

Role of Environmental Heterogeneity in the Species Distribution of Vascular Plants in Periods of High and Low Emissions from a Copper Smelter

M. R. Trubina^{a, *} and D. V. Nesterkova^a

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

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

Received June 7, 2023; revised June 20, 2023; accepted June 22, 2023

Abstract—Environmental heterogeneity can significantly modify the rate of species extinction with an increase in anthropogenic load and the rate of recolonization of disturbed territories after a decrease in load, but this issue is poorly understood. The distribution of 14 species of the herb–dwarf shrub layer of forests on an area of 1734 km² in two natural regions of the eastern and western macroslope of the Urals during periods of high (1995–1998) and low (2014–2016) emissions from the Middle Ural Copper Smelter has been analyzed. With an increase or decrease in load, the pattern of dynamics and the magnitude responses are species-specific and significantly depend on habitat conditions, but the main contribution to the spatiotemporal dynamics of species affects the load level. During the period of high emissions, the environmental heterogeneity slows down the decrease in area of species distribution along a load gradient, but the distribution decreases under very heavy pollution, regardless of habitats or species. After the reduction of emissions, the distribution of most species in the heavily polluted areas has changed little for 19 years; the elimination and reduction in the distribution of the most sensitive species continues. Positive shifts have been revealed mainly in less polluted areas; the rates of recolonization vary in different habitats. Depending on habitat conditions, the species response to an increase or decrease in pressure can be “fast” (relatively high rates of change) or “slow” (lower rates of change and even a continued decline in distribution, despite reductions in pressure).

Keywords: extinction, fragmentation, recolonization, dispersal, recovery, pollution, heavy metals, sulphur dioxide

DOI: 10.1134/S1995425524010141

INTRODUCTION

The spatiotemporal dynamics of species under changing environmental conditions is one of the central topics of modern ecology. Climate change and anthropogenic impacts, including environmental pollution, are among the main reasons for the currently observed changes in the composition of communities and a decrease in their diversity (Pereira et al., 2012; Di Marco et al., 2019; Sánchez-Bayo and Wyckhuys, 2021; Kharuk et al., 2023). Questions regarding the rate and pattern of biota degradation under different types and levels of anthropogenic impact and the ability of biota to self-recovery after a reduction/cessation of impact, as well as identifying factors that significantly modify the rate of species extinction and recolonization of disturbed areas, are especially relevant.

The presence of a time lag in the extinction or dispersal of species when environmental conditions change has been shown in a number of studies (Kolk and Naaf, 2015; Naaf and Kolk, 2015; Ash et al., 2017; Trubina, 2020). In addition to the inherent characteristics of species, factors influencing these processes include the heterogeneity of environmental conditions

(Hylander and Ehrlén, 2013; Alexander et al., 2018). Different magnitudes of response of different communities when pollutants enter (Trubina, 2002; Per-ring et al., 2018; Hedwall et al., 2021) and after load reduction (Rose et al., 2016) indirectly indicate the significant role of habitat conditions in species dynamics. However, the question of the influence of habitat conditions on the rate of extinction of local populations of plant species during the long-term input of pollutants and the rate of recolonization of contaminated areas by species after a reduction in emissions remains open.

The purpose of this work is to assess the influence of habitat conditions on the distribution of vascular plant species during periods of high and low emissions from a copper smelter. In this work, we focused on species of the herb–dwarf shrub layer of forests. The attached lifestyle and low rate of dispersal of most of these species (Baeten et al., 2009; Brunet et al., 2021) make them extremely vulnerable to loss, fragmentation, and changes in habitat quality (Nordén et al., 2014; Haddad et al., 2015; Paal et al., 2017; Trubina, 2020). In this work we tested the following hypothesis:

habitat conditions have a significant influence on the distribution of species upon the entry and reduction of pollutants, but the main contribution to the spatiotemporal dynamics of species is made by the level of load.

MATERIALS AND METHODS

The studies were carried out in the vicinity of the Middle Ural copper smelter, located on the outskirts of the city of Revda, 50 km west of Yekaterinburg. Emissions are mainly gaseous compounds of sulfur, fluorine, and nitrogen, as well as dust particles with sorbed heavy metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). The enterprise has been operating since 1940. In 1980, its emissions were 225000, in 1990—148000, in 1994—96000, in 2000—63000, in 2004—28000, and (after a radical reconstruction of the enterprise) in 2010 3000—5000 t of pollutants/year (Vorobeichik and Kaygorodova, 2017).

According to physical–geographical zoning (Kapu-stin, 2009), near the city of Revda there is a boundary between two natural regions: the low mountains of the Middle Urals and the eastern foothills of the Urals, which differ in thermal and water availability. To the west of this border, fir–spruce forests with a high participation of nemoral species are predominantly widespread and, to the east, pine forests with a high participation of boreal species, which is due to less precipitation and a more continental climate on the eastern macroslope (Igoshina, 1964). According to the soil–geographical zoning (Gafurov, 2008), the territory under consideration belongs mainly to the Pervouralsky (eastern sector) and Kuzino-Polevsky (western sector) districts of the Middle Ural southern taiga soil province. The Pervouralsky district as a whole is characterized by a predominance of soddy–podzolic soils, while the Kuzino-Polevsky district is characterized by a predominance of mountain forest brown soils. Mapping of the territory based on field diagnostics of the mechanical composition of mineral horizons at a depth of 20–30 cm also showed a clear differentiation of soils in the western and eastern sectors (Vorobeichik and Nesterkova, 2015).

To analyze the distribution of species, we used the results of descriptions of vegetation cover carried out during the period of high (1995–1998) and low (2014–2016) plant emissions. Aspects concerning the dynamics of species richness of mosses and vascular plants with different modes of distribution of generative diaspores have been discussed earlier (Trubina, 2020; Trubina and Dyachenko, 2020). In each of the periods, descriptions were carried out on 110 sample plots (SPs) measuring 25 × 25 m located in forest phytocenoses at a distance of at least 1 km from each other around the smelter within an area of 1734 km². The sites differed in landscape type (eluvial, transitional, and accumulative), soil type (gray forest, brown mountain forest, and soddy–podzolic), and vegetation (birch, pine–birch, pine, and spruce–fir forests

of various associations). The criteria for selecting SP were the absence of fresh fires and severe anthropogenic disturbances not associated with pollution, distance from highways of at least 100 m, and the age of edificators of the tree layer of at least 80 years. The locations of the SPs in the first and second periods could be slightly different, since in the first period the SP positions were recorded manually on a map at a scale of 1 : 100000.

To assess the toxic load, we used the toxicity index, which characterizes the average excess of the regional background for acid-soluble forms of four metals (Cu, Cd, Pb, and Zn) in the forest litter (Vorobeichik, 2003). The load index varied from 2.3 to 132.1 arb. units. During analysis, the gradient was divided into five pollution zones providing a similar (21–23) number of SPs in each one: (1) very strong (40.0–132.1), (2) strong (16.7–37.4), (3) moderate (7.0–16.6), (4) weak (4.4–6.9), and (5) background (2.3–4.35). Within the same pollution zones, monitoring of epiphytic lichens (Mikhailova, 2022) and mosses (Trubina and Dyachenko, 2020) is carried out. The average load indices in the same zone of different sectors did not differ.

The areas of pollution zones and species distribution were calculated in QGIS 3.16.5. The local coordinate system was used: MSK66, zone 1. The inverse square method was used for interpolation. A map of the work area with the boundaries of contamination zones and the location of the SPs is shown in Fig. 1. The species distribution area for each load zone and for each sector was calculated separately. When calculating areas, the areas of the 11 largest reservoirs were subtracted (total area 50.39 km²). Due to differences in the area of pollution zones, the original data on the area of distribution of species were recalculated into the relative area of distribution (Sr).

A preliminary analysis of the data showed the presence of significant differences in the distribution of most species in the background areas of the eastern and western sectors, which is quite expected given the location of the sectors in different natural areas. To minimize the contribution of the initial spatial unevenness of species distribution, testing of the hypothesis was carried out for species that have a high (more than 55%) and nearby distribution area in the background territories of both sectors. Only 14 species (*Angelica sylvestris* L., *Betonica officinalis* L., *Calamagrostis arundinacea* (L.) Roth, *Geranium sylvaticum* L., *Fragaria vesca* L., *Lathyrus vernus* (L.) Bernh., *Maianthemum bifolium* (L.) FW Schmidt, *Melampyrum pratense* L., *Pyrola rotundifolia* L., *Pulmonaria mollis* L., *Rubus saxatilis* L., *Thalictrum minus* L., *Trientalis europaea* L., and *Veronica chamaedrys* L.) meet this requirement and were included in the analysis.

To compare changes in Sr of species in different load zones in different sectors and dynamics over time, the Wilcoxon test was used to determine the level of significance of differences using the Monte Carlo method (9999 permutations). The contribution of fac-

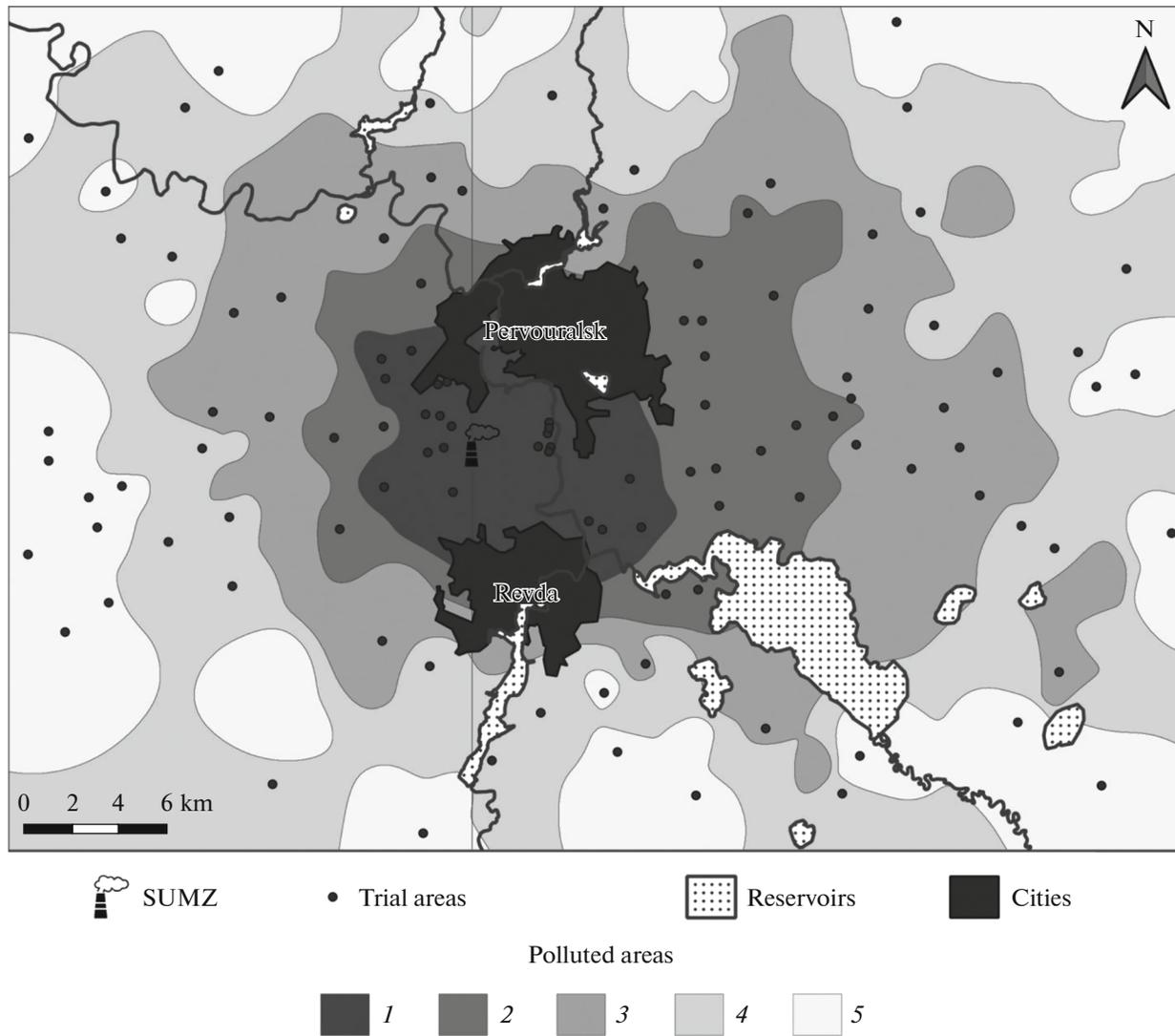


Fig. 1. Map of the study area with the boundaries of pollution zones.

tors (time, sector, and load zone) to the dynamics of Sr in contaminated areas was assessed using the analysis of variance components. To determine the significance of changes in the Sr of specific species, we calculated the standard deviation (σ) during the first observation period in the background areas of the eastern and western sectors, as well as in the areas of background and weak pollution in each sector. For the background territories of the sectors, this value was 0.077, in the western sector it was 0.076, and in the eastern sector it was 0.078. Changes $Sr \geq 0.16$ (maximum rounded value 2σ) were considered statistically significant. In absolute terms, this corresponded to 270 km². Data analysis was performed in the Statistica 8.0 and Past 4.0 package.

RESULTS

A decrease in the Sr of species along the load gradient during the period of high emissions was noted in all

species, regardless of the sector under consideration (Table 1), but the magnitude and pattern of the response of species to the increase in load varied.

In the eastern sector, a significant decrease in Sr in zone 3 was noted in *Angelica sylvestris* and *Pulmonaria mollis*, in zone 2 in seven species, and in five species in zone 1 only. *Angelica sylvestris* and *Melampyrum pratense* disappeared in zone 1; close to zero values of Sr were revealed in *Pulmonaria mollis*, *Trientalis europaea*, and *Veronica chamaedrys*. Relatively high Sr values (more than 0.2) in zone 1 in this sector were retained only in *Calamagrostis arundinacea* and *Geranium sylvaticum*.

In the western sector, a decrease in Sr in most species was observed only in zone 1. In zone 1, *Melampyrum pratense* disappeared, and close to zero values of Sr were revealed in *Veronica chamaedrys*. Six out of 14 species preserved a value of Sr more than 0.2 in zone 1 in this sector. In some species (*Maianthemum*

Table 1. Relative distribution area (Sr) of species in the first (1995–1997, values above the line) and second (2014–2016, values below the line) observation period

Species	Eastern sector					Western sector					Entire territory
	1 (79.7)	2 (140.4)	3 (233.7)	4 (331.0)	5 (217.4)	1 (38.1)	2 (47.8)	3 (134.6)	4 (269.3)	5 (191.7)	
	Pollution zone (area without large bodies of water, km ²)										
<i>Angelica sylvestris</i>	0/<0.01	0.08/0.26	0.28/0.58	0.57/0.62	0.58/0.71	0.08/0.06	0.30/0.23	0.15/0.07	0.41/0.34	0.65/0.60	1683.9
<i>Betonica officinalis</i>	0.01/0	0.30/0.30	0.69/0.80	0.53/0.61	0.70/0.71	0.16/0	0.61/0.13	0.57/0.60	0.54/0.48	0.76/0.66	0.39/0.45
<i>Calamagrostis arundinacea</i>	0.25/0.66	0.81/1	0.95/1	0.99/1	0.94/1	0.59/0.81	0.77/1	0.97/0.75	0.96/0.94	0.83/1	0.55/0.55
<i>Fragaria vesca</i>	0.02/0.01	0.42/0.31	0.63/0.84	0.64/0.97	0.73/0.99	0.36/0.16	0.64/0.77	0.81/1	0.80/1	0.87/1	0.91/0.84
<i>Geranium sylvaticum</i>	0.38/0.29	0.81/0.83	0.97/0.99	0.97/1	1/1	0.33/0.34	0.96/0.92	0.93/1	0.97/0.85	0.82/0.85	0.66/0.84
<i>Lathyrus vernus</i>	0.16/0.19	0.61/0.71	0.85/0.99	0.98/1	1/1	0.16/0.31	0.81/0.73	0.95/0.91	0.86/0.77	0.80/0.93	0.90/0.89
<i>Maianthemum bifolium</i>	0.12/0.23	0.83/0.80	0.84/0.97	0.83/1	0.83/1	0.40/0.43	0.97/0.92	0.96/1	0.80/1	0.54/1	0.83/0.86
<i>Melampyrum pratense</i>	0/0.05	0.27/0.52	0.64/0.98	0.65/0.87	0.82/0.87	0/0	0.22/0.01	0.58/0.37	0.56/0.40	0.62/0.77	0.77/0.93
<i>Pulmonaria mollis</i>	<0.01/0	0.21/0.13	0.37/0.59	0.66/0.91	0.61/0.86	0.07/0	0.73/0.27	0.63/0.62	0.56/0.71	0.80/0.81	0.56/0.65
<i>Pyrola rotundifolia</i>	0.18/<0.01	0.71/0.82	0.58/0.71	0.77/0.73	0.61/0.63	0.31/0.07	0.83/0.59	0.68/0.53	0.76/0.51	0.62/0.34	0.65/0.57
<i>Rubus saxatilis</i>	0.07/0.32	0.79/0.87	0.94/0.99	0.93/1	0.86/1	0.31/0.46	0.84/0.92	0.79/1	0.76/0.85	0.70/0.94	0.79/0.91
<i>Thalictrum minus</i>	0.05/0.05	0.35/0.34	0.52/0.57	0.73/0.82	0.68/0.77	0.09/0.14	0.53/0.31	0.85/0.87	0.72/0.68	0.59/0.87	0.60/0.66
<i>Trientalis europaea</i>	<0.01/<0.01	0.25/0.42	0.80/0.88	0.86/0.97	0.66/0.93	0.05/0.02	0.52/0.38	0.73/0.97	0.78/0.94	0.57/0.97	0.65/0.82
<i>Veronica chamaedrys</i>	<0.01/0	0.33/0.30	0.83/0.87	0.54/0.83	0.79/0.94	<0.01/0	0.44/0.07	0.70/0.35	0.67/0.74	0.59/0.91	0.59/0.68

bifolium, *Trientalis europaea*, *Thalictrum minus*, and *Pyrola rotundifolia*) at intermediate load levels, higher Sr values were noted than in zone 5.

The smallest changes in distribution with increasing load levels in both sectors were found in *Calamagrostis arundinacea*, *Geranium sylvaticum*, *Lathyrus vernus*, *Maianthemum bifolium*, and *Rubus saxatilis*.

The pattern and magnitude of a species' responses to emission reductions varied across pressure zones and sectors (Table 1). In zone 1 of both sectors, the Sr of most species did not change; three species with low Sr in the first observation period (*Betonica officinalis*, *Pulmonaria mollis*, and *Veronica chamaedrys*) disappeared; the distribution continued to decline in *Pyrola rotundifolia*. A significant increase in the eastern sector was noted in *Calamagrostis arundinacea* and *Rubus saxatilis*, but, in the western sector, it only occurred in the first species. However, in zones 2–4, species responses to emission reductions varied across sectors. For example, a significant decrease in zones 2 and 3 of the western sector was noted in four and three species, respectively, and in none in the eastern sector. An increase in Sr was observed in *Melampyrum pratense* and *Angelica sylvestris* in the eastern sector in these areas; however, in the western sector, Sr of the first one decreased, while that of the second remained at the same level. Maps of species distributions during periods of high and low emissions are shown in Figs. 2–4.

During the period of high emissions, a significant decrease along the load gradient of Sr species in general in the eastern sector was observed in zone 2 ($z = 3.05$, $P < 0.001$) (Fig. 5a) and, in the western sector, in zone 1 ($z = 3.30$, $P < 0.001$) (Fig. 5b). The index values in the western sector, when compared to the eastern sector, were higher in zones 1 and 2 ($z = 2.34$, $P < 0.017$; $z = 3.05$, $P < 0.001$). The contribution of the contamination zone was 61.4% ($F_{4,130} = 22.81$; $P < 0.005$), sector \times zone interaction was 3.1% ($F_{4,130} = 2.23$; $P < 0.070$), and unaccounted factors were 35.5.

After emissions were reduced, the increase in Sr of species in the eastern sector were revealed in zones 3–5 and in the western sector only in zone 5. In zone 2 of the western sector, there was a significant decrease in Sr. The contribution of load zones in the dynamics of species in contaminated areas (zones 1–4) amounted to 57.4% ($F_{3,208} = 31.05$; $P < 0.004$), period \times sector interaction was 2.8% ($F_{1,208} = 15.18$; $P < 0.030$), sector \times zone interaction was 2.7% ($F_{3,208} = 9.09$; $P < 0.051$), period \times sector \times zone interaction was 0.4%, and unaccounted factors were 36.7%. When zone 5 was included in the analysis, the results were similar: the proportion of variance associated with load zone was 58.2%, with the time \times sector interaction 1.7%, with the sector \times zone interaction 2.3%, and with the period \times sector \times zone interaction 0.8%; unaccounted for factors were 37%.

The area of uninhabited territory as a whole during the period of high emissions varied from 158 (*Calama-*

grostis arundinacea) to 1020 km² (*Angelica sylvestris*) (Fig. 6a). After reducing emissions, the distribution area of most species changed little (Fig. 6b); a statistically significant increase in distribution was noted in *Fragaria vesca*, *Maianthemum bifolium*, and *Trientalis europaea*.

DISCUSSION

Spread during high emission periods. The different responses of species to impacts are a known fact, and the data from our work are consistent with it. Reductions in area distribution were observed across different species at different stress levels, and some species in the western sector even showed increases in distribution at intermediate stress levels. The magnitude of the response also varied: the distribution area within the same sector for different species in very heavily polluted areas varied tens of times (see Table 1). At the same time, the composition of species sensitive and weakly sensitive to pollution in the sectors was exactly the same; only the magnitude of the response to the load differed. The species-specific response partially explains the high proportion of residual variance when assessing the influence of the load zone and sector on the dynamics of the species as a whole.

An analysis of the reasons for the species-specificity of the reaction was not part of the scope of the work, but it is important to note the following. A higher tolerance of widespread species to changes in habitat conditions has been shown in a number of works (Trubina, 1992; Chichorro et al., 2019; FINDERUP Nielsen et al., 2019; Staude et al., 2020). The data from our work are consistent with them to a certain extent. Elimination and a decrease in the distribution area to almost zero values, as a rule, were observed only among species with Sr less than 0.8 (see Table 1). At the same time, none of these species is included in the category of rare species for the territory under consideration: their initial Sr was higher than 0.57, and *Melampyrum pratense* was 0.82. This indicates that the probability of species extinction due to long-term pollution can be determined not only by the width of the ecological niche, but also by the sensitivity of the species to ongoing changes in conditions. However, this issue requires studies using more extensive material.

The distribution area in different sectors at high load levels for the same species could differ several times (see Table 1) and, for species as a whole, twice (see Fig. 5). One possible reason for the slower rate of decline in species distribution in the western sector may be differences in the buffering capacity of the prevailing soils. Mountain forest brown soils, widespread in the western sector, in comparison with the soddy-podzolic soils prevailing in the eastern sector, are characterized by a higher content of carbon, nitrogen, exchangeable bases, and the proportion of clay (Gafurov, 2008). When heavy metals enter the environment,

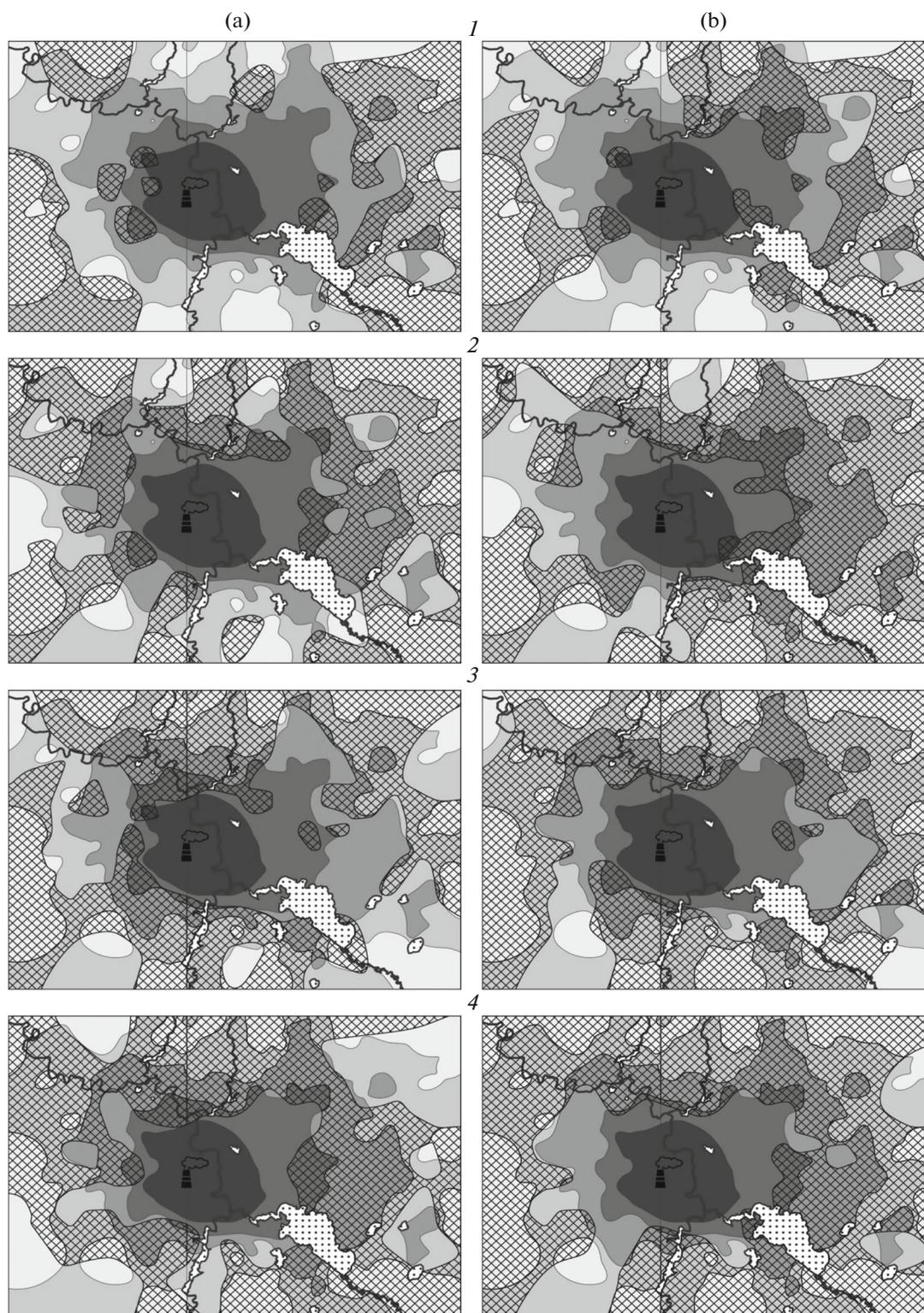


Fig. 2. Distribution of *Angelica sylvestris* (1), *Melampyrum pratense* (2), *Pulmonaria mollis* (3), and *Veronica chamaedrys* (4) in 1995–1997 (a) and 2014–2016 (b). Here and in Figs 3, 4, the territory inhabited by species is shaded.

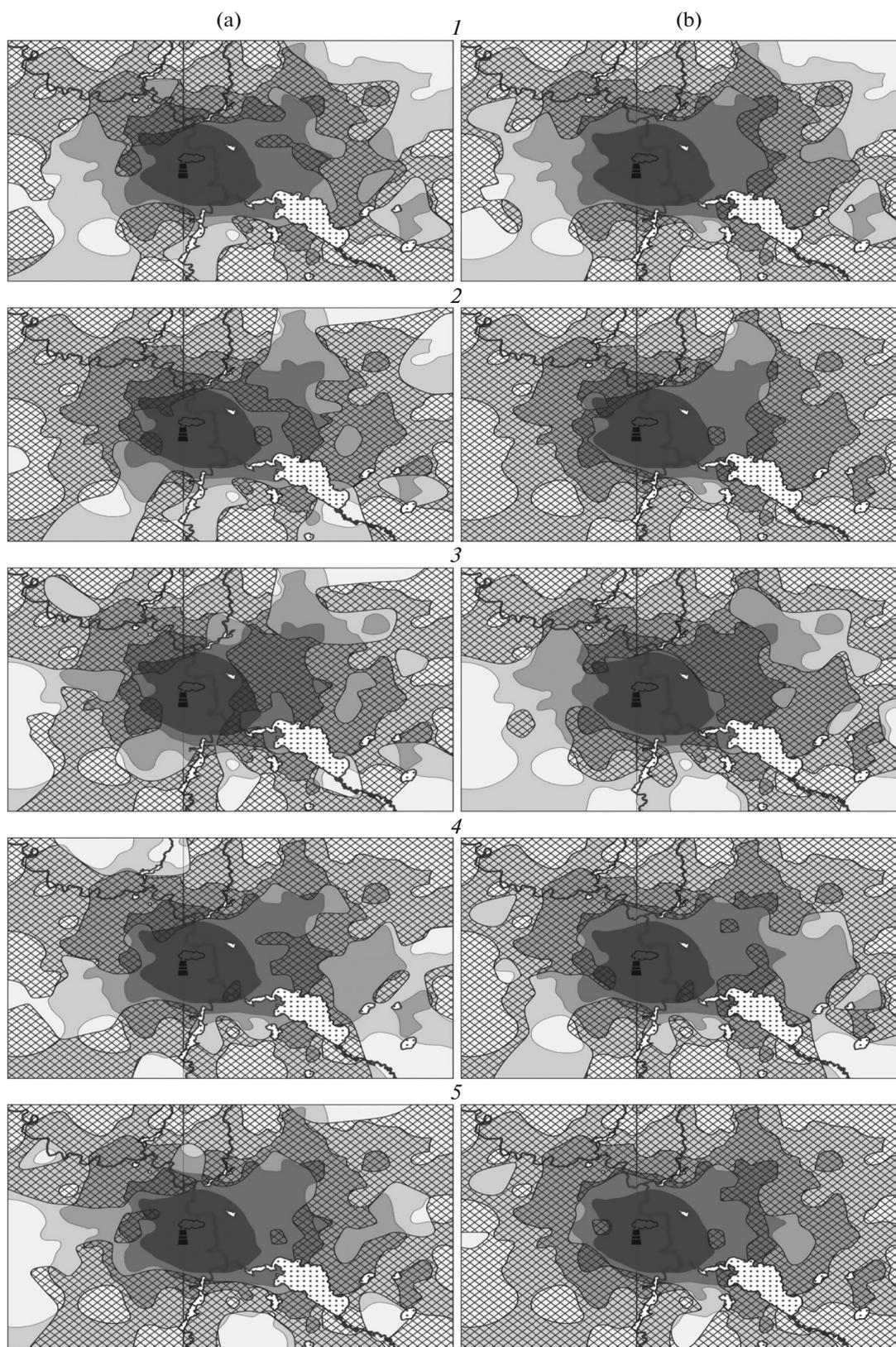


Fig. 3. Distribution of *Betonica officinalis* (1), *Fragaria vesca* (2), *Pyrola rotundifolia* (3), *Thalictrum minus* (4), and *Trientalis europaea* (5) in 1995–1997 (a) and 2014–2016 (b).

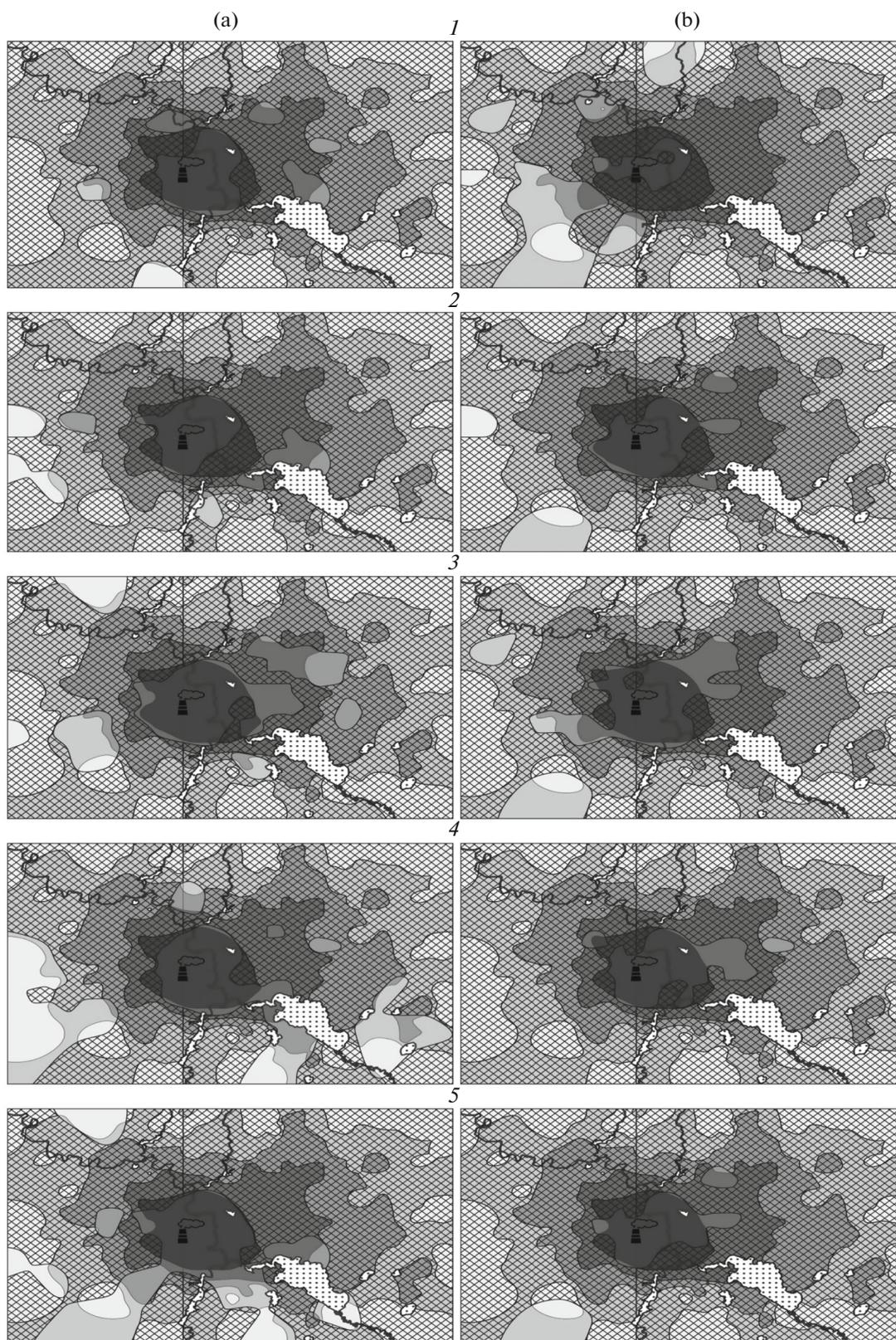


Fig. 4. Distribution of *Calamagrostis arundinacea* (1), *Geranium sylvaticum* (2), *Lathyrus vernus* (3), *Maianthemum bifolium* (4), and *Rubus saxatilis* (5) in 1995–1997 (a) and 2014–2016 (b).

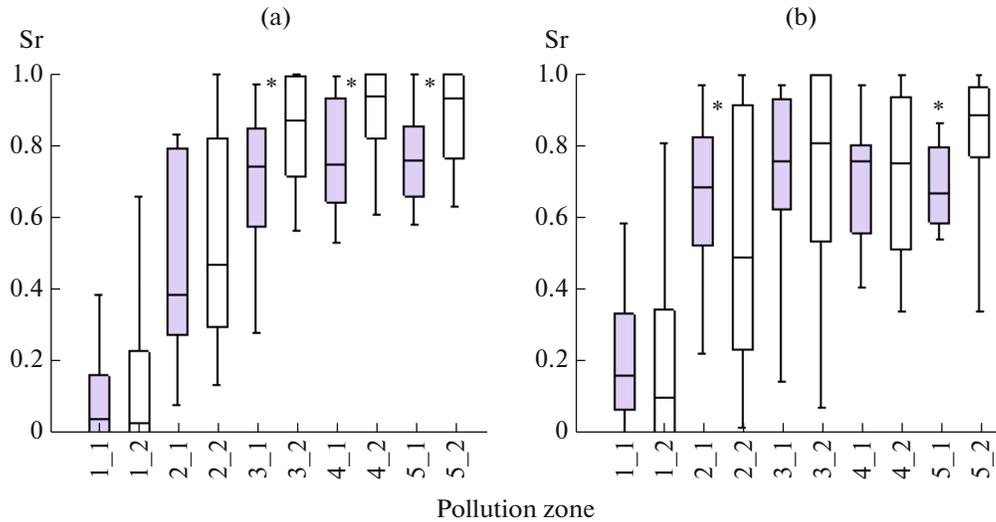


Fig. 5. Relative area of distribution of species in the eastern (a) and western (b) sectors in 1995–1997 (gray shading) and 2014–2016 (without shading). Median, interquartile range, and limits are shown; * significant differences between observation periods.

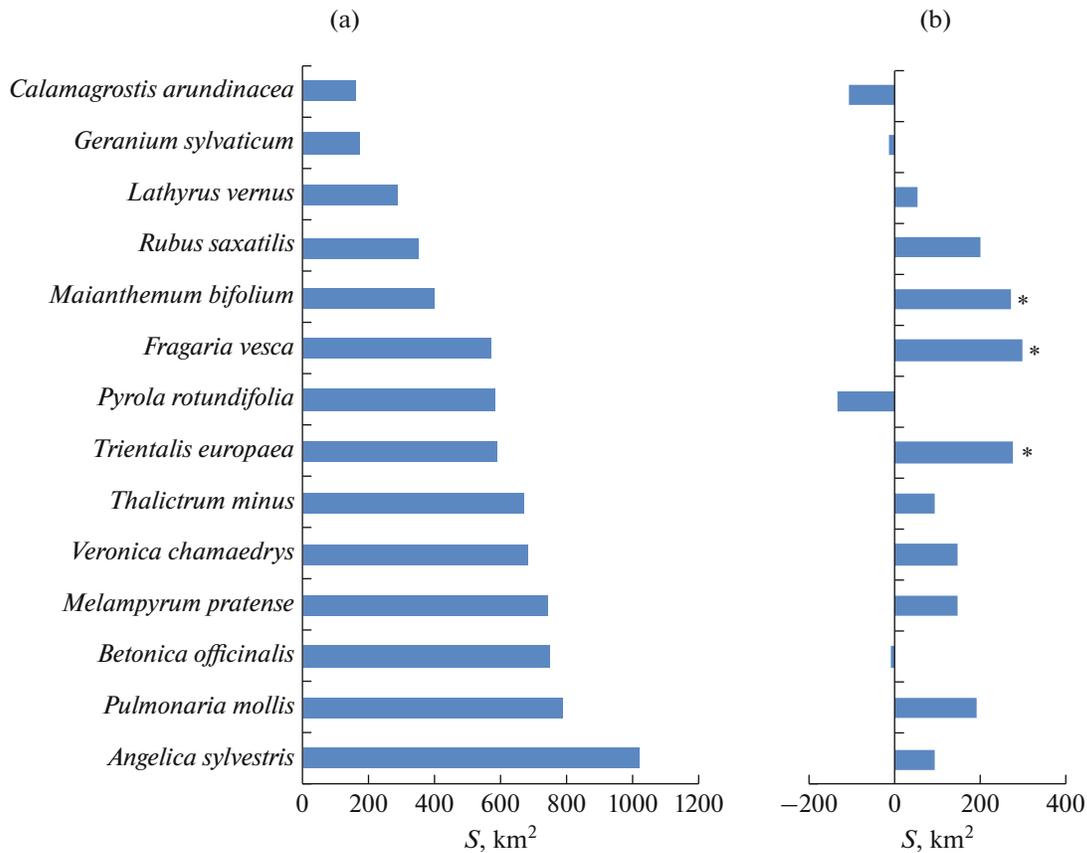


Fig. 6. Area of uninhabited territory in 1995–1997 (a) and the magnitude of the change in distribution area after emissions reduction (b); * significant differences between observation periods.

high values of these parameters significantly reduce the mobility of heavy metals and their availability to plants (Dube et al., 2001). However, in addition to soil characteristics, the distribution of species is influenced by a number of other factors, for example, the light regime of habitats and biotic interactions (Perring

et al., 2018; Hedwall et al., 2021). As was mentioned above, the eastern and western sectors are located in different natural areas, differing not only in soil characteristics, but also in the ratio of pine and fir–spruce forests, as well as thermal and water availability. For example, an analysis of dose-effect relationships for

different types of communities in the smelter's area of influence showed that the decrease in species richness along the load gradient in fir–spruce forests occurs more slowly than in birch and pine forests (Trubina, 2002). Thus, the observed spatial unevenness in changes in the distribution of species along the load gradient most likely reflects the influence of a whole complex of factors.

The uneven decline in the distribution of species was also observed within the same load zone of the same sector, and the preservation of small areas of inhabited areas in individual species was noted even under very high loads (see Figs. 2–4). This effect, without the division of the territory into zones and sectors, was also noted for epiphytic lichens (Mikhailova, 2022). The presence of areas with higher diversity in heavily polluted areas has been shown for the herb-dwarf shrub layer of forests (Trubina and Vorobeichik, 2012; Trubina, 2020), small mammals (Mukhacheva et al., 2012), fungi (Mikryukov et al., 2015), and earthworms and mollusks (Vorobeichik et al., 2020). Refugia can be floodplain areas of rivers and small water-courses (Mukhacheva et al., 2012; Nesterkova, 2014) and various microsites, in particular, large woody remains (Vorobeichik et al., 2020; Mikryukov et al., 2021) and windfall complexes (Trubina, 2009). The modifying influence of the heterogeneity of the environment on the survival of local populations of species, together with the species-specific response, to a certain extent explains the slow decline in the gamma diversity of plant communities in the territory under consideration along the load gradient (Trubina and Vorobeichik, 2012).

The decline in the distribution area along the load gradient up to the complete elimination of individual species occurred regardless of the sector or species under consideration, and the main contribution to the dynamics was made by the level of load. The lack of studies on the dynamics of the distribution of vascular plant species depending on the level of load and heterogeneity of habitats in the vicinity of other plants does not allow us to compare the degree of generality of the estimates of the contribution of factors. However, it is important to note the following. The formation of technogenic “deserts” near copper smelters has been shown for earthworms (Vorobeichik, 1998), epiphytic lichens (Mikhailova, 2022), and the European mole (Vorobeichik and Nesterkova, 2015), and the harmful effects are associated with the combined effect of acid gases and heavy metals (Vorobeichik et al., 2019). Our estimates of the area of uninhabited territory during the period of high smelter emissions for the most sensitive species (see Table 1 and Fig. 6a) are comparable with estimates for individual sensitive species of epiphytic lichens (Mikhailova, 2022) and the distribution of moles in the area of the smelter. In particular, the area of the “mole desert” in the first observation period in the territory under consideration was 563 km² (Vorobeichik and Nesterkova, 2015).

Dynamics after emissions reduction. Positive shifts were expressed mainly in less polluted areas (see Fig. 5), which is consistent with data on the dynamics of the distribution of epiphytic lichens (Mikhailova, 2022) and moles (Vorobeichik and Nesterkova, 2015) in the same territory. Moreover, the distribution area of most species after the reduction of emissions across the entire territory has changed little, and over the past 19 years an increase has been noted in only three species (see Fig. 6b). Research on the dynamics of communities of different groups of biota on permanent sample plots in the area of the smelter (Vorobeichik et al., 2014; Vorobeychik et al., 2019; Mukhacheva, 2021; Nesterkov, 2022) also indicate a load-dependent response to emission reductions.

One of the main reasons for the low rate of recolonization of contaminated areas may be the persistence of high concentrations of heavy metals in the litter and upper soil horizons for decades after emission reductions (Vorobeichik and Kaygorodova, 2017). The dispersal of herbaceous plants can be limited by the lack of diaspore arrival, especially given the observed scale of reduction in the area of distribution and increased fragmentation in general. The influence of the availability of diaspores and the quality of habitats on the dynamics of forest species after the cessation of agricultural land use, as well as the negative effect of habitat fragmentation on the processes of immigration of species, has been shown in a number of works (Flinn, 2007; Baeten et al., 2009; Paal et al., 2017). The processes of species dispersal in contaminated habitats can also be limited by litter, the increase in thickness of which in the area of the plant is well documented (Vorobeichik, 1995). The negative effect of thick litter on plant renewal is well known. However, additional studies, including experimental ones, are needed to separate the contribution of different factors to the dynamics of species in contaminated areas.

One unexpected and extremely important result of this work is to continue eliminating and reducing the distribution of species in contaminated areas. A decrease in abundance or distribution during recovery successions is quite expected for species that, in the absence of pollution, are characterized by extremely low participation in communities, but are able to exist and even increase their participation in the presence of high levels of pollution. This type of dynamics after a reduction in emissions is shown for birds (Belsky and Lyakhov, 2021) and epiphytic lichens (Mikhailova, 2022). However, the data from our work indicate that negative changes occurred mainly among species sensitive to pollution (see Table 1), some of which are typical forest species. Fragmentation in distribution and spatial isolation of local populations along the load gradient were most pronounced for these species (see Fig. 2). The results of modeling the behavior of herbaceous plant species in highly fragmented landscapes indicate that the elimination of local populations of species as

a result of stochastic processes can occur without further increasing fragmentation (May et al., 2013).

Data on the slower recolonization of contaminated areas in the western sector when compared to the eastern sector are consistent with the results of an analysis of the dynamics of mole distribution in the surveyed area (Vorobeichik and Nesterkova, 2015). The authors consider a possible reason for the observed phenomenon to be the slower release of toxicants from soils of heavy mechanical composition that predominate in the western sector, but this assumption needs to be verified. The slow pace of recolonization in the western sector was due not only to the weak expression of the positive response, but also to the continued reduction in the area of distribution of species in contaminated areas (see Table 1). The presence of negative trends in the herb–shrub layer of fir–spruce forests after a reduction in emissions was shown by us when analyzing the temporal dynamics of the state of the vegetation cover on permanent sample plots established in the western sector (Vorobeichik et al., 2014).

The data generally indicate that the low rate of recovery of the diversity of plant communities after emission reductions is due not only to the lack of dispersal of most species and the small number of species capable of recolonizing heavily polluted areas, but also to the continued elimination of local populations of species. However, the reasons for the different rates of recolonization in different natural areas and the continuing decline in the area of distribution of sensitive species after emission reductions remain open.

CONCLUSIONS

The results of this work indicate that, when pollutants arrive and decrease, the magnitude of the response and the pattern of the dynamics are species-specific and significantly depend on habitat conditions, but the main contribution to the spatiotemporal dynamics of species is made by the load level. This completely confirms the original hypothesis.

During periods of high emissions, the reduction in the distribution area of different species occurred at different levels of load, and the magnitude of the response of species to an increase in load varied several times. Environmental heterogeneity contributed to a significant slowdown in the rate of decline in species distribution, but the share of variance associated with the modifying influence of this factor, compared with the level of load, was generally small. At high stress levels, reductions in area distribution occurred regardless of the sector or species considered.

The increased load led to the emergence of vast uninhabited areas around the plant and a significant increase in fragmentation in the distribution of species in contaminated areas in general. Although it is impossible to accurately estimate the time lag in the extinction of local populations of species using the

method of spatiotemporal analogies, our data show that, even for widespread species, this value may be only a few decades.

After reducing emissions, the distribution area of most species in heavily polluted areas changed little over the course of 19 years. Positive changes were noted mainly in less contaminated areas and were more pronounced in the eastern sector than in the western sector. Moreover, the elimination and reduction in distribution in the most sensitive species continued, with negative trends in the western sector being more pronounced than in the eastern sector.

Changes in the area of distribution of species in general during both observation periods in the western sector occurred more slowly than in the eastern sector. This indicates that, depending on habitat conditions, the type of response of communities to increasing/decreasing load can be fast (low resistance and inertia) or slow (high resistance and inertia). Differences in the type of response must be taken into account when developing acceptable anthropogenic load levels. It is also important to note that the work examined the dynamics of a limited number of species and it remains unclear whether the identified dynamics features will appear when analyzing more extensive material.

ACKNOWLEDGMENTS

We express deep gratitude to E.L. Vorobeichik for providing data on the content of metals in the litter and valuable comments during our work on the manuscript.

FUNDING

Research in 1995–1997 was carried out with financial support from INTAS, project no. 93-1645, and in 2015–2016 with support from the Russian Foundation for Basic Research, project no. 15-04-06828. Data collection in 2014, interpretation of the results and, preparation of the manuscript were carried out as part of the State Task of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

Alexander, J.M., Chalmandrier, L., Lenoir, J., et al., Lags in the response of mountain plant communities to cli-

- mate change, *Global Change Biol.*, 2018, vol. 24, no. 2, pp. 563–579.
- Ash, J.D., Givnish, T.J., and Waller, D.M., Tracking lags in historical plant species' shifts in relation to regional climate change, *Global Change Biol.*, 2017, vol. 23, no. 3, pp. 1305–1315.
- Baeten, L., Jacquemyn, H., Van Calster, H., et al., Low recruitment across life stages partly accounts for the slow colonization of forest herbs, *J. Ecol.*, 2009, vol. 97, no. 1, pp. 109–117.
- Bel'skii, E.A. and Lyakhov, A.G., Dynamics of the community of hole-nesting birds upon reduction of industrial emissions (the example of the Middle Ural Copper Smelter), *Russ. J. Ecol.*, 2021, vol. 52, no. 4, pp. 296–306.
- Brunet, J., Hedwall, P.-O., Lindgren, J., et al., Immigration credit of temperate forest herbs in fragmented landscapes—Implications for restoration of habitat connectivity, *J. Appl. Ecol.*, 2021, vol. 58, no. 10, pp. 2195–2206.
- Chichorro, F., Juslén, A., and Cardoso, P., A review of the relation between species traits and extinction risk, *Biol. Conserv.*, 2019, vol. 237, pp. 220–229.
- Di Marco, M., Harwood, T.D., Hoskins, A.J., et al., Projecting impacts of global climate and land-use scenarios on plant biodiversity using compositional-turnover modelling, *Global Change Biol.*, 2019, vol. 25, no. 8, pp. 2763–2778.
- Dube, A., Zbytniewski, R., Kowalkowski, T., et al., Adsorption and migration of heavy metals in soil, *Pol. J. Environ. Stud.*, 2001, vol. 10, no. 1, pp. 1–10.
- Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M., et al., More is less: net gain in species richness, but biotic homogenization over 140 years, *Ecol. Lett.*, 2019, vol. 22, no. 10, pp. 1650–1657.
- Flinn, K.M., Microsite-limited recruitment controls fern colonization of post-agricultural forests, *Ecology*, 2007, vol. 88, no. 12, pp. 3103–3114.
- Gafurov, F.G., *Pochvy Sverdlovskoi oblasti* (Soils of Sverdlovsk Region), Ekaterinburg: Ural. Univ., 2008.
- Haddad, N.M., Brudvig, L.A., Clobert, J., et al., Habitat fragmentation and its lasting impact on Earth's ecosystems, *Sci. Adv.*, 2015, vol. 1, no. 2, p. e1500052.
- Hedwall, P.-O., Uria-Diez, J., Brunet, J., et al., Interactions between local and global drivers determine long-term trends in boreal forest understorey vegetation, *Global Ecol. Biogeogr.*, 2021, vol. 30, no. 9, pp. 1765–1780.
- Hylland, K. and Ehrlén, J., The mechanisms causing extinction debts, *Trends Ecol. Evol.*, 2013, vol. 28, no. 6, pp. 341–346.
- Igoshina, K.N., *Vegetation of the Urals*, Tr. Bot. Inst. Akad. Nauk SSSR, 1964, pp. 83–230.
- Kapustin, V.G., Physical-geographical zoning of the Sverdlovsk region, *Materialy Conferentsii "Geografia i sovremennye problemy estestvennonauchnogo poznaniya"* (Proc. Conf. "Geography and Modern Problems of Natural Science Knowledge"), Ekaterinburg, 2009, pp. 11–24.
- Kharuk, V.I., Petrov, I.A., Im, S.T., et al., Subarctic 2023. Vegetation under the mixed warming and air pollution influence, *Forest*, 2023, vol. 14, no. 3, p. 615.
- Kolk, J. and Naaf, T., Herb layer extinction debt in highly fragmented temperate forests – Completely paid after 160 years?, *Biol. Conserv.*, 2015, vol. 182, pp. 164–172.
- May, F., Giladi, I., Ristow, M., et al., Metacommunity, mainland-island system or island communities? Assessing the regional dynamics of plant communities in a fragmented landscape, *Ecography*, 2013, no. 36, pp. 1–12.
- Mikhailova, I.N., Dynamics of distribution boundaries of epiphytic macrolichens after reduction of emissions from a copper smelter, *Russ. J. Ecol.*, 2022, vol. 53, no. 5, pp. 335–346.
- Mikryukov, V.S., Dulya, O.V., and Vorobeichik, E.L., Diversity and spatial structure of soil fungi and arbuscular mycorrhizal fungi in forest litter contaminated with copper smelter emissions, *Water, Air, Soil Pollut.*, 2015, vol. 226, no. 114, pp. 1–14.
- Mikryukov, V.S., Dulya, O.V., Bergman, I.E., et al., Sheltering role of well-decayed conifer logs for forest floor fungi in long-term polluted boreal forests, *Front. Microbiol.*, 2021, vol. 12, p. 729244.
- Mukhacheva, S.V., Long-term dynamics of small mammal communities in the period of reduction of copper smelter emissions: 1. Composition, abundance, and diversity, *Russ. J. Ecol.*, 2021, vol. 52, no. 1, pp. 84–93.
- Mukhacheva, S.V., Davydova, Y.A., and Vorobeichik, E.L., The role of heterogeneity of the environment in preservation of the diversity of small mammals under the condition of strong industrial pollution, *Dokl. Biol. Sci.*, 2012, vol. 447, pp. 338–341.
- Naaf, T. and Kolk, J., Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation, *Biol. Conserv.*, 2015, vol. 182, pp. 155–163.
- Nesterkov, A.V., Recovery signs in grass-stand invertebrate communities after a decrease in copper-smelting emissions, *Russ. J. Ecol.*, 2022, vol. 53, no. 6, pp. 553–564.
- Nesterkova, D.V., Distribution and abundance of european mole (*Talpa europaea* L.) in areas affected by two Ural copper smelters, *Russ. J. Ecol.*, 2014, vol. 45, no. 5, pp. 429–436.
- Nordén, B., Dahlberg, A., Brandrud, T.E., et al., Effects of ecological continuity on species richness and composition in forests and woodlands: A review, *Ecoscience*, 2014, vol. 21, no. 1, pp. 34–45.
- Paal, T., Kütt, L., Lõhmus, K., et al., Both spatiotemporal connectivity and habitat quality limit the immigration of forest plants into wooded corridors, *Plant Ecol.*, 2017, vol. 218, no. 4, pp. 417–431.
- Pereira, H.M., Navarro, L.M., and Martins, I.S., Global biodiversity change: the bad, the good, and the unknown, *Annu. Rev. Environ. Resour.*, 2012, vol. 37, pp. 25–50.
- Perring, M.P., Diekmann, M., Midolo, G., et al., Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition, *Environ. Pollut.*, 2018, vol. 242, pp. 1787–1799.
- Rose, R., Monteith, D.T., Henrys, P., et al., Evidence for increases in vegetation species richness across UK Environmental Change Network sites linked to changes in air pollution and weather patterns, *Ecol. Indic.*, 2016, vol. 68, pp. 52–62.

- Sánchez-Bayo, F. and Wyckhuys, K.A.G., Further evidence for a global decline of the entomofauna, *Aust. Entomol.*, 2021, vol. 60, no. 1, pp. 9–26.
- Staude, I.R., Waller, D.M., Bernhardt-Römermann, M., et al., Replacements of small-by large-ranged species scale up to diversity loss in Europe's temperate forest biome, *Nat. Ecol. Evol.*, 2020, vol. 4, no. 6, pp. 802–808.
- Trubina, M.R., Trends in dynamics of composition of eco-morphs under aerotechnogenic pollution, in *Tekhnogennye vozdeistviya na lesnye soobshestva i problemy ikh vosstanovleniya i sokhraneniya* (Technogenic Impacts on Forest Communities and Problems of their Restoration and Conservation), Makhnev, A.K. and Koltunov, E.V., Eds., Ekaterinburg, 1992, pp. 93–104.
- Trubina, M.R., Plant communities of the different landscape elements under long-term disturbance, *Materialy Conferentsii "Ekologicheskie problemy gornykh territorii"* (Proc. Conf. "Environmental Problems of Mountain Areas"), Ekaterinburg: Akademkniga, 2002, pp. 240–244.
- Trubina, M.R., Species richness and resilience of forest communities: combined effects of short-term disturbance and long-term pollution, *Plant Ecol.*, 2009, vol. 201, no. 1, pp. 339–350.
- Trubina, M.R., Vulnerability to copper smelter emissions in species of the herb-dwarf shrub layer: role of differences in the type of diaspore dispersal, *Russ. J. Ecol.*, 2020, vol. 51, no. 2, pp. 107–117.
- Trubina, M.R. and Dyachenko, A.P., Current state of forest moss communities after reduction of emissions from the Middle-Ural Copper Smelter, *Biol. Bull.*, 2020, vol. 48, pp. 1924–1931.
<https://doi.org/10.1134/S1062359021100265>
- Trubina, M.R. and Vorobeichik, E.L., Severe industrial pollution increases the β -diversity of plant communities, *Dokl. Biol. Sci.*, 2012, vol. 442, pp. 17–19.
- Vorobeichik, E.L., Changes in thickness of forest litter under chemical pollution, *Russ. J. Ecol.*, 1995, vol. 26, pp. 252–258.
- Vorobeichik, E.L., Populations of earthworms (Lumbricidae) in forests of the Middle Urals in conditions of pollution by discharge from copper works, *Russ. J. Ecol.*, 1998, vol. 29, no. 2, pp. 85–91.
- Vorobeichik, E.L., Reaction of forest litter and its relationship with soil biota under toxic pollution, *Lesovedenie*, 2003, no. 2, pp. 32–42.
- Vorobeichik, E.L. and Kaigorodova, S.Y., Long-term dynamics of heavy metals in the upper horizons of soils in the region of a copper smelter impacts during the period of reduced emission, *Eurasian Soil Sci.*, 2017, vol. 50, no. 8, pp. 977–990.
- Vorobeichik, E.L. and Nesterkova, D.V., Technogenic boundary of the mole distribution in the region of copper smelter impacts: Shift after reduction of emissions, *Russ. J. Ecol.*, 2015, vol. 46, no. 4, pp. 377–380.
- Vorobeichik, E.L., Trubina, M.R., Khantemirova, E.V., et al., Long-term dynamic of forest vegetation after reduction of copper smelter emissions, *Russ. J. Ecol.*, 2014, vol. 45, no. 6, pp. 498–507.
- Vorobeichik, E.L., Ermakov, A.I., and Grebennikov, M.E., Initial stages of recovery of soil macrofauna communities after reduction of emissions from a copper smelter, *Russ. J. Ecol.*, 2019, vol. 50, no. 2, pp. 146–160.
- Vorobeichik, E.L., Ermakov, A.I., Nesterkova, D.V., et al., Coarse woody debris as microhabitats of soil macrofauna in polluted areas, *Biol. Bull.*, 2020, vol. 47, no. 1, pp. 87–96.

Publisher's Note. Pleiades Publishing remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.