.9	34.4 $\pm$ 6.8
Aranei	47.8 $\pm$ 7.3	18.7 $\pm$ 4.9	30.0 $\pm$ 4.9	35.6 $\pm$ 6.9	30.0 $\pm$ 6.2
Opiliones	–	–	–	–	3.3 $\pm$ 1.9
Lithobiidae	35.6 $\pm$ 7.5	25.7 $\pm$ 5.2	22.2 $\pm$ 5.7	17.8 $\pm$ 5.2	33.3 $\pm$ 7.3
Geophilidae	20.0 $\pm$ 4.5	18.7 $\pm$ 4.6	22.2 $\pm$ 5.0	7.8 $\pm$ 3.1	12.2 $\pm$ 3.5
Diplopoda	2.2 $\pm$ 1.6	–	1.1 $\pm$ 0.9	–	–
Hemiptera (im + l)	13.3 $\pm$ 3.9	7.0 $\pm$ 3.2	–	3.3 $\pm$ 2.4	7.8 $\pm$ 2.7
Carabidae (im + l)	51.1 $\pm$ 9.1	21.1 $\pm$ 4.4	20.0 $\pm$ 4.8	32.2 $\pm$ 7.1	20.0 $\pm$ 5.7
Staphylinidae (im + l)	93.3 $\pm$ 13.3	38.6 $\pm$ 6.9	27.8 $\pm$ 8.4	28.9 $\pm$ 7.2	35.6 $\pm$ 7.2
Elateridae (im + l + p)	6.7 $\pm$ 2.5	19.9 $\pm$ 6.9	13.3 $\pm$ 4.3	18.9 $\pm$ 5.0	20.0 $\pm$ 4.8
Other Coleoptera (im + l + p)	25.6 $\pm$ 4.8	8.2 $\pm$ 2.8	17.8 $\pm$ 4.9	7.8 $\pm$ 2.7	23.3 $\pm$ 5.9
Lepidoptera (l + p)	5.6 $\pm$ 2.3	1.2 $\pm$ 1.0	–	4.4 $\pm$ 2.6	2.2 $\pm$ 1.5
Hymenoptera, Symphyta (l + p)	2.2 $\pm$ 1.5	1.2 $\pm$ 1.0	1.1 $\pm$ 0.9	2.2 $\pm$ 1.5	–
Diptera (l + p)	23.3 $\pm$ 7.1	9.4 $\pm$ 2.9	13.3 $\pm$ 3.9	16.7 $\pm$ 4.6	10.0 $\pm$ 3.4
Gastropoda	3.3 $\pm$ 1.9	17.5 $\pm$ 4.2	17.8 $\pm$ 3.8	10.0 $\pm$ 4.4	15.6 $\pm$ 5.2
Other invertebrates	22.2 $\pm$ 5.5	10.5 $\pm$ 3.5	1.1 $\pm$ 0.9	1.1 $\pm$ 0.9	5.6 $\pm$ 2.8
Total abundance	428.9 $\pm$ 32.9	273.9 $\pm$ 26.6	282.2 $\pm$ 23.2	203.3 $\pm$ 17.7	304.4 $\pm$ 28.0

A dash indicates the absence of a taxon. Development stages: (im) imago, (l) larva, and (p) pupa or puparium.

with the HTC in biotope III ( $r = 0.94$ ). Spiders, stone centipedes, and ground beetles, on the other hand, in the conditions of the waterlogged season, were notable for their low abundance both in the strongly disturbed biotope and in biotopes I and II (Table 3). The abundance of rove beetles in this year was characterized by low values in the weakly and strongly disturbed habitats, while in the undisturbed biotope their abundance was maximum, which can be explained both by the redistribution of insects in microstations due to precipitation, and by the direct destructive effect of storm currents on small species in the biotope with poorly developed litter.

In the driest year of 2016, with the lowest HTC value for the period under study (Table 1), rove beetles prevailed in biotopes I and II, while in biotope III their abundance was significantly lower. The abundance of spiders decreased in the series of biotopes I – II – III, while the number of ground beetles, on the contrary, increased (Table 3). In a dry summer season unfavorable for earthworms, the values of their abundance in biotopes II and III were higher than in undisturbed habitats. Our early studies [38] show that in the Visim Reserve earthworms are most abundant in meadow communities, their abundance is also higher in birch forests than in fir-spruce forests. The development of reed grass in biotopes II and III forms a weakly decomposed turf densely intertwined with roots. Moisture is better preserved under the turf layer, which creates favorable conditions for the life of geobionts: earthworms, enchytraeids, stone centipedes, soil centipedes and other groups.

The study of long-term values of the total abundance of invertebrates shows that they are similar in biotopes I, II, and III. During the study period, the change in the variable was asynchronous, with the exception of 2013 and 2014 (Fig. 3). Under the influence of similar weather factors, asynchronous dynamics can be caused by the distinctive features of biotopes: the structure of the vegetation cover, the hydrothermal regime of soils, which are most dynamic in open habitats—in burnt-out areas. In contrast to undisturbed habitats with a preserved tree layer and a developed crown, the soil cover in the cleared burnt-out areas warms up more strongly and to a greater depth, the fluctuations of the maximum and minimum temperatures on the soil surface are much higher, the thickness of the litter and its moisture content are reduced, and the qualitative composition changes. The values of the total abundance of invertebrates in biotope III during the entire period, except for 2016, occupied an intermediate position in comparison with biotopes I and II. In the undisturbed habitat, the total abundance of soil mesofauna was characterized by increased values in only two cases out of five (in 2015 and 2016) (Fig. 3). In 2013 and 2014, the dynamics of the indicator values was synchronous, which was broken in subsequent years. Asynchrony manifested itself to a greater extent in 2017, when the

total abundance in biotopes II and III increased, while in biotope I it decreased, and only in that year the values of the indicator had highly significant biotopic differences ( $F_{2,116} = 7.10, p < 0.001$ ). A similar asynchrony of fluctuations in the total abundance of soil mesofauna in burned areas of green moss pine forests was observed in the Oka Nature Reserve, which persisted for more than 20 years of observations, while the dynamics in pine forests undisturbed by fires was synchronous in all the years [37].

Analysis of the variability of abundance parameters of different taxa in the compared communities of soil mesofauna revealed their significant differences. The range of interannual variability of the abundance of the most numerous group of rove beetles in different biotopes was 110.0–14.4 specimens/m<sup>2</sup>, whereas the abundance of ground beetles differed more than 50-fold (Table 3). Statistically significant biotopic variability in the abundance of invertebrates was found for all taxonomic groups, with the exception of Aranei, Opiliones, and Diptera (Table 4). The lack of variability in abundance in the last two groups can be explained by their low abundance in all compared habitats, and the absence of biotopic differences in one of the numerous taxa, spiders, may be due to the peculiarities of their recovery in pyrogenic territories [25, 27]. It is known that in the groups of soil-litter invertebrates from the biotopes disturbed by fires, significant changes in the composition are observed: taxa with a higher species diversity are the most resistant to the effects of adverse factors due to the biological diversity of their constituent species, and also more resistant to the negative effects of external factors [39].

The results of the analysis of the total abundance of communities of soil-litter invertebrates indicate the absence of its biotopic variability, while the level of its interannual differences, on the contrary, proved to be highly significant. The spread of long-term values of the total abundance of soil mesofauna in late summer – early fall of 2013–2017 was much smaller in comparison with the range of variability in the abundance of individual taxa of the community. The minimum variation in the total abundance was noted in biotope I, where the values differed by a factor of 1.7, while in the communities of disturbed biotopes II and III, they changed by a factor of 2.1 (Table 3). The smaller range of variability of this variable in the undisturbed biotope indicates more stable environmental conditions in this habitat, which is confirmed by the results of a comparative analysis of the microhabitat characteristics of the three biotopes (Table 2).

The results obtained indicate the biotopic “stability” of total abundance of soil-litter invertebrates, which determines the food supply of the common shrew habitats in ecologically contrasting environmental conditions, which can be explained from the standpoint of the “principle of compensation” or replacement of missing elements through the forma-

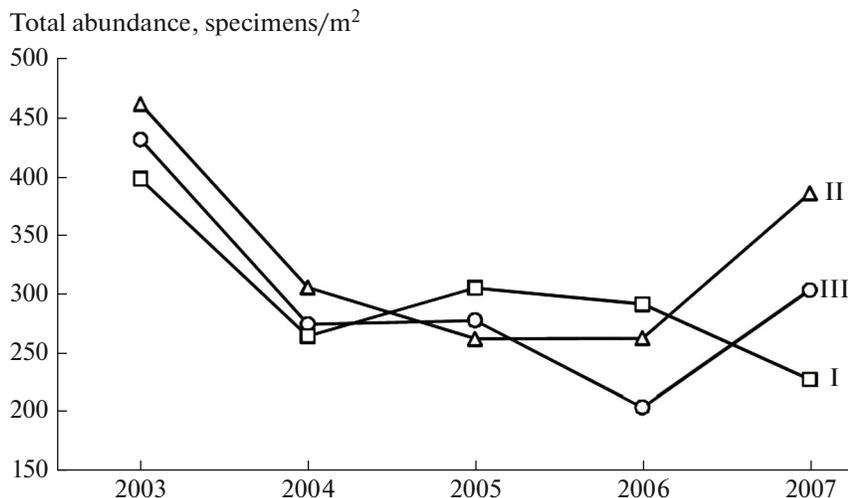


Fig. 3. Long-term change in the total abundance of soil mesofauna in biotopes with varying degrees of disturbance.

tion of replacing structures, which is one of the fundamental properties of biological systems [40]. In general, communities of invertebrates, both in undisturbed biotopes and in habitats with varying degrees of impact of natural catastrophic factors, remain stable due to the redistribution of the number of different taxonomic groups in them in the course of long-term dynamics.

**Assessment of the association between the abundance of the common shrew and the total abundance of invertebrates.** We did not find a relationship between the number of shrews and the total abundance of soil mesofauna in the current year, which reflects the actual food supplies of small insectivores. However, a positive correlation was revealed between the population size of the current year and the total abundance of soil-litter invertebrates in the previous year, which characterizes the accumulated food reserves of the common shrew (Table 5). This relationship was most pronounced in all compared habitats in 2014, when the shrew population was characterized by the maximum abundance values for the entire study period (Fig. 2), and the previous year, 2013, was characterized by the highest indices of the total abundance of soil-litter invertebrates (Table 3), and, consequently, the maximum level of the index of food supply for the common shrew habitats. This agrees with the opinion that the stock of potential food rigidly determines the spatial distribution of small insectivorous mammals at the maximum abundance of the latter, and with a decrease in the number of animals, the relationship between the biomass of potential food and the distribution of shrews weakens [41]. The close relationship between the abundance of the common shrew and the total abundance of its potential food objects in the previous year, which characterizes the stocks accumulated over the winter, found in a strongly disturbed

biotope, is illustrated by data for a longer (1998–2019) period of our observations (Fig. 4).

Thus, our hypothesis about the presence of a relationship between the abundance of the common shrew and the total abundance of invertebrates, which characterizes the food supply of habitats, is substantiated and confirmed by the results of the study. The revealed dependence of the abundance of *S. araneus* in the current year on the food supply of its habitats in the previous year can be explained from the standpoint of the spatiotemporal heterogeneity of the composition of invertebrate communities. Almost all groups of soil mesofauna are characterized by seasonal fluctuations in abundance, especially pronounced in earthworms, spiders, beetles, and dipterans [36, 42]. The composition and dynamics of the number of invertebrates are largely determined by the characteristics of the biotope and the weather conditions of the growing season. An important role is played by such ecological and biological aspects of the life of invertebrates as the duration of the life cycle, confinement to habitats and food selectivity. In the fall period, a relatively stable composition of the soil-litter population is formed, and the litter, along with this, is enriched by invertebrates that inhabit it for the coming winter period. Consequently, in different communities, the maximum concentration of invertebrates is observed in the fall season, when the composition leaving for wintering is completely formed in the soil [42], and, therefore, the accumulated winter food supply of the previous season actually determines the food supply of shrews in the next year.

## CONCLUSIONS

The ecological characteristics of a population of the common shrew and its potential food objects—

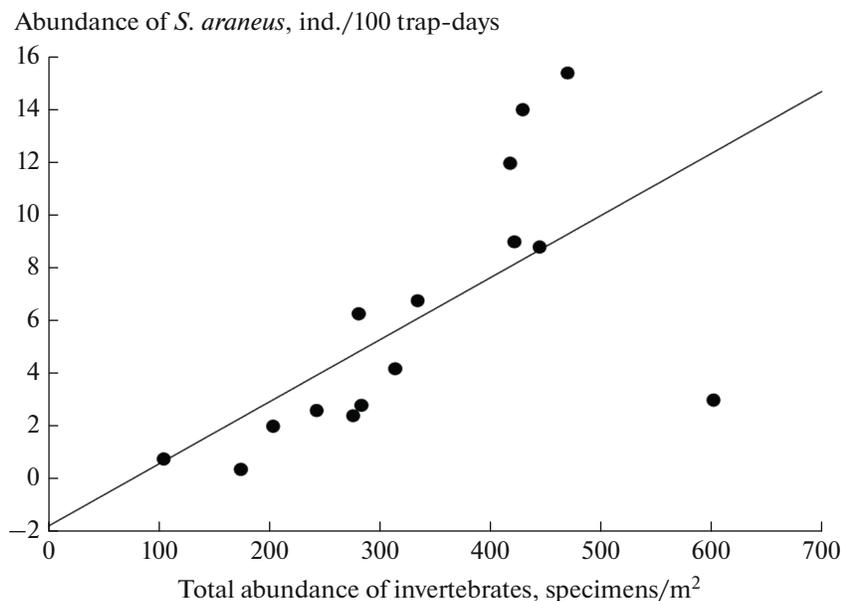
**Table 4.** Biotopic and chronographic variability of the abundance of the main groups of soil mesofauna

Taxonomic group	Source of variability	<i>df</i>	Sum of squares	Mean square	<i>F</i> -criterion	Level of significance, <i>p</i>
Lumbricidae	Biotope	2	25.53	12.77	11.14	<0.001
	Year	4	55.89	13.97	12.19	<0.001
	“Biotope” × “year”	8	39.04	4.88	4.26	<0.001
	Intergroup	581	666.07	1.15		
	Total	595	786.53			
Enchytraeidae	Biotope	2	16.82	8.41	12.08	<0.001
	Year	4	11.42	2.85	4.10	<0.05
	“Biotope” × “year”	8	27.54	3.44	4.95	<0.001
	Intergroup	581	404.34	0.70		
	Total	595	460.12			
Aranei	Biotope	2	1.61	0.81	0.77	ns
	Year	4	63.44	15.86	15.26	<0.001
	“Biotope” × “year”	8	7.19	0.90	0.87	ns
	Intergroup	581	603.71	1.04		
	Total	595	675.95			
Opiliones	Biotope	2	0.32	0.16	2.96	ns
	Year	4	0.29	0.07	1.35	ns
	“Biotope” × “year”	8	0.52	0.07	1.20	ns
	Intergroup	581	31.55	0.05		
	Total	595	32.68			
Lithobiidae	Biotope	2	65.24	32.62	23.53	<0.001
	Year	4	42.65	10.66	7.69	<0.001
	“Biotope” × “year”	8	35.69	4.46	3.22	<0.001
	Intergroup	581	805.39	1.39		
	Total	595	948.97			
Geophilidae	Biotope	2	3.15	1.57	3.19	<0.05
	Year	4	6.09	1.52	3.08	<0.05
	“Biotope” × “year”	8	8.25	1.03	2.09	<0.05
	Intergroup	581	286.97	0.49		
	Total	595	304.46			
Diplopoda	Biotope	2	13.26	6.63	26.60	<0.001
	Year	4	2.68	0.67	2.69	<0.05
	“Biotope” × “year”	8	3.23	0.40	1.62	ns
	Intergroup	581	144.82	0.25		
	Total	595	163.99			
Carabidae	Biotope	2	35.21	17.61	46.16	<0.001
	Year	4	5.50	1.38	3.61	<0.05
	“Biotope” × “year”	8	10.20	1.28	3.34	<0.001
	Intergroup	581	221.58	0.38		
	Total	595	272.49			
Staphylinidae	Biotope	2	38.69	19.35	9.62	<0.001
	Year	4	151.77	37.94	18.87	<0.001
	“Biotope” × “year”	8	22.12	2.77	1.38	ns
	Intergroup	581	1168.14	2.01		
	Total	595	1380.72			

Taxonomic group	Source of variability	<i>df</i>	Sum of squares	Mean square	<i>F</i> -criterion	Level of significance, <i>p</i>
Elateridae	Biotope	2	11.87	5.94	18.73	<0.001
	Year	4	9.46	2.36	7.46	<0.001
	“Biotope” × “year”	8	8.38	1.05	3.31	<0.001
	Intergroup	581	184.11	0.32		
	Total	595	213.82			
Diptera	Biotope	2	2.50	1.25	2.35	ns
	Year	4	7.90	1.98	3.72	<0.05
	“Biotope” × “year”	8	14.02	1.75	3.30	<0.001
	Intergroup	581	308.76	0.53		
	Total	595	333.18			
Gastropoda	Biotope	2	2.40	1.20	4.43	<0.05
	Year	4	3.39	0.85	3.13	<0.05
	“Biotope” × “year”	8	2.19	0.27	1.01	ns
	Intergroup	581	157.35	0.27		
	Total	595	165.33			
Total abundance	Biotope	2	68.79	34.40	2.54	ns
	Year	4	858.26	214.56	15.85	<0.001
	“Biotope” × “year”	8	422.15	52.77	3.90	<0.001
	Intergroup	581	7865.76	13.54		
	Total	595	9214.96			

large soil-litter invertebrates—in contrasting biotopic conditions of the taiga forests of the Middle Urals have been studied. The ecological contrast of the animal habitat in the three compared biotopes, disturbed by natural catastrophic factors to varying degrees, is con-

firmed by the different levels of chronographic and biotopic variability of microhabitat parameters. The abundance of the common shrew was characterized by higher indices in a strongly disturbed biotope (windfall and two fires), which may indicate more favorable



**Fig. 4.** Dependence of the abundance of the common shrew of the current year on the total abundance of soil mesofauna in the previous year for 1998 – 2019 in a biotope disturbed by a windfall and two fires.

**Table 5.** Relationship between the abundance of the common shrew and the total abundance of invertebrates in biotopes with varying degrees of disturbance

Biotope	Current year		Previous year	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
I	0.13	ns	0.68	ns
II	0.28	ns	0.96	*
III	0.29	ns	0.94	*

(*r*) Pearson correlation coefficient; (*p*) the significance level; (\*)  $p < 0.05$ ; (ns) the values are statistically insignificant.

conditions in comparison with weakly disturbed and undisturbed habitats. In the conditions of a strongly disturbed biotope, common shrew individuals are more “attached” to areas with better protective conditions.

The long-term values of abundance of the most numerous representatives of communities of soil-litter invertebrates differed in contrasting biotopic conditions, which is associated with the biological and ecological characteristics of the compared taxa. The contribution of individual taxonomic groups of soil mesofauna to the total variability of the compared biotopes differs in different years. The food supply, which is equivalent to the indicator of the total abundance of invertebrates, is a stable biotopic characteristic reflecting the state of the food supply of shrews, the stability of which is ensured by the numerical redistribution of different taxonomic groups of soil mesofauna in an ecologically contrasting habitat environment. The discovered positive correlation between the abundance of the common shrew of the current year and the total abundance of soil-litter invertebrates in the previous year indicates an important role of the stock of potential food accumulated by winter during the previous summer–fall period in the life of shrews.

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#### CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest and confirm that applicable ethical standards were followed in handling animals.

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