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Daily Dynamics of Grass Stand Invertebrate Communities Exposed to Emissions from the Middle Ural Copper Smelter

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Abstract—The study investigated the daily dynamics of the invertebrate communities in the meadow grass stands along the pollution gradient of the Middle Ural Copper Smelter. In the most polluted area, the abundance of invertebrates in the upper part of the grass stand increases in the second half of the day, both in total (1.9 times) and in the groups of herbivores, both sucking (3.2 times) and chewing (2.2 times). This leads to a significant decrease in the similarity of the shape of the curves of circadian dynamics in the background and most polluted areas. In the other trophic groups considered, circadian changes are less pronounced. The obtained results confirm the hypothesis about modification of daily dynamics of grass stand invertebrates under industrial pollution. The most probable reasons for the changes are general degradation of invertebrate habitat, destabilization of temperature regime in it, as well as changes in the composition and structure of invertebrate communities themselves.

Keywords: Circadian dynamics, relative abundance, meadow communities, herbivores, predators, industrial pollution, metallurgical plant

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INTRODUCTION

Among the characteristic features of the invertebrate communities of the grassland are high abundance and diversity, close connection with herbaceous vegetation and “extremely strong diurnal dynamism” [1]. Daily dynamics refers to the vertical movements of invertebrates in the thickness of the grass stand, as a result of which one group or another ends up in its upper part. It is postulated that all groups of invertebrates visit the upper layers of the grass layer during the day [1]. The ecological meaning of daily migrations lies, on the one hand, in avoiding extreme environmental conditions and, on the other, in searching for the most favorable conditions [1, 2].

The causes of the daily dynamics of invertebrates were most actively studied in the second half of the 20th century. According to the generally accepted point of view, it is based on endogenous (not associated with the influence of the environment) physicochemical cellular mechanisms caused by the transcription of mRNA [3], the transport of small molecules through membranes [4, 5], or complex mutually coordinated transformations of compounds [6, 7]. The presence of such mechanisms allows us to “anticipate” future changes in environmental conditions (for example, the onset of daytime heat or nighttime cold) and prepare for them in advance [2]. External factors (illumination, meteorological conditions, habitat characteristics, trophic links in communities, etc. [1, 2, 8]) mainly synchronize endogenous rhythms with the current state of the environment [9]. According to another point of view, environmental factors are of primary importance, and endogenous rhythms are secondary, since it is impossible to completely isolate organisms from the environment [10].

In the second half of the 20th century, the specifics of the daily dynamics of invertebrates in the grass stand were described (strictly regular character, expressed in all natural zones, shift of the maximum rise of invertebrates to the upper part of the grass stand at night [1]), and basic studies of undisturbed communities and agroecosystems were carried out [11–14]. In recent decades, laboratory experiments on vertebrates have shown the modifying effect of metals on circadian rhythms [15–18]. For invertebrates, we know of only one work [19] that confirms the possibility of such a modification. To determine whether it is realized in natural conditions, field research data are needed. This will make it possible to make a contribution to understanding the mechanisms of biota adaptation to toxic load and, consequently, the principles of ecosystem functioning under pollution conditions, which determines the relevance of this work.

To date, the impact of industrial pollution on the daily dynamics of invertebrates has been virtually unstudied, although it could potentially be large. Near metallurgical plants, whose activities cause soil acidification, the diversity of meadow grasses is greatly reduced, in some cases to just a few species [20–22]. This inevitably simplifies the structure and architecture of the grass stand [21] and leads to a change in the temperature regime in it [23]. As a result, both the habitats themselves and the microclimatic conditions of the invertebrate habitats of the grassland change. No less significant are the changes in the invertebrate communities themselves. Most groups show a significant reduction in abundance and species richness [20, 21]; some taxa (e.g., harvestmen and terrestrial mollusks) may disappear completely near the plant [23–25]. The abundance of cicadas, on the contrary, can increase significantly with severe pollution [20, 21, 26]. As a consequence, the ratio of trophic groups in heavily polluted and background areas can differ significantly [20, 21, 26, 27], which means a modification of trophic links in invertebrate communities. The change in the ratio of trophic groups is also described for a different type of emission source, a phosphate fertilizer plant that alkalizes the upper soil horizons [28]. Consequently, in contaminated areas there are prerequisites for changes in the daily dynamics of invertebrate communities.

Previously, we have already attempted to analyze the impact of pollution on the daily dynamics of grass invertebrates, giving an approximate estimate of its consistency in different pollution zones [29]. The results led us to the conclusion about the insignificant influence of pollution on daily dynamics, preliminary, since it was based on an indirect indicator. In this work, a more powerful criterion is used, a direct assessment of the similarity of the shape of time series in areas with different levels of pollution.

Objective—To qualitatively establish the presence of the effect of industrial pollution on the daily dynamics of grass invertebrates. The presence of pronounced changes in invertebrate communities and their habitats allowed us to hypothesize that the influence of pollution is capable of modifying daily dynamics.

MATERIALS AND METHODS

Characteristics of the Study Area

The study area is located in the least elevated part of the Ural ridge (150–400 m above sea level) in the southern taiga subzone. The work was carried out in the vicinity of the Middle Ural Copper Smelter (MUCS, 56.8515° N, 59.9069° E). MUCS has been in operation since 1940 and its main emissions include sulphur dioxide, fluorine compounds, nitrogen oxides, metals and metalloids (Cu, Pb, Zn, Cd, Fe, and As). The annual volume of emissions in 1980 reached 225000 tons, after which it began to decline: to 148000 tons in 1990, 63000 tons in 2000, 28000 tons in 2004, and to 3000–5000 tons after 2010 [30].

The study sites are located in the western direction from the MUCS (against the prevailing winds) on secondary dry meadows formed as a result of forest clearing about 70 years ago. The meadows are located in low relief elements in forest clearings of approximately 5000 m^2 in size. The sampling plots are confined to three pollution zones: background (30 km from MUCS, pollution at the regional background level), buffer (4 km, moderate pollution) and impact (1 km, strong pollution). The reasons for identifying pollution zones were discussed in detail earlier [30, 31]. The floristic composition and structure of meadow vegetation vary greatly between zones, which is due to the disappearance of sensitive species of herbs and their replacement by grasses near the plant. In the background zone there are herb meadows, in the buffer zone there are herb–grass meadows, in the impact zone there are grass meadows, with absolute dominance of *Agrostis tenuis* Sibth. The average (± error) height of herbage in 2008 was 109.1 ± 4.7 cm in the background zone, 113.2 ± 4.0 cm in the buffer zone, and 55.5 ± 1.4 cm in the impact zone (based on 10 measurements in each test plot). The herbage was described in more detail earlier [21]. At the time of the research, there was no grazing or haymaking in any of the areas.

Collection and Processing of Invertebrates

The surveys were conducted in 2004 in three rounds, in the second half of June, July, and August. In each of the contamination zones, three sampling plots measuring 50 × 50 m (9 in total) were laid out. The plots within the contamination zone were selected based on the presence of meadows of a similar type in individual forest clearings, at least 100–300 m apart and located at a comparable distance from the plant.

The daily dynamics of trophic and large taxonomic groups of invertebrates were studied in the upper part (20–30 cm) of meadow herbage. In this case, it was not the absolute abundance of invertebrates per unit of space that was assessed, but its analog: the relative abundance normalized to the standard sampling effort. Discussions about the increase or decrease in abundance further in the text of the work are applicable only in the context of the analysis of daily dynamics. Samples were collected at 0:00, 4:00, 8:00, 12:00, 16:00, and 20:00 h, the daily cycle consisted of six censuses. Mowing was done with a standard entomological net (hoop diameter 30 cm, nylon mesh bag depth 70 cm, handle length 130 cm). Each sample included 20 sweeps of the net; successive censuses in the daily cycle were made in different parts of the sample plots to prevent “exhaustion” of invertebrates.

Two researchers participated, each of whom performed a full daily cycle on each sample plot in each census round. The researchers alternated between the contamination zones and the sample plots (Appendix, Table S1). The use of two researchers helps to minimize the bias in the obtained abundance estimates caused by the influence of their individual characteristics. The structure of the experiment includes two types of experimental units: spatial (sample plots) and temporal (days of sampling); samples are considered as the statistical units (Appendix, Fig. S1). A total of 324 samples were collected (6 samples per day × 2 researchers × 3 sample plots in each zone × 3 pollution zones × 3 rounds) and more than 292000 specimens of invertebrates.

The collected invertebrates, together with plant fragments, were shaken out of the net into a wide-mouthed container with a 70% ethanol solution (to facilitate subsequent packaging), after which they were strained into a nylon mesh bag, labeled, and stored in a 70% ethanol solution. Determination of taxonomic affiliation (up to the family level) and trophic specialization of invertebrates was carried out in the laboratory. In total, six trophic groups have been identified: sucking and chewing herbivores, sucking and chewing predators, hemophages, and others [20]. The "other" group also included ants, which are difficult to clearly classify into one of the main trophic groups. The method of accounting used is focused on representatives of macrofauna; representatives of mesofauna (Collembola, Thysanoptera, Acariformes) included in the samples were excluded from further analysis.

Analysis of Daily Dynamics of Invertebrates

All calculations were performed in the R software environment [32]. The curves of daily dynamics of the total abundance and main trophic groups of invertebrates are visualized in the ggplot2 package [33]. In each of the pollution zones, the mean and standard error were calculated for the total abundance, main trophic, and most abundant taxonomic groups of invertebrates for each time of day (3 areas × 3 rounds, $n = 9$), as well as average daily values ($n = 6$). In this case, the data on the evaluation units (samples) were averaged within each sample plot ($n = 2$). In subsequent data processing, the individual influence of researchers was minimized by z-normalizing the abundances of each of the considered groups by the mean and standard deviation for each researcher:

$$d'_{ij} = \frac{d_{ij} - \bar{x}_j}{\sigma_j},$$

where d'_{ij} is the normalized value of abundance in the i-th sample collected by the j-th researcher; d_{ij} is the initial value of abundance; $\bar{x}_j$ is the average value of the abundance of the group collected by the j-th researcher in all load zones; and σ_j is the standard deviation of the value of the group collected by the j-th researcher in all pollution zones.

We then analyzed z-normalized abundance of invertebrates. The analysis of the influence of the factors "pollution zone," "census round," and "time of day" was performed in the LMERConvenienceFunctions package [34]. Linear models with mixed factors were used (fixed factors—zone, census round, and time of day; random factor—sample plot). Multiple comparisons (Tukey's test) were also performed between the pollution zones for each of the considered groups within each time of day (multcomp package [35]).

Analysis of the Similarity of the Shape of Time Series

The specificity of changes in the daily dynamics of invertebrates in the pollution gradient was revealed using the method of assessing the similarity of the shape of time series (Shape-Based Distances, SBD) in the dtwclust [36] and proxy [37] packages. The SBD method, based on the procedure k-Shape-clustering, is currently one of the fastest and most accurate methods of time series analysis. The method is aimed at identifying minor changes in the shape of the compared series, caused, for example, by a shift in values or a change in their scale. The SBD index values range from 0 to 2, where 0 means perfect similarity of time series [38]. The work compared time series consisting of data from one day of sampling at each sample plot (series length is six measurements). Based on the SBD values obtained for each invertebrate group considered, the mean and confidence interval limits were calculated for each pair of pollution zones. The significance of the confidence interval estimates was tested using the BCa bootstrap method (99,999 permutations) in the boot package [39]. SBD values obtained for total abundance and major trophic groups were visualized in the ggplot2 package.

Analysis of Temperature Parameters

Data on the temperature regime in the grass stand were collected in 2010–2011 (from June 1 to August 31) using iButton DS 1921 thermochrons with a minimum gradation of recorded temperature of 0.5°C. Thermochrons were installed on supports at each of the test plots at four random points at a distance of 15–20 m from each other. At points 1–3, two thermochrons were placed: the first one was 2–3 cm above the soil surface, the second one was in the thickness of the grass stand (at a height of about 30 cm). At point 4, one thermochron was installed 10–15 cm above the grass stand. All thermochrons were protected from direct sunlight by protective caps. Each year, 63 thermochrons were installed (7 in each test area); air temperature was measured every 2 h (12 measurements per day). For the obtained data, the average daily, maximum daily, and range (the difference between the maximum and minimum values) of daily temperatures at the soil surface, in the middle of the grass stand and above the grass stand were calculated. Average temperature values are calculated for each summer month

Table 1. Results of the analysis of a linear model with mixed factors (fixed factors – zone, tour, and time of day; random factor – sample plot)

Groups	Factors					
	zone	tour	time of day	zone × tour	zone × time	tour × time
Total abundance	<0.0001	<0.0001	<0.0001	<0.0001	0.0289	0.1002
Sucking herbivores	<0.0001	<0.0001	0.0002	<0.0001	0.0742	0.4468
Chewing herbivores	<0.0001	0.0008	0.0458	<0.0001	0.0001	0.0006
Sucking predators	<0.0001	<0.0001	0.0007	<0.0001	0.2255	0.0026
Chewing predators	<0.0001	<0.0001	<0.0001	0.0328	0.8077	<0.0001
Hemophages	0.1637	0.6930	0.3528	0.0510	0.1296	0.3733
Others	<0.0001	0.5484	<0.0001	0.5878	<0.0001	0.1095

The achieved significance is given.

and for the summer period as a whole; confidence intervals for these values are also calculated.

The standardized precipitation evapotranspiration index (SPEI) was calculated in the SPEI package [40] for a set of values of average monthly air temperature and total monthly precipitation from January 1959 to December 2021 based on data from the Revda weather station (WMO ID 28430, [41]), the results are visualized in the ggplot2 package [33]. The SPEI index is designed to take into account the relationship between precipitation and potential evapotranspiration in any area on a global scale; the index values can be significantly refined by using local meteorological observations over a sufficiently long period (30–50 years or more). The index allows one to evaluate the moisture conditions in the period of interest in relation to the long-term average. Thus, the SPEI 1 index form characterizes the conditions of the specified month, the SPEI 4 form characterizes the average conditions of 4 months, the specified month and the three preceding ones. Index values below –1.5 correspond to drought, while those above +1.5 correspond to excess moisture.

RESULTS

Daily Dynamics of Invertebrates

According to the results of the linear mixed-factor model analysis, the total abundance of invertebrates was significantly affected by the pollution zone, the census round, and the time of day. All interactions of factors are also significant, with the exception of "census round × time of day" (Table 1). In all major trophic groups, the influence of the pollution zone, the census round, and the time of day is also significant. For sucking herbivores, the most abundant trophic group, the interactions of the factors "pollution zone × time of day" and "census round × time of day" are insignificant. In other groups, the trends are in different directions (see Table 1).

The overall abundance of invertebrates in the background zone was lowest in the early morning hours and highest around midday and before midnight (Fig. 1a; Appendix, Table S2). In the buffer zone the trend is similar. In the impact zone, the overall abundance is increased: 1.9 times higher than the background, 1.5 times higher than the buffer. The daily dynamics generally correspond to the background zone, although the "midday" increase in abundance is more pronounced and lasts longer in time.

The daily dynamics of sucking herbivores correspond to the trends described for the total abundance (Fig. 2a; Appendix, Table S2). The abundance in the impact zone increased more significantly: 3.2 times compared to the background, 2.0 times compared to the buffer. The daily dynamics of other trophic groups have specific features. In the group of chewing herbivores in the background and buffer zones, the greatest abundance was also noted around midday and before midnight (Fig. 2b; Appendix, Table S2). In the impact zone, on the contrary, the abundance was reduced: 2.2 times compared to the background, 1.4 times compared to the buffer. The daily dynamics in the impact zone have changed. The "midday" increase in abundance is clearly shifted to the right, towards the evening, when abundance decreases in the background and buffer zones. As a result, the peak abundance of the group in the impact zone reaches background values (Fig. 2c, Appendix Table S2). The daily dynamics of sucking predators in all zones is weakly expressed, although the abundance of the group increases slightly around midday and midnight (Fig. 2c; Appendix, Table S2). The daily dynamics of chewing predators is also weakly expressed and similar in all pollution zones. The "midday" and "midnight" increases in abundance are still noticeable and are somewhat shifted to the left, to earlier hours (Fig. 2g; Appendix, Table S2). The daily dynamics of hemophages generally coincide with that described for chewing predators (Appendix, Table S2). In the "other" group, which unites taxa with a different trophic specialization, the general nature of daily dynamics is determined by

Hymenoptera microparasitica. In the background and buffer zones their abundance is similar, with a tendency to increase around midday. In the impact zone, a “midday” peak is expressed, 3.2 times exceeding the background values (Appendix, Table S2).

Analysis of the Similarity of the Shape of Time Series

The curves of daily dynamics of total abundance were most similar in the background and buffer zones. When comparing the background and impact zones, the similarity of the curves decreased significantly; the confidence interval of the distance between the zones did not intersect with the intervals of other compared pairs of pollution zones (Fig. 1b; Table 2). When comparing the buffer and impact zones, the similarity decreased somewhat, although the distance between the zones did not increase significantly. In the group of sucking herbivores the situation is similar, although the confidence intervals in all compared pairs of zones do not intersect (Appendix, Fig. S2a; Table 2). The curves of the daily dynamics of chewing herbivores were most similar in the buffer and impact zones, and least similar in the background and impact zones. Moreover, the confidence intervals of all compared pairs of zones also did not intersect (Appendix, Fig. S2b; Table 2). In the group of sucking predators, the curves of daily dynamics in the background zone were similar to both the buffer and impact zones (Appendix, Fig. S2c; Table 2). In chewing predators, the daily dynamics curves were similar in all pollution zones (Appendix, Fig. S2d; Table 2). In hemophages, the daily dynamics are most similar in the background and impact zones, and least similar in the buffer and impact zones. In the “other” group, no differences in dynamics between zones were identified (see Table 2).

Analysis of Temperature Parameters

According to the SPEI values, the total amount of precipitation in the summer and spring months in 2004 and 2011 was within the almost 80-year norm. Precipitation during the summer months of 2010 was also within the norm, but taking into account the spring months, July and August were somewhat drier than usual (Appendix, Fig. S3).

In the background and buffer zones, the daily dynamics of air temperature were similar at all measurement points: above the grass stand, in the middle of the grass stand, and above the soil surface. In the impact zone, lower temperatures were observed over the grass stand during the daytime (Fig. 3a). In the middle of the grass stand, the temperature was generally higher (Fig. 3b), and above the soil surface it was significantly higher during the daytime (Fig. 3c). Average daily temperatures, maximum daily temperatures, and the range of daily temperatures in all zones were comparable (Appendix, Table S3).

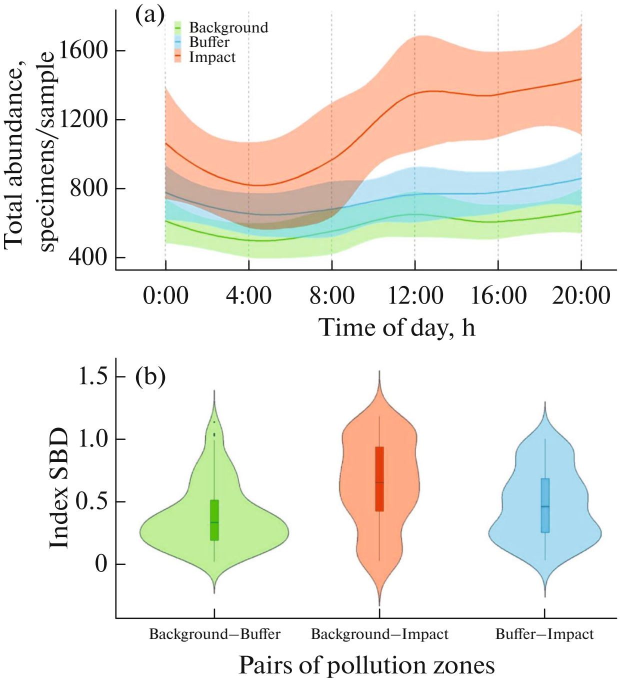

Fig. 1. Daily dynamics of total abundance (a) and distribution of SBD index values when comparing pairs of pollution zones (b) in grassland invertebrate communities: (a) average and 95% confidence interval limits, statistical unit—3 sample plots × 3 census round ($n = 9$); (b) median, quartiles and outliers; statistical unit—9 comparisons between sample plots in a statistical unit × 4 comparisons between days of sampling (researchers) in a round × 3 census round ($n = 108$).

DISCUSSION

In the impact zone, the daily dynamics of invertebrate communities in the grassland undergo changes. Between midday and sunset, the total abundance and abundance of herbivores increase greatly. In this case, the differences with the background zone increase in sucking herbivores, while in chewing ones, on the contrary, they decrease. The shapes of the curves of the daily dynamics of the indicated groups differ most significantly in the background and impact zones. Taking into account that the sample plots were maximally unified in ecotopic conditions, and the dynamics of weather conditions in the studied gradient (about 30 km) are largely synchronous, the most probable cause of the described changes should be considered the direct or indirect effect of industrial pollution.

For the overall abundance and all the groups considered, a strong influence of the “census round” factor was noted (see Table 1), obviously caused by seasonal changes in taxonomic composition. Representatives of some species emerge from the egg stage and appear in samples, while representatives of others go into diapause and are no longer counted. When changing age stages, a change in trophic specialization is possible (for example, in Lepidoptera, Hymenop-

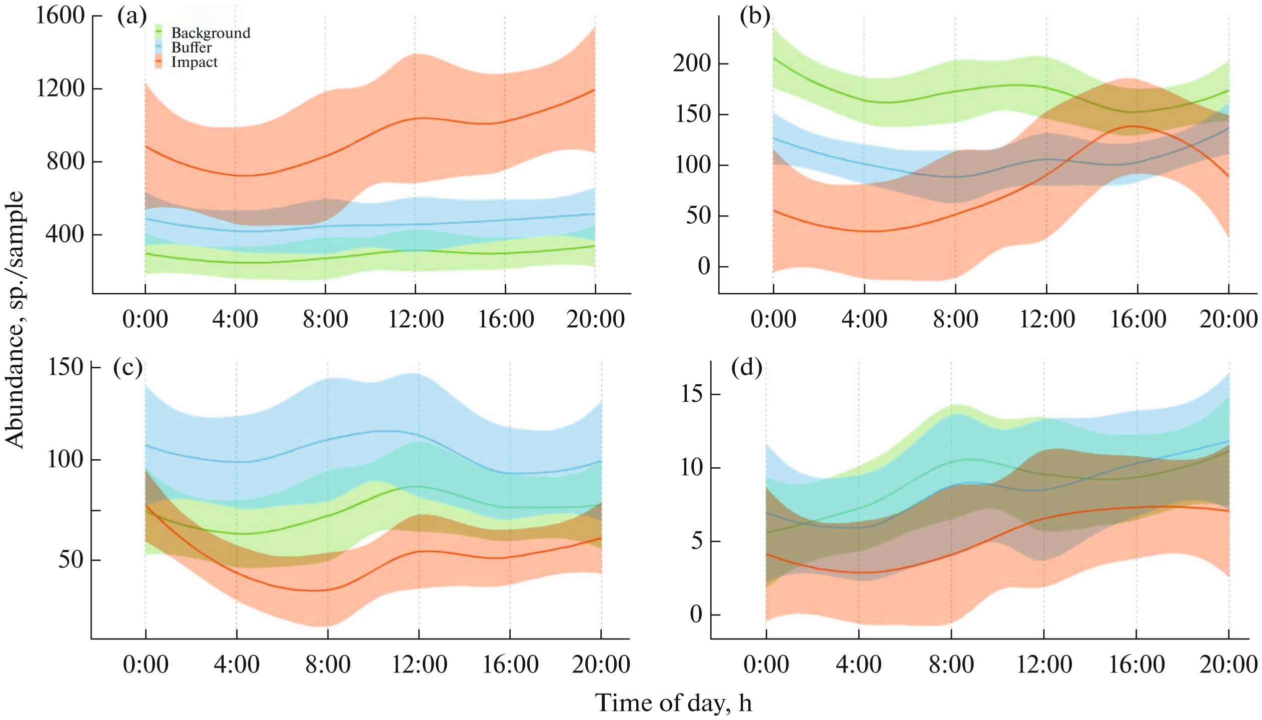

Fig. 2. Daily dynamics of the main trophic groups in the communities of invertebrates of the grass stand: (a) sucking herbivores, (b) chewing herbivores, (c) sucking predators, (d) chewing predators. The averages and the limits of the 95% confidence interval are given, the accounting unit is 3 sample plots × 3 census rounds ($n = 9$).

tera symphyta, etc.). However, during the analysis, materials from different census rounds were combined. The data are deliberately "roughened" in order to establish, in a first approximation, "in broad strokes," whether there is an effect of industrial pollution in relation to the daily dynamics of invertebrates. The prerequisites for such an approach are present in the results of the linear model analysis. The absence of a significant interaction between the factors "census round × time of day" means that for the community as a whole, the trend in abundance change during the day is the same in all census rounds (see Table 1). For individual trophic groups, this trend is expressed less strongly and is manifested mainly in sucking herbivores (see Table 1 and Appendix, Fig. S4), which are the most abundant in the herbage.

The reasons for changes in the daily dynamics of invertebrate communities in the grassland in the contaminated area may lie in the influence of several interrelated factors. Firstly, under the influence of pollution, the abundance and ratio of many taxonomic and trophic groups, and therefore the trophic structure of communities, can change. Secondly, pollution can modify the composition and architecture of meadow grassy vegetation, the habitat of invertebrates. Thirdly, the transformation of the grass layer can lead to a change in the microclimatic conditions within it. The potential significance (outside the context of pollution) of all three groups of factors for the daily dynamics of invertebrates has been emphasized repeatedly [1, 2, 8].

The main components of MUCS emissions include metals, whose ability to modify circadian rhythms in vertebrates is well recognized. Using the example of cyprinid fish [15, 17] and rats [16, 18], it has been shown that exposure to metals (Cd, Cu, and Pb) disrupts the coordination of several enzymatic reactions and the expression of individual genes, and this disrupts the synchronization of endogenous rhythms with the environment. For invertebrates, we know of only one study describing a change in the ratio of sleep and activity in the daily cycle of Drosophila under the influence of methylmercury [19], which confirms the fundamental possibility of modifying daily rhythms by industrial pollution.

The general nature of changes in the trophic structure of communities of terrestrial non-soil invertebrates in areas with different types of pollution consists of an increase in the abundance of herbivores and a decrease in the abundance of predators [42]. Changes in invertebrate communities generally correspond to the given trend and are most fully described for the MUCS vicinity. In the buffer zone, the abundance of sucking predators (nabiid bugs and some spiders; Appendix, Table S2, [23]) and some chewing herbi-

Table 2. Dissimilarity (SBD indices) of daily dynamics of abundance of grass invertebrates in different pollution zones

Group/Taxon	Background – buffer	Background – impact	Buffer – impact
Total abundance	0.38 [0.34–0.43]^{a}	0.64 [0.57–0.70] ^{b}	0.47 [0.42–0.53] ^{a}
Sucking herbivores	0.34 [0.28–0.41] ^{a}	0.70 [0.62–0.77] ^{b}	0.49 [0.43–0.55] ^{c}
Cicadinea	0.38 [0.32–0.45] ^{a}	0.66 [0.58–0.74] ^{b}	0.52 [0.45–0.60] ^{ab}
Miridae	0.40 [0.32–0.48] ^{a}	0.52 [0.44–0.60] ^{a}	0.36 [0.30–0.43] ^{a}
Diptera brachycera anthophaga	0.20 [0.17–0.25] ^{a}	0.82 [0.74–0.88] ^{b}	0.75 [0.68–0.80] ^{b}
Chewing herbivores	0.64 [0.59–0.69] ^{a}	0.77 [0.71–0.83] ^{b}	0.47 [0.43–0.51] ^{c}
Diptera nematocera anthophaga	0.48 [0.43–0.53] ^{a}	0.51 [0.45–0.56] ^{a}	0.42 [0.36–0.49] ^{a}
Lepidoptera larvae	0.54 [0.49–0.59] ^{a}	0.70 [0.64–0.76]^{b}	0.55 [0.48–0.63] ^{a}
Symphyta larvae	0.67 [0.61–0.73] ^{a}	0.95 [0.90–1.0] ^{b}	0.64 [0.56–0.72] ^{a}
Pulmonata	0.83 [0.79–0.87]	–	–
Sucking predators	0.45 [0.39–0.52] ^{a}	0.45 [0.40–0.51] ^{a}	0.59 [0.53–0.65] ^{b}
Nabiidae	0.54 [0.49–0.60] ^{a}	0.57 [0.51–0.63] ^{a}	0.83 [0.77–0.88] ^{b}
Linyphiidae	0.46 [0.39–0.52] ^{ab}	0.33 [0.28–0.39] ^{a}	0.51 [0.44–0.58] ^{b}
Salticidae	0.48 [0.43–0.53] ^{a}	0.65 [0.60–0.69] ^{b}	0.75 [0.69–0.80] ^{b}
Thomisidae	0.57 [0.52–0.63] ^{a}	0.53 [0.47–0.60] ^{a}	0.59 [0.52–0.65] ^{a}
Chewing predators	0.36 [0.32–0.39] ^{ab}	0.40 [0.36–0.44] ^{a}	0.28 [0.25–0.32] ^{b}
Cantharidae	0.15 [0.12–0.20] ^{a}	0.14 [0.10–0.18] ^{a}	0.11 [0.09–0.14] ^{a}
Coccinellidae	0.49 [0.44–0.53] ^{a}	0.64 [0.58–0.69] ^{b}	0.60 [0.55–0.65] ^{b}
Phalangiidae	0.76 [0.71–0.81]	–	–
Hemophage	0.41 [0.35–0.47] ^{ab}	0.32 [0.27–0.37] ^{a}	0.51 [0.44–0.58] ^{b}
Other groups	0.42 [0.38–0.46] ^{a}	0.50 [0.46–0.54] ^{a}	0.45 [0.41–0.49] ^{a}
Hymenoptera microparasitica	0.43 [0.38–0.47] ^{a}	0.50 [0.46–0.55] ^{a}	0.42 [0.38–0.46] ^{a}

The mean and bootstrap-verified 95% confidence intervals for pairs of contamination zones within individual groups/taxa are presented. Statistical unit: 9 comparisons between sample plots in a census round × 4 comparisons between days of sampling (researchers) in a round × 3 census rounds ($n = 108$); dash – absence of a group in the impact zone. SBD indices are calculated for each of the days of days of sampling (six time points in total). Letter indices are the result of comparison of confidence interval boundaries; identical letters mean no differences between SBD indices within individual groups/taxa.

vores (Diptera nematocera anthophaga, [20, 21]) has increased. The abundance of other groups is similar to the background or reduced. In the impact zone, the total abundance and abundance of sucking herbivores (primarily cicadas and mirid bugs) are greatly increased, while the abundance of other groups is reduced (Appendix, Table S2) [20, 21, 26]. In addition, a decrease in species richness was recorded for all groups considered. Thus, the number of spider species near the plant has been reduced by almost 2 times – from 90 to 48; dominance in communities has increased significantly [23]. The species richness of aphids decreased threefold, from 30 to 9 species [43]; harvestmen [23] and gastropods [24, 25] completely disappeared.

Data for other meadow ecosystems near point sources of pollution are rare, but in all cases the structure of invertebrate communities changes under the influence of pollution. In the impact zone of the Karabash copper smelter (Karabash, Southern Urals), the overall abundance of invertebrates is reduced by 1.4–2.9 times. The abundance of the main trophic groups did not change significantly, although a tendency towards its decrease was noted among herbivores (sucking and chewing) [27]. In meadows near a phosphate fertilizer plant in Germany, alkalization of the upper soil horizons (pH increased from 7 to 9) led to a decrease in the species richness and diversity of sucking (cycads) and chewing (coleoptera) herbivores, as well as sucking predators (hemipterans) [28].

Thus, the daily increase in abundance in the MUCS impact zone is most likely due to sucking herbivores, the most abundant group, the features of the daily dynamics of which are manifested against the background of a decrease in the abundance of all other groups. Species richness indices in plants and inverte-

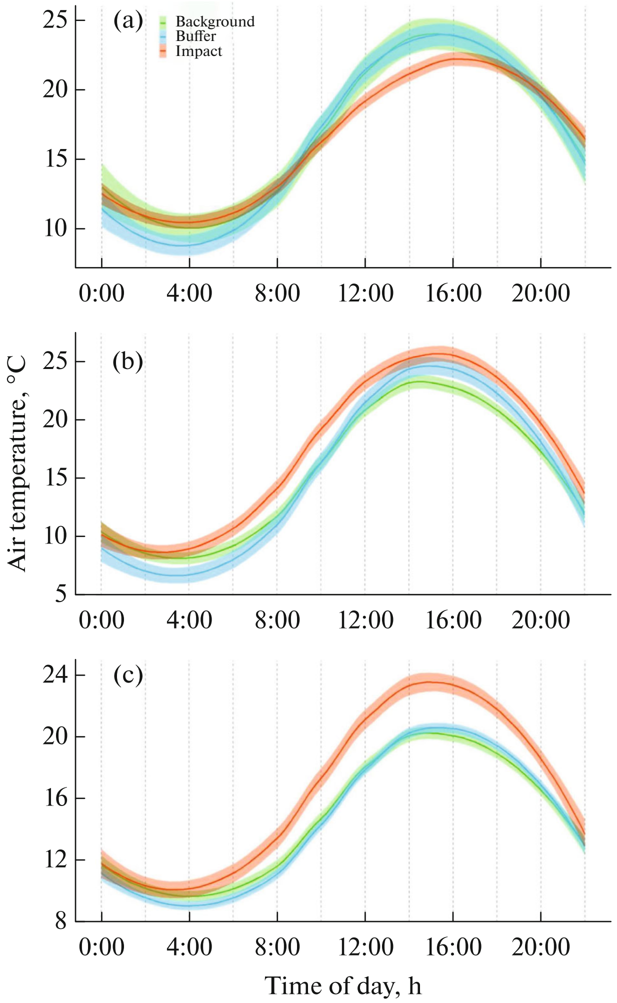

Fig. 3. Daily dynamics of air temperature in different pollution zones: (a) – above the grass stand, (b) – in the grass stand, (c) – near the soil level. The averages and the limits of the 95% confidence interval are given; the statistical unit is the sample plot ($n = 3$).

brates typically change in similar ways [44, 45], so a decrease in plant richness in an impact zone likely means a decrease in the richness of sucking herbivores. In this case, the daily dynamics in the contaminated area may be due to the specificity of one or several species of cicadas and leafhoppers that have adapted to the conditions of the impact zone and have increased their numbers many times over. This assumption seems plausible but requires verification at the species level of communities.

The transformation of invertebrate communities correlates well with the degradation of their habitat. According to the general trend, the phytomass of herbaceous vegetation decreases near non-ferrous metallurgy enterprises [46]. In the MUCS impact zone, the total phytomass (twofold) and species richness (from 63–69 to 3–5 species) are reduced; the herbage is absolutely dominated by *Agrostis tenuis* (94–99% of the total phytomass) [20, 21]. The projective cover of meadows decreased from 90–100% in the background and buffer zones to 50–80% in the impact zone [47]. In the impact zone of the Karabash Copper Smelter, the phytomass of meadow grasses is also reduced (by 2–7 times), and the proportion of graminoids is increased (from 36–45 to 53–85%) [27]. A strong decline in diversity was noted near a copper smelter in England, where grasslands were dominated by *Agrostis stolonifera* L. and *Festuca rubra* L. [22]. Species richness and diversity of meadow plants were reduced near a phosphate fertilizer plant in Germany (from 42–64 to 2 species) [28].

The structure of terrestrial invertebrate communities is determined by the composition and structure of plant associations [44, 45, 48]. The complex architecture of the vegetation prevents the free movement of air, creating a gradient of microclimatic conditions. This, together with the high taxonomic diversity of food plants, provides a large set of ecological niches for invertebrate habitation [49]. A decrease in plant diversity leads to a decrease in invertebrate diversity [44, 45]. The presence of graminoids in the herbage itself does not have a negative effect on meadow communities; their high productivity contributes to an increase in the species richness of herbivores and the abundance of predators [45]. However, under pollution, plant diversity is sharply reduced, and graminoids can dominate absolutely. Their vertical-linear organization with weakly expressed branching of the stem leads to a simplification of the overall architecture of the grass layer of the contaminated area. In addition, the grass stand of the impact zone meadows is sparse, as evidenced by the decrease in projective cover [47]. For herbivores and predators, this means a shift in the range of food objects and the loss of habitats for waiting and reproduction. In addition, sparse grass stands compensate for weather fluctuations less effectively, and temperature and humidity fluctuations should be more pronounced [50], which is unfavorable for many groups of invertebrates [51]. An increase in the range of daily temperatures in the impact zone was also noted for birch forests [52].

The results confirm the assumption about the change of daily air temperature dynamics in the contaminated area. During the hottest time of day, after midday, temperatures near the soil surface and in the grass layer in the impact zone are noticeably higher than in the background zone (see Fig. 3). Apparently, the sparse grass cover of the impact zone does not shield the soil surface from heating by the sun, which is why the temperature in it is equalized throughout the entire depth. The greatest abundance of invertebrates in the upper part of the grass stand during the daytime corresponds to the highest temperatures (around midday), and at night, to the lowest (around midnight). In the background and buffer zones, the increase in abundance is relatively small. In the impact zone it is more pronounced, and daylight lasts longer and occupies most of the daylight hours (see Figs. 1 and 3).

Vertical migrations of grass invertebrates are associated with the search for favorable environmental conditions, primarily temperature and humidity [1, 2, 14]. The ascent to the upper part of the herbage during the night is accompanied by the greatest feeding activity; at least for some groups this has been confirmed by analysis of intestinal contents [1]. Rising during daylight hours is unlikely to be related to nutrition, since, as noted above, this process should be timed to favorable, not extreme, temperatures. It is probably due largely to avoidance of the sun-heated soil surface.

If we accept this assumption, then the influence of air temperature on the daily dynamics of invertebrates under pollution can be described as follows. At night, the temperature in the herbage is minimal. After dawn, temperatures near the soil surface begin to increase and invertebrates begin to move up into the upper part of the grass stand. In the middle of the day, temperatures near the soil and in the grass stand are maximum (3–4°C higher than those measured above the grass stand), as is the abundance of invertebrates (see Figs. 1 and 3). Apparently, the soil surface in the impact zone becomes a "hot frying pan," forcing invertebrates to rise higher to avoid overheating. It can be assumed that in the impact zone, the ability to compensate for overheating in this way is one of the survival factors that ensures the existence of only stable groups. This is indirectly confirmed by the change in the ratio of life forms of spiders near the plant, where the proportion of xerophilic species increases and the proportion of hygro- and mesophilic species decreases [23]. In the afternoon, the temperature in the herbage decreases and after sunset it becomes equal in all pollution zones. The high total abundance of invertebrates in the impact zone also persists at least until sunset beyond the forest boundary (19–21 h local time, depending on the round of census). This is probably due to the feeding of the most abundant groups (mainly sucking herbivores) in the upper part of the grass stand when favorable temperature conditions occur. Further decreases in temperature lead to a decrease in the abundance of invertebrates, reaching minimum values after midnight.

Thus, all three groups of factors considered (changes in the composition and structure of the grass stand, changes in the trophic structure of invertebrate communities, and changes in the temperature regime in the grass stand) can lead to a modification of the daily dynamics in the MUCS impact zone. The modification itself is confirmed by a decrease in the similarity of the curves of daily dynamics when approaching the plant. A decrease was noted not only for the total abundance, but also for sucking herbivores (see Table 2), for which, according to the results of the analysis of the linear model, the influence of pollution on daily dynamics was not established (absence of significant interaction between the factors "zone" and "time of day", see Table 1). However, the magnitude of the changes was smaller than would be expected given the scale of community transformation. The SBD index estimates obtained by comparing communities in the background and impact zones do not exceed the value of one on average, i.e., half of the maximum possible value of dissimilarity (see Table 2 and Appendix, Fig. S2). The relatively high consistency of the daily dynamics in the pollution gradient confirms the results obtained earlier [29]. This is probably largely due to the ecotopic unification of the sample plots and the uniformity (due to the slight geographical distance) of the weather conditions on them. It should be noted that in the year considered, weather conditions in the territory under consideration were close to the long-term norm (see Appendix, Fig. S3). At the same time, the SBD index estimates may be somewhat biased due to the fact that the surveys in different zones in some cases were carried out on different days (see Appendix, Table S1). This could lead to some error due to the dynamics of weather conditions. In addition, the relatively high consistency of the daily dynamics of invertebrate grass stands in different zones may be based on the action of endogenous intracellular mechanisms [3–7], the discussion of which, however, is beyond the scope of this study.

CONCLUSIONS

Under the influence of industrial pollution, the daily dynamics of invertebrate communities in the grassland have undergone changes. In the impact zone, the overall abundance and abundance of several groups (sucking and chewing herbivores) are greatly increased in the second half of the day. As a result, the similarity of the shape of the daily dynamics curves in the background and impact zones significantly decreased. In the other trophic groups considered, the changes are less pronounced. The most probable reasons for the modification of daily dynamics in the impact zone are the general degradation of the grass stand (the habitat of invertebrates), the destabilization of the temperature regime in it, as well as changes in the composition and structure of the invertebrate communities themselves. The obtained results confirm the proposed hypothesis about the possibility of modifying the daily dynamics of grass invertebrates under industrial pollution.

SUPPLEMENTARY INFORMATION

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

By the decision of the Bioethics Commission of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (minutes No. 13 dated November 1, 2022), the Commission's permission to use materials or data collected before the date of creation of the Bioethics Commission at the Institute of Plant Genetics and Society of the Ural Branch of the Russian Academy of Sciences (i.e., before May 14, 2020) is not required.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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