

Long-term Dynamics of Small Mammal Communities in the Period of Reduction of Copper Smelter Emissions: 2. β -Diversity

S. V. Mukhacheva^{a, *} and A. N. Sozontov^a

^a Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

*e-mail: msv@ipae.uran.ru

Received April 2, 2021; revised May 31, 2021; accepted June 10, 2021

Abstract—The long-term dynamics of β -diversity of small mammal (SM) communities in the vicinity of a large copper smelter has been analyzed during the periods of high (1990–1997), reduced (1998–2009), and almost terminated emissions (2010–2020). The results show that the β -diversity of communities increases as the smelter is approached, with the level of pollution playing a key role in the formation of community structure (up to 25%). Throughout the 30-year observation period, the background communities have been less variable than the buffer and impact communities; i.e., the more unstable the environment, the higher the community variability. Structural rearrangements in the impact and buffer communities in the period of emission reduction have resulted in the progressive divergence between the communities of background and polluted areas.

Keywords: rodents, shrews, community similarity, diversity, dynamics, industrial pollution, natural recovery

DOI: 10.1134/S1067413621060084

The diversity of biotic communities is traditionally evaluated in term of inventory community (refers to Whittaker's α and γ diversity) and differentiation (β) diversity [1–4]: the former reflect the species diversity of communities on the local (α) or regional scale (γ), while the latter characterize similarity of communities in space and time.

Anthropogenic impact may cause differently directed transformations in the structure of communities, which depend on a variety of factors: the pattern and intensity of impact [5, 6], its spatial scale [7–9], the quality of habitats [6, 10, 11], and specific features of the study objects [10, 12–14]. Such transformations may lead to either homogenization or divergence of biotic communities. The best studied from this aspect are some taxa of vascular plants, invertebrates, and birds. Studies on small mammals (SMs) as model objects are relatively few. It has been found that the β diversity of SM communities increases under conditions of industrial pollution [15] and in agricultural landscapes [14]. Similarity of these communities in habitats transformed by felling operations may increase [9], decrease [11], or remain unchanged [16]. A stable composition is also characteristic of some SM communities inhabiting agricultural landscapes exploited with different intensity [12, 13, 17].

Studies on β -diversity are not only of theoretical interest but also relevant for choosing the most efficient strategies for the improvement of stability of natural and human-modified ecosystems [5, 10]. Similar-

ity of communities on a local scale depends on the dynamic balance between the processes of homogenization and divergence. The former processes are conditioned by the disappearance of certain species from communities under a direct (selective elimination) or indirect impact (the loss of suitable habitats) [18–21]; the latter, by disturbances if the exchanges of species between local communities because of fragmentation of habitats [13, 22–24]. Ecological processes leading to convergence of communities does not necessarily involve extinction or invasion of certain species [25]. They usually manifest themselves in the replacement of dominants and an increase in the proportion of widespread and ecologically flexible species (“winners”) at the expense of rare and specialized species (“losers”) [18, 26, 27].

This paper is the second part of the study on the long-term dynamics of SM communities in polluted areas in the periods of high, reduced, and almost terminated emissions from the Middle Ural Copper Smelter (MUCS). The data presented in the first part [28] concern the dynamics of inventory (α and γ) diversity of the species composition and abundance of communities. They show that the response of SM communities to pollution has not basically changed over 30 observation years (1990–2019): in each of the three periods, their α -diversity and total abundance were found to decrease significantly as the MUCS was approached, while parameters of γ -diversity remained unchanged along the pollution gradient. Therefore, it is of interest to ana-

lyze the dynamics of β -diversity. We are not aware of studies where the results of long-term annual censuses have been used to evaluate the β -diversity of SM communities inhabiting areas with different pollution levels in the periods before and after reduction of emissions.

The purpose of this study was to analyze long-term changes in the β -diversity of SM communities in background and polluted areas. The following hypotheses were tested: (1) when emissions are high, β -diversity is higher in polluted areas; (2) As emissions are reduced, similarity between communities of background and polluted areas increases; and (3) impact communities are more variable in time than background communities.

MATERIAL AND METHODS

Collection of the Material

The study region, key plots, and the procedure of sample collection are described in detail in the first part of this paper [28]. Studies were performed over 30 years that covered the periods of high (1990–1997, period I), reduced (1998–2009, period II), and almost terminated emissions (2010–2020, period III). Seven key plots were established in three zones with different pollution levels: the impact (heavy pollution; 1, 1.5, and 2 km from the MUCS), buffer (moderate pollution, 4 and 6 km), and background zone (pollution at the regional background level, 20 and 30 km). Small mammals were trapped every year (in May, July, and September) in all plots simultaneously using wooden snap traps arranged in lines at stationary positions. Each line consisted of 25 traps set at intervals of 5–7 m, which were exposed for 3–5 days and inspected once a day. Two to four lines per plot were laid out during each trapping round. A total of more than 100000 trap–days were conducted, and almost 6000 animals were trapped.

A key plot was taken as a statistical unit. The abundance of individual species (ind./100 trap–days) was estimated as the total number of animals of a given species trapped in a plot over the year (during all trapping rounds) normalized relative to sampling effort (number of traps \times number of trapping days). In certain years of depression in SM population size, “zero” samples ($n = 7$) containing not a single animal were obtained with a standard sampling effort in some plots of the impact zone. For the unambiguous interpretation of the presented data, the results of calculations based on the numbers of animals of individual species were referred to as absolute abundance, and variants taking into account the proportions of species, as relative abundance.

Data Analysis

The β -diversity of SMs was evaluated using the Whittaker index β_w and the Bray–Curtis distance I_{BC} . The former was calculated as the ratio of the total

number of species (γ) to the average number of species per sample (α) and interpreted as a measure of variation in species composition. Analyzing the dynamics of β -diversity over the entire pollution gradient, α -diversity was determined as the number of species recorded in each key plot over the year, and γ -diversity, as the total number of species in all key plots over the year. Analysis of β -diversity in time within a key plot was performed using the number of species recorded per year as α -diversity and the total number of species recorded over a given period as γ -diversity.

The Bray–Curtis distance characterizes differences between communities in both species composition and species abundance ratio, varying from 0 (communities are identical) to 1 (communities are absolutely different). Similarity between two “zero” samples was scored 0. β -Diversity in time within a plot was calculated as the average distance between samples from this plot taken over the test period, and that in the entire pollution gradient, as the average distance between samples from all key plots over the year.

The number of recorded species closely depends on the amount of material, while the Whittaker index may prove to be insensitive to sample size. Therefore, we calculated the indices of β -diversity that take into account only species composition: β_{-1} according to Routledge, β_{-2} according to Harrison, β_{-3} according to Williams, and “Czekanowski–Sørensen similarity index [29]. In our case, the results obtained with these metrics led to similar conclusions and were not included in this paper.

The dynamics of similarity between communities from different zones was analyzed by principal component analysis (PCA) based on the Bray–Curtis distance [30], with the effect of environmental factors on it being estimated by the PERMANOVA algorithm (9999 permutations) [31]. For this purpose, the initial data were grouped by 3-year intervals corresponding to cyclic changes in the abundance of dominant species (*Myodes glareolus* and *M. rutilus*, which accounted for 70–80% of the total SM abundance in each zone), thereby reducing the influence of interannual fluctuations on the structure of communities from different zones. The cycle of 1999–2001 was not included in calculations because of data incompleteness. The statistical significance of trends in the dynamics of β -diversity was estimated using general linear models (LM) with the year as an independent variable.

The existence of 3-year cycles in the abundance of SMs allowed us to arrange the values of similarity between communities into time series. Each value of the initial parameter in the additive model used in the study is the sum of three components: trend, periodic component, and random noise [30, 32]. Decomposition of the time series made it possible to analyze each of the three components separately and compare them with each other. Missing values were reconstructed

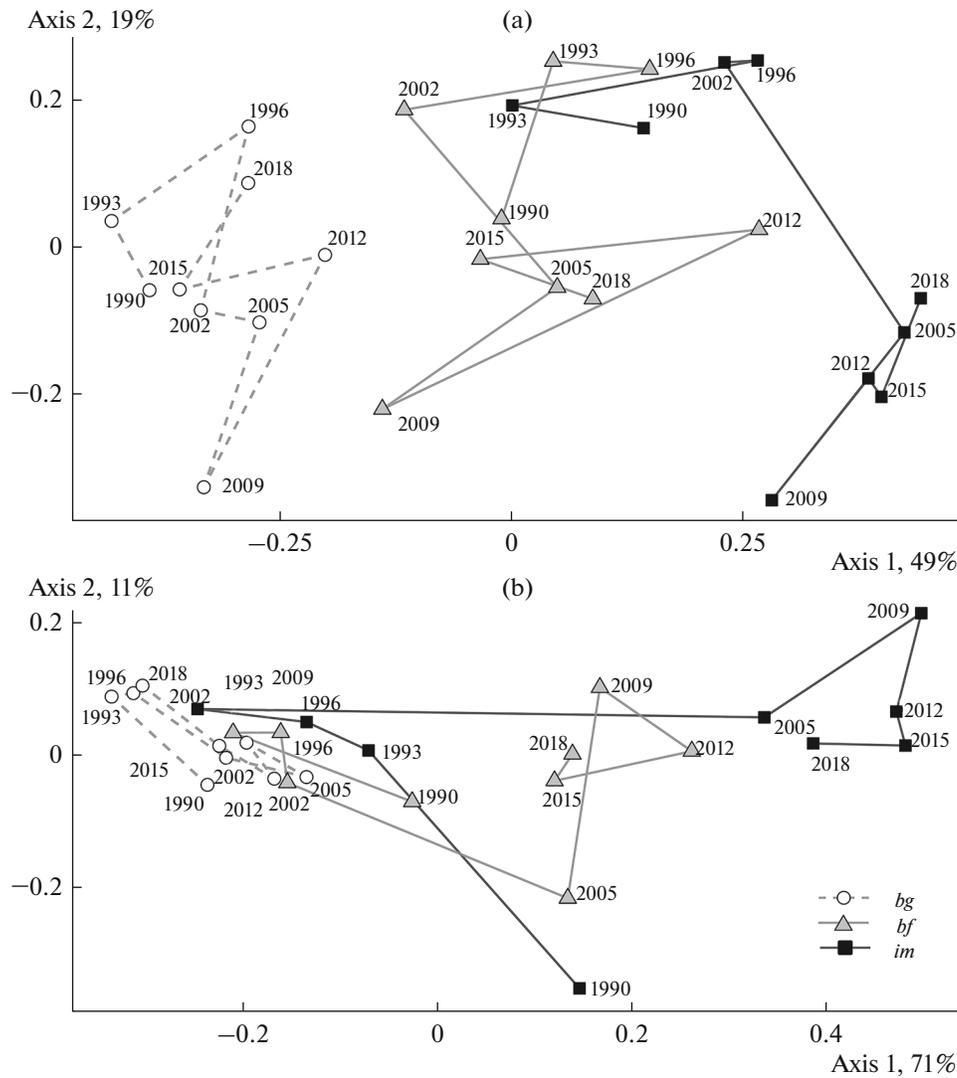


Fig. 1. Time ordination of small mammal communities from different pollution zones based on (a) the absolute abundance of species and (b) their proportions in communities. Zones: *bg*, background; *bf*, buffer; *im*, impact. The data are grouped by 3-year intervals, the starting year of each interval is indicated.

using the Kalman filtering algorithm [33] in the `zoo` package [34].

The results of statistical tests were considered significant at $p < 0.05$. Bootstrap confidence intervals for β_W and I_{BC} were computed based on 9999 iterations. Calculations and data visualization were performed in the R v. 4.0.3 environment [35] using software packages `ape` [36], `vegan` [37], and `ggplot2` [38]. The initial data and code are available at github.com/ANSozontov/betadiv_2020.

RESULTS

Long-Term Dynamics of Community Similarity

Throughout the 30-year observation period, the highest magnitude of difference was between the com-

munities of background and impact zones, with those of the buffer zone being intermediate between them (Fig. 1). Variation of the background community in time was higher in terms of absolute rather than relative abundance. Conversely, the impact community was characterized by consistently low values of absolute abundance, and higher variation was revealed in case of ordination by relative abundance (proportions of species). The community of the buffer zone occupied an intermediate position with respect to both topology in the space of principal coordinates and the magnitude of variation: it “tended” toward the background zone in terms of absolute abundance and to the impact zone in terms of relative abundance.

The spatial factor (pollution zone) and temporal factor (period of study) differently contributed to vari-

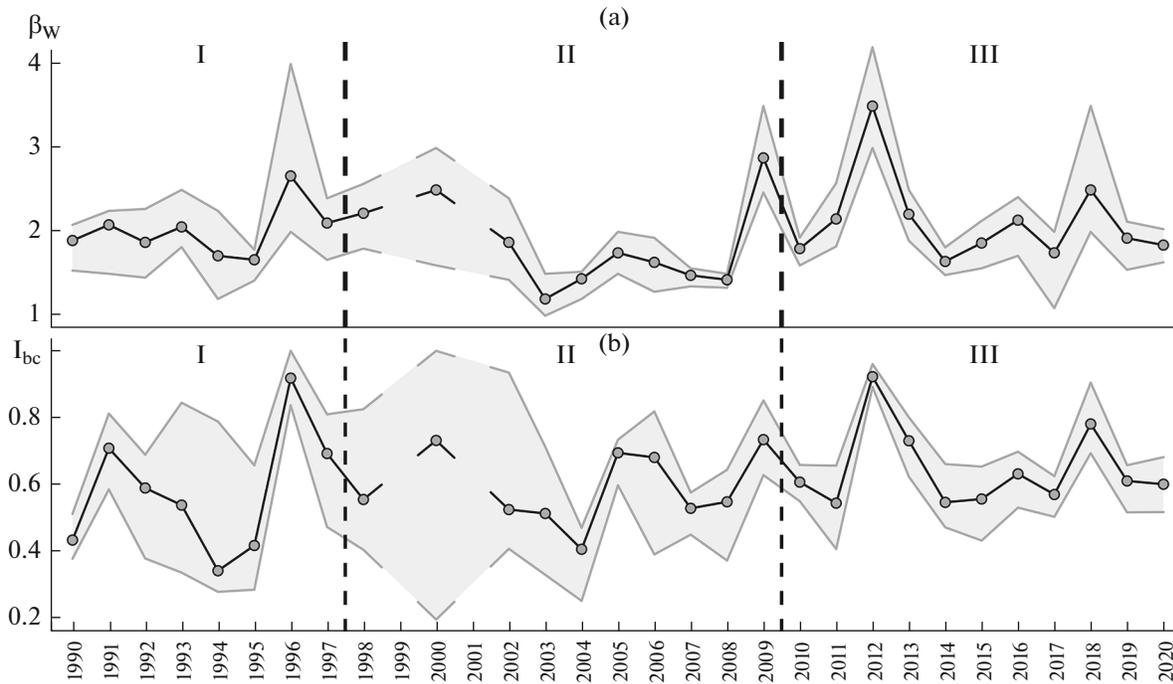


Fig. 2. Long-term dynamics of (a) β_W and (b) I_{BC} in small mammal communities over the entire pollution gradient. Vertical dashed lines mark the boundaries between the periods of (I) high, (II) reduced, and (III) almost terminated emissions. Data on years 1999 and 2001 are missing. Gray color indicates 95% confidence interval.

ation in the composition of SM communities, accounting for 24 and 9% of the total variance, respectively; the role of their interaction (9%) was also significant (Table 1). On the whole, the proportion of explained variance reached 42%.

Dynamics of β -diversity over the Entire Pollution Gradient

Parameters of β -diversity calculated for the pollution gradient based on annual data were variable, with β_W ranging from 1.20 to 3.50 and I_{BC} , from 0.35 to 0.92 (Fig. 2). No distinct temporal trends were reeled ($b = 0.003-0.004$, $p = 0.2-0.7$). As a rule, the highest values were recorded at the phase of population depression (1996, 2005, 2009, 2012, 2018), and the lowest

values, at the phase of population peak (1995, 2004, 2014, 2017).

β -Diversity in Time on the Scale of Key Plots

During the period of high emissions, the β_W index was found to increase slightly with a decrease in distance from the MUCS ($b = -0.35$, $p = 0.057$), but no directed changes were revealed after emissions were reduced (period II, $b = 0.21$, $p = 0.431$; period III, $b = -0.08$, $p = 0.655$) (Fig. 3a). Changes in I_{BC} were similar during all the three periods, with its values increasing as the MUCS was approached: in period I, $b = -0.15$, $p = 0.115$; in periods II and III $b = -0.10$ to -0.22 , $p = 0.001-0.005$ (Fig. 3b). The β -diversity of SM communities in the background zone remained at approximately the same level over 30 years, with β_W ranging from 1.83 to 2.06 and I_{BC} from 0.52 to 0.67. These parameters in the buffer area varied more distinctly: β_W from 1.72 to 2.10 and I_{BC} from 0.51 to 0.68. The β -diversity in the impact zone reached the highest level: $\beta_W = 1.00-2.52$, $I_{BC} = 0.62-1.00$.

Table 1. Results of PERMANOVA based on the proportions of species

Factor of variance	df	F.Model	R ²	p
Zone	2	14.1	0.24	0.0001
Period	2	5.1	0.09	0.0005
Zone × period	4	2.6	0.09	0.0062
Residual variance	69		0.58	

Designations: df, number of degrees of freedom; F.Model, F-statistics value; R², coefficient of determination; p, significance level.

Dynamics of Components of Community Similarity

Figure 4 shows decomposition of the time series of Bray-Curtis distances (1) into components such as trend line (2), 3-year cycle changes (3), and residue (4). All pairwise comparisons provided evidence for the divergence of communities increasing over time

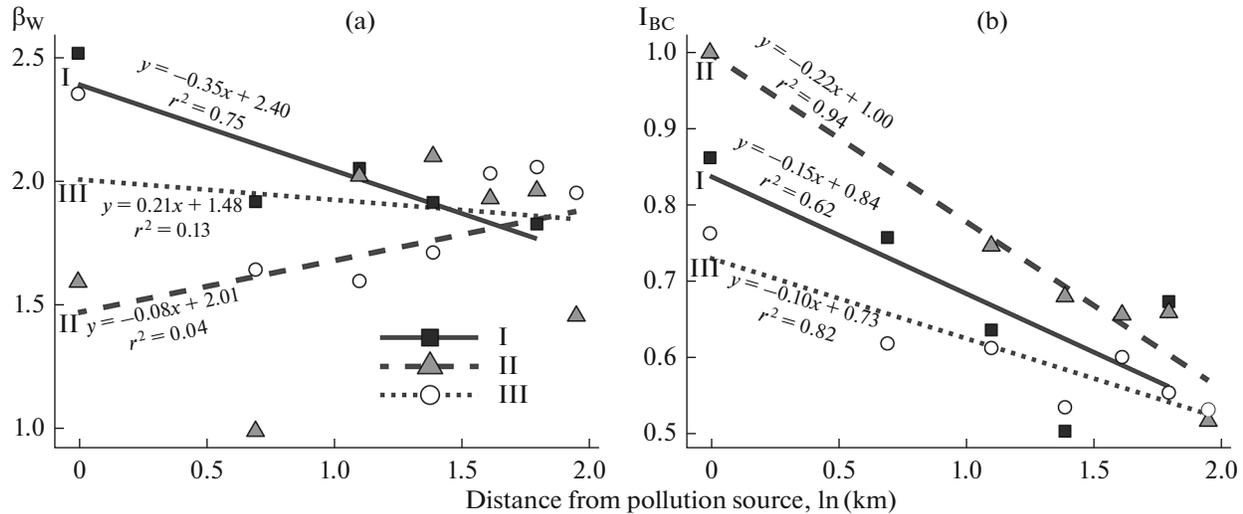


Fig. 3. Time variation of (a) β_W and (b) I_{BC} within key plots in the periods of (I) high, (II) reduced, and (III) almost terminated emissions. Different markers show the values of parameters for each plot and indicate corresponding regression lines.

(Table 3). The most distinct changes were recorded for the distance between the background and impact zones. The initial stage of emission reduction coincided with an abrupt drop in similarity between these communities, which subsequently stabilized at a higher level and has remained so since then. Similarity between the communities of buffer and impact zones showed significant interannual fluctuation during the entire 30-year period, while similarity between the communities of background and buffer zones remained at a high level. In all pairwise comparisons, the most variance in similarity was accounted for by the contribution of trend (89–99%) and random factors (about 5%). The contribution of cyclic component was minor and did not exceed 4% in most cases.

DISCUSSION

How Does Pollution Affect β -diversity of SM Communities?

There is no consensus on this question: on the one hand, the pattern and direction of changes in β -diversity depend on a number of factors; on the other hand, quantitative data on the β -diversity of local communities of the terrestrial vertebrates under industrial pollution are very scarce. By analogy with other types of anthropogenic impact, both monotonic (increase/decrease) and non-linear (U- or bell-shaped) changes in β -diversity along the pollution gradient may be expected. Dominance of generalist species and elimination of rare and specialized species combined with the ability of most species for effective dispersal will result in homogenization of communities, i.e., to a reduction in β -diversity. For example, such changes have been observed in SM communities inhabiting areas of tropical forests transformed by felling operations [9], and also in spider and

hoverfly communities from agrocenoses with different pesticide loads [10]. Conversely, disturbances in the metapopulation dynamics of certain species combined with high degree of habitat fragmentation create prerequisites for the formation of unique communities in certain areas, i.e., for an increase in β -diversity. For example, this is the case with mammal communities inhabiting areas with different levels of economic development such as agrolandscapes [14], the vicinities of industrial facilities [15], or felling areas in forests [11]. In some cases, nonlinear changes in β -diversity were observed: upon reduction in the number of suitable habitats was, similar communities initially began to differ from each other, but then similarity between them has increased again [23]. Such a pattern of change in β -diversity has been observed in the communities of true bugs and plants [10]. Compared to other taxonomic groups, small mammal communities often prove to be more tolerant to disturbances in the environment. For example, the loss or replacement of species were observed in bird and invertebrate communities under the impact of agricultural intensification, whereas the species composition of SM communities remained unchanged in the gradient of load [12, 13].

The results of our studies showed that the β -diversity of SM communities gradually increased as the MUCS was approached (Fig. 3). This increase was most distinct during the initial period (I), when industrial emissions from this source greatly exceeded the present level (total emissions, by a factor of 50; emissions of SO_2 , Cu, and Pb, by factors of 80, 3000, and 9, respectively) [39], and disturbances of the environment in its vicinity were most severe [40]. Variation in species composition (β_W) was especially sensitive to pollution: the values of this index in the impact community exceeded the back-

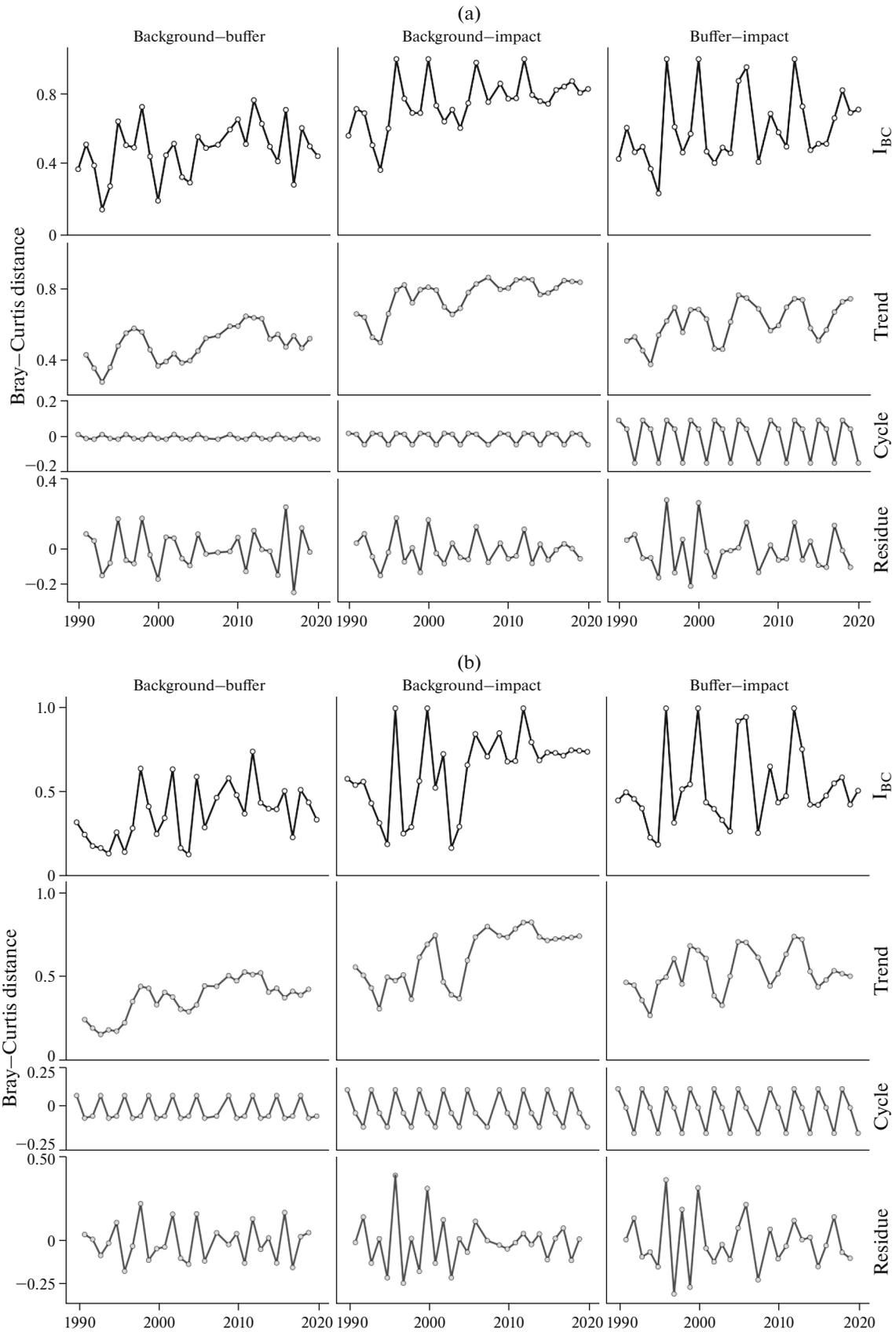


Fig. 4. Dynamics of Bray–Curtis distance (I_{BC}) between communities of different pollution zones and decomposition of this series into components with account of (a) the abundance of species and (b) their proportions in communities,

Table 2. Results of regression analysis of trends in the dynamics of community β -diversity

Zones compared	b_1	t	p
With account of the abundance of species			
Background–buffer	0.006	3.28	0.003
Background–impact	0.008	4.77	<0.0001
Buffer–impact	0.006	2.81	0.009
With account of the proportions of species			
Background–buffer	0.009	5.21	<0.0001
Background–impact	0.013	5.36	<0.0001
Buffer –impact	0.004	1.54	0.135

Designations: b_1 , regression coefficient; t , t -test value; p , significance level.

ground level. This effect was less distinct with respect to variation in community composition and species abundance ratio (I_{BC}) during period I but was also observed during periods II and III (Fig. 3).

The most specific SM community was formed in the plots bordering on a technogenic desert at 1–1.5 km from the MUCS. Strongly fragmented habitats were hardly suitable for the survival of SMs during the complete life cycle. Such depopulated fragments were periodically (during the snow-free period) colonized by single individuals of various murine rodent and small insectivore species, with resources available in each fragment being sufficient for only a limited set of species (individuals). In addition to typical forest species, there also occurred synanthropic species (*Mus musculus*) and species characteristic of open areas (*Apodemus agrarius*, *Microtus arvalis*), and the γ -diversity of SMs could therefore be considerable at extremely low parameters of α -diversity and species abundance [28]. As a result, the SM community in close proximity to the MUCS in the period of high emissions was characterized by the highest variability. Parameters of the SM community of the buffer zone (β_w , I_{BC}) were highly similar to those in the community of the adjacent impact plot (2 km), which may be explained by comparable habitat conditions for the animals [28] and territorial proximity between these communities, which facilitated species exchange between them [41]. The community of the background zone was distinguished by the presence of a superdominant (*M. glareolus*), with other species being few in numbers and occurring in catches irregularly, which accounted for minimal changes in the β -diversity of this community in the period of high emissions.

Thus, the results of our study support the hypothesis that the β -diversity of SM communities increases with an increase in technogenic load during the period of high emissions.

How Does β -diversity of SM Communities Change after Reduction of Emissions?

It is logical to expect that reduction of industrial emissions will initiate the processes of natural recovery of forest phytocenoses, with consequent improvements in the quality and quantity of habitats for different SM species. These changes in the environment will probably lead to increasing similarity between the communities of background and polluted areas. As shown in the first part of this study [28], the rate of such changes is not uniform: positive shifts in the structure of SM communities in the buffer zone are more distinct than in impact plots and involve different trophic groups.

Unexpectedly, similarity between the communities of polluted and background zones has not increased after reduction of emissions. Conversely, all pairwise comparisons provided evidence for their significant divergence (Fig. 4, Table 2). Since parameters β_w and I_{BC} in the community of the buffer zone varied insignificantly during the 30-year period, it appears that the decrease in its similarity with the communities of buffer and impact zones is due to structural rearrangements occurring in polluted territories.

The loss of rare species, the replacement of dominants, and changes in the proportions of individual species may lead to homogenization of communities. All these events have occurred in the impact community during the past two decades [28]. The decrease in technogenic load due to reduction of emissions was accompanied by the replacement of dominant species, with *M. glareolus* being substituted by *M. rutilus* and *Sorex araneus* by *caecutiens*. These changes occurred abruptly and an effect on the proportions (of both species) and the abundance of species (*Sx. caecutiens*) in the community. Moreover, the abundance of rodent species (except *M. rutilus*) decreased by the end of observations. This may be due to gradual improvement of food resources for small insectivores [42] in the absence of positive shifts in the composition and abundance of diet for phytophages [43]. The effect of cardinal changes that occurred in 2002–2007 proved to be so strong that the community of the impact zone before and after reduction of emissions is represented in the plot by two isolated clusters (Fig. 1a). These changes have resulted in segregation of this community, which increases over time. It is noteworthy that, after an upswing that coincided with the onset of emission reduction, dissimilarity between the background and impact communities has stabilized at a new, higher level (Fig. 4).

Structural rearrangements in the buffer community involved an increase in the number of dominant species (from two to four) accompanied by an equivalent increase in their proportions (except for *M. glareolus*) and abundance, with these positive trends being observed in different trophic groups: zoophages, phytophages, and granivores [28]. In our opinion, these

changes are a consequence of gradual recovery of the environment, including the abundance and diversity of food resources, which provided for increasing dissimilarity between the buffer community and other communities (Fig. 4).

Thus, the hypothesis that similarity between communities of buffer and polluted zones increases after reduction of emissions is not confirmed. On the contrary, our results provide evidence for the divergence of background, buffer, and impact communities.

Which Communities Are More Variable, Background or Impact?

The results presented above show that, compared to communities of the buffer and impact zones, background communities are less variable in time, which follows from the minimum level of changes in its structure (Fig. 1) and low variation in β_W and I_{BC} indices over the 30-year observation period. Such changes in the buffer and, especially, impact communities had wide amplitude and showed more distinct trends, up to replacement of the dominant complex. The variation range of β_W in the background buffer zones was 10 and 20%, while that in the impact zone reached 250%, overlapping both buffer and background values. A similar picture was observed for I_{BC} : 30% in the background and buffer zones vs. up to 60% in the impact zone. In our opinion, such major differences may be explained by living conditions for animals in zones with different pollution levels: the more unstable the environment, the higher the variability of communities. Thus, the hypothesis that background communities are less variable in time is fully confirmed.

Our results also allow the conclusion that the initial level of pollution has played a key role in the formation of SM community structure (see Table. 1): this spatial factor still accounts for about 25% of variability even after two decades since the onset of emission reduction. The contribution of temporal factor (period of study) and the interaction of factors is significantly lower (9% for each of them).

The effect of pollution level on the composition and abundance of SMs in the environs of the MUCS is mediated through the quality of habitats and the diversity and abundance of resources. Our results well agree with published data [44–46]. We consider that the direct impact of pollution leading to selective elimination of individuals is not a significant factor for murine rodents and small insectivores due to their ecological flexibility and high mobility. The main mechanism of response allowing these animals to minimize the adverse effect of chronic pollution involves the uneven distribution of individuals in microareas with most suitable conditions for a given species [15, 47] in combination with high migration mobility of the animals [41] and their selective feeding on the least contaminated food objects [48–50].

CONCLUSIONS

We are not aware of long-term studies on SM communities in the gradient of industrial pollution in which the results of annual censuses have been used to compare the dynamics of species composition before, during, and after reduction of emissions. Our results confirm the hypothesis that the β -diversity of SM communities increases along the pollution gradient under increasing technogenic load in the period of high emissions: the β -diversity was found to increase regularly as the polluter was approached. Furthermore, the minimum similarity was observed between communities of the background and impact zones, while the buffer community occupied an intermediate position, tending toward the impact community with respect to species composition and to the background community with respect to the abundance of species. The initial level of pollution played a key role in the formation of SM community structure, with its contribution reaching 25%. Technogenic pollution led to a significant increase in the variability of species composition and, to a lesser extent, in the species abundance ratio. The variability of communities was increasing with an increase in instability of the environment near the MUCS.

The hypothesis of structural convergence between the background, buffer, and impact communities of SMs after multifold reduction of emissions was not confirmed: all pairwise comparisons provided evidence for their increasing divergence over time. The expected improvements in the quality of habitats in polluted areas, primarily in their foraging and protective properties combined with increasing ecological capacity and decreasing fragmentation, will create prerequisites for an increase in the α -diversity of communities and abundance of individual species. These factors should have a significant effect on similarity between the above communities. It appears that a 20-year period is insufficient for the evident recovery of SM communities in heavily polluted areas.

ACKNOWLEDGMENTS

The authors are grateful to Yu.L. Sumorokov, E.Yu. Sumorokova, S.Yu. Sumorokov, and A.A. Gerasimov for their help in field studies and to E.L. Vorobeichik and anonymous reviewers for their constructive comments on the manuscript.

FUNDING

Data analysis of preparation of the manuscript were performed under a state contract with the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.

COMPLIANCE WITH ETHICAL STANDARDS

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

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Translated by N. Gorgolyuk