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Vulnerability to Copper Smelter Emissions in Species of the Herb–Dwarf Shrub Layer: Role of Differences in the Type of Diaspore Dispersal

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Abstract—The type of diaspore dispersal may have a significant effect on the vulnerability of herbaceous plants to anthropogenic transformation of ecosystems. However, there is still no unified opinion on the relationship between the type of diaspore dispersal and the processes of extinction and colonization. Here, descriptions of vegetation performed in the zone of impact from the Middle Ural Copper Smelter in the periods of high and low emission levels (1995–1998 and 2014–2016, respectively) have been analyzed to test two hypotheses: (1) the type of diaspore dispersal has an effect on plant vulnerability, with the species whose diaspores are dispersed farther being less vulnerable to habitat transformation; and (2) irrespective of the type of dispersal, recolonization is less intense under high than under low pollution levels. It has been found that the species richness of all plant groups highly varies in space: it decreases sharply in the zone of heavy toxic loads, but localities with high species richness occur even under conditions of heavy pollution. With the increasing pollution level, the species diversity within plant groups on a mesoscale (hundreds of meters) decreases more strongly than that on a macroscale (kilometers). Species with different types of diaspore dispersal differ from each other both in sensitivity to pollution and in the capacity for recolonization after reduction of emissions, but the relationship between vulnerability and the distance of diaspore dispersal is ambiguous. High sensitivity to pollution and low recolonization capacity have been revealed in species characterized by either the lowest (autochores) or the highest dispersal distance (epi- and endozoochores), with anemochores being the least vulnerable. The diversity of most groups in the zone of heavy pollution has remained low over the past 20 years; some positive shifts have occurred in myrmecochores and typical anemochores, with the dynamics of the latter being independent of pollution level.

Keywords: temporal dynamics, diversity, loss of species, plant dispersal, recolonization, heavy metals, reduction of emissions

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Anthropogenic impact on ecosystems is often accompanied by significant fragmentation of habitats and deterioration of their quality, which leads to a sharp loss of biodiversity [1, 2]. As a consequence, ecosystem fuctions may be disturbed, and not only on a local but also on a global scale [3–5]. Therefore, studies on the consequences of ecosystem transformation are relevant in modern ecology. It is important to analyze the vulnerability of the biota to external influences, including the assessment of both its sensitivity to load and ability to recover after load reduction, and also identification of factors having an effect on the processes of extinction and recolonization.

Species of the herb–dwarf shrub layer in forests of the temperate zone form the basis of plant diversity and play a major role in regulation the fluxes of biogenic elements and maintaining the diversity of other groups of biota [6–8]. Many herbaceous plant species are vulnerable to fragmentation of habitats and deterioration of their quality because of a low velocity of dispersal [9–12], which may be limited due to a small number of generative diaspores [13] and a low distance of their dispersal [14–16]. In turn, this distance depends on the type of dispersal [14, 15, 17, 18], which may have an effect on the vulnerability of species.

There is still no unified opinion on the relationship between the type of diaspore dispersal and the processes of extinction and colonization. Some studies show that such a relationship is absent [19, 20], while others provide evidence for its existence [21–23]. Plant sensitivity to anthropogenic transformation of the environment is also estimated differently [22, 23]. The inconsistency of these data is most likely due to the fact that the processes of species extinction and dispersal may depend on a number of factors [24], including habitat quality [10, 25, 26], characteristics of species [27–30], selective diaspore ingestion and transfer by animals [31–34], and changes in the contribution of dispersal vectors [22]. However, a deficit of information on the dynamics of species with different types of dispersal in transformed ecosystems does not allow any generalizations to be made. Although atmospheric pollution significantly contributes to the degradation of natural ecosystems, vulnerability to its impact has not yet been compared among species with different types of diaspore dispersal.

The purpose of this study was to compare vulnerability to emissions from a copper smelter among species of the herb–dwarf shrub layer differing in the type of dispersal of generative diaspores in order to test the following hypotheses.

The first is that the type of diaspore dispersal has a significant effect on plant vulnerability, with the species whose diaspores are dispersed farther being less vulnerable to habitat transformation. This hypothesis is based on the assumption that such species have higher probability of occurrence in habitat fragments with favorable environmental conditions, which allows them to survive under long-term pollution and more rapidly colonize vacant areas after reduction of emissions. On the other hand, the dependence between the type of dispersal and its range may be very weak [19, 20] due to the probability of accidental transfer of diaspores for very long distances [14, 18], an equalizing effect of other factors [24, 35], or changes in the contribution of dispersal vectors [22].

The second hypothesis is that, irrespective of the type of diaspore dispersal, recolonization is less intense under high than under low pollution levels, since the dispersal of species over an area may be limited both by the absence of diaspores [36] and by environmental conditions unfavorable for their survival [10, 25, 37]. Despite significant reduction of emissions, toxicant concentrations in the soil and litter in the vicinities of copper smelters remain very high for decades [38–40]. This factor, combined with the low numbers and abundance of plant species and high level of habitat fragmentation around the emission source [41], can significantly limit the dispersal of species in the period after emission reduction.

MATERIAL AND METHODS

Studies were performed in the region around the Middle Ural Copper Smelter (MUCS) located in the suburbs of Revda, 50 km from Yekaterinburg. The main components of emissions are gaseous compounds of sulfur, fluorine, and nitrogen and dust particles with adsorbed heavy metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). The MUCS has been in operation since 1940. The total amount of emissions in the 1980s reached 150–225 × 10^3 t/year, but it was reduced to 65 × 10^3 t/year at the turn of the century and to 25 × 10^3 t/year by the mid-2000s (decade). A crucial overhaul of the smelter in 2010 resulted in its further reduction to less than 5 × 10^3 t/year [49]. According to physiographic zoning, the study region is in the southern taiga subzone of the low-mountain province of the Middle Urals with elevations of 100 to 450 m a.s.l [42].

Geobotanical descriptions used for analysis were made during the periods of high and low emission levels (1995–1998 and 2014–2016) in an area of 56 × 36 km around the MUCS, where 110 sampling plots (25 × 25 m) were established in forest phytocenoses at distances of no less than 1 km from each other. The plots differed with respect to landscape type (eluvial, transitional, or accumulative), soil type (gray forest, brown mountain-forest, or soddy podzolic soils), and vegetation (birch, pine–birch, and pine forests of different associations). Criteria for selecting the plots were as follows: the absence of damage from recent fires and serious anthropogenic disturbances unrelated to pollution, location no closer than 100 m to motor roads, and the edificator tree stand age of no less than 80 years. Locations of the plots during the first period were manually marked on a 1 : 100000 map and could therefore be slightly different during the second period.

According to the classifications proposed previously [14, 17], all the recorded species were divided into six groups with respect to the type of diaspore dispersal (Table 1). Since many species employ several types of dispersal (see Annex in the online version), their attribution to a certain group was based on morphological criteria (primarily characteristics of fruits).

Toxic load was evaluated using the index characterizing the average excess over the regional background concentrations of acid-soluble forms of Cu, Cd, Pb, and Zn in the forest litter (in this study, their concentrations in forests of Sysert district, Sverdlovsk oblast: 23.6 μg/g Cu, 1.1 μg/g Cd, 17.4 μg/g Pb, 147.8 μg/g Zn). Metal concentrations were determined in litter samples collected in 1995–1998 (three averaged samples per plot). A sample was suspended in a tenfold volume of 5% HNO_3, shaken up, and extracted for 24 h. Measurements were made with an AAS-3 atomic absorption spectrometer (Analytik Jena, Germany). The toxic load index varied from 2.30 to 132.14 arbitrary units along the pollution gradient. In the course of analysis, this gradient was divided into two zones (light and heavy pollution, 55 plots in each), with the above index varying from 2.30 to 10.63 arb. units in the former and from 10.86 to 132.14 arb. units in the latter zone.

Sensitivity to pollution and recolonization capacity were estimated from the degree of change in the diversity of groups along the pollution gradient before and after emission reduction. Two parameters were used to characterize the diversity of groups: species richness (the number of species per 625-m^2 plot) and the total

Table 1. Traits and representatives of species with different types and distances of dispersal of generative diaspores

Type of dispersal		Main traits and representatives	Dispersal distance, m	
			50–99% of diaspores	maximum
Autochores	Without devices for dispersal (WD)	Diaspores fall down under their own weight or when stems are lodged or shaken (*Veronica* sp., *Campanula* sp.)	0.1–1 [14]	1 [14]
	Automechanochores (AM)	Diaspores are actively scattered due to specific features of fruit structure (*Geranium* sp., *Vicia* sp.)	1–5 [14]	7 [14]
Anemochores	Semianemochores (SA)	Diaspores with small winglike extensions, light and fragile inflorescences, caryopses covered with glumes, considerable plant height (families Poaceae, Apiaceae)	2–150 [14]	200 [14]
	Typical anemochores (TA)	Very small and light diaspores, plumed seeds (families Asteraceae, Pyrolaceae; horsetails, ferns, club mosses))	10–500 [14]	3600 [14]
Zoochores	Myrmecochores (M)	Diaspores have elaiosomes and are actively dispersed by ants (*Viola* sp., *Myosotis* sp.)	2–15 [14]	70 [14, 17]
	Epi- and endozoochores (EE)	Bright and juicy fruits and fruits with devices for attachment to hair or feathers (*Vaccinium* sp., *Geum* sp.)	400–1500 [14]	6000 [31]

number of species within the zone, with the former characterizing species diversity on a mesoscale (hundreds of meters), and the latter, in a macroscale (kilometers). Differences in sensitivity to toxic load were estimated from the slope of regression lines (for species richness) and the proportion of extinct species relative to the total species number (for the macroscale diversity). Differences in the capacity for recolonization after emission reduction were estimated from the presence or absence of a statistically significant increase in the species diversity of groups over the past 20 years and the dynamics of the total number of species per group. As an accessory parameter, the proportion of uncolonized plots in very heavily polluted areas (over 49.76 arb. units) before and after emission reduction was determined.

The influence of the type of diaspore dispersal and load level on the dynamics of species richness in groups during the high-emission period was evaluated for each zone by analysis of covariance (a model for estimating the homogeneity of regression slopes). Since the response to increasing toxic load differed between the groups, a covariance model for data sets with different regression slopes was used. The data on species richness were subjected to square root transformation prior to analysis. Multiple comparisons were made with Tukey's test. Two-tailed *t*-test was used to compare species of different groups with respect to the proportion of plots not colonized by them and the dynamics of this parameter in time. All calculations were made with Statistica v. 7.0 (StatSoft, Inc.).

RESULTS

Species richness. The data on the period of 1995–1998 show that the species richness of most groups in the zone of light pollution remained unchanged under increasing toxic load but became higher in epi- and endozoochores (EE) and lower in semianemochores (SA) (Table 2, Fig. 1a). The combined effect of factors "group × load index" was statistically significant ($F_{5,308} = 2.29$, $p < 0.046$), while that of the latter factor alone was not ($F_{1,308} = 0.01$, $p < 0.917$). In the zone of heavy pollution, a significant decrease in species richness under increasing toxic load was observed in all groups ($F_{5,\,308} = 209.48$, $p < 0.001$) (Table 2, Fig. 1b). Adverse changes in the groups of typical anemochores (TA) and semianemochores (SA) were least prominent (group × load index: $F = 2.78_{5,308}$, $p < 0.018$).

The species richness of groups in the light pollution zone increased between the first and second observation periods ($F_{1,308} = 13.75$, $p < 0.001$), but significant shifts were revealed only in myrmecochores (M) ($p < 0.001$) and TA ($p < 0.001$) (period × group × load index: $F_{5,308} = 3.15$, $p < 0.001$). This increase in M was observed mainly in the region of low loads; in TA, along the entire part of pollution gradient. The species richness of groups in the heavy pollution zone also increased between the observation periods ($F_{1,308} = 7.80$, $p < 0.005$), but this increase was statistically significant only in TA ($p < 0.037$) (period × group × load index: $F_{5,308} = 40.75$, $p < 0.001$).

The species richness of groups widely varied over the study area and could be fairly high in certain plots within the heavy pollution zone (Table 3). However, its average values in the heavy pollution zone were significantly lower than in the light pollution zone both in the first and second observation periods.

The highest proportions of uncolonized plots in very heavily polluted area were revealed for M and AM, and the lowest proportions, for SA and TA (Fig. 2).

Table 2. Results of regression analysis for the effect of toxic load level on species richness in groups with different types of diaspore dispersal

Group	Pollution zone (load index, arb. units)					
	light pollution (2.3–10.6)			heavy pollution (10.9–132.1)		
	β (SE)	R^2	P	β (SE)	R^2	P
1995–1998						
Without devices for dispersal (WD)	–0.026 (0.054)	0.00	0.631	–0.032 (0.004)	0.49	0.000
Automechanochores (AM)	–0.007 (0.037)	0.00	0.840	–0.024 (0.003)	0.51	0.000
Myrmecochores (M)	0.004 (0.029)	0.00	0.884	–0.025 (0.004)	0.42	0.000
Epi- and endozoochores (EE)	0.076 (0.032)	0.10	0.022	–0.022 (0.003)	0.49	0.000
Semianemochores (SA)	–0.107 (0.048)	0.09	0.030	–0.015 (0.004)	0.24	0.000
Typical anemochores (TA)	0.050 (0.049)	0.02	0.312	–0.015 (0.004)	0.23	0.000
2014–2016						
No devices for dispersal (ND)	–0.09 (0.045)	0.07	0.050	–0.031 (0.005)	0.42	0.000
Automechanochores (AM)	–0.023 (0.033)	0.01	0.492	–0.027 (0.004)	0.45	0.000
Myrmecochores (M)	–0.055 (0.028)	0.07	0.059	–0.031 (0.004)	0.49	0.000
Epi- or endozoochores (EE)	0.021 (0.022)	0.02	0.356	–0.023 (0.003)	0.53	0.000
Semianemochores (SA)	–0.125 (0.046)	0.12	0.009	–0.014 (0.003)	0.29	0.000
Typical anemochores (TA)	0.092 (0.031)	0.15	0.004	–0.024 (0.003)	0.47	0.000

Designations: β (SE), standardized regression coefficient with standard error; R^2, determination coefficient; P, significance level for regressions.

Table 3. Species richness in groups with different types of diaspore dispersal in zones of light and heavy pollution during different observation periods, arithmetic means ± standard error and limits (in parentheses)

Group	Pollution zone (load index, arb. units)			
	light pollution (2.3–10.6)		heavy pollution (10.9–132.1)	
	1995–1998	2014–2016	1995–1998	2014–2016
Without devices for dispersal (WD)	9.0 ± 0.55 (2–18)	10.2 ± 0.53 (3–20)	4.9 ± 0.61 (0–17)	4.5 ± 0.59 (0–16)
Automechanochores (AM)	4.0 ± 0.25 (0–7)	4.9 ± 0.21 (0–8)	2.6 ± 0.28 (0–7)	3.0 ± 0.33 (0–7)
Myrmecochores (M)	5.6 ± 0.24 (2–9)	8.9 ± 0.29 (3–13)	1.9 ± 0.31 (0–9)	2.9 ± 0.42 (0–11)
Epi- and endozoochores (EE)	4.6 ± 0.23 (1–7)	5.0 ± 0.17 (2–7)	3.3 ± 0.27 (0–7)	3.3 ± 0.26 (0–6)
Semianemochores (SA)	7.6 ± 0.45 (1–15)	9.2 ± 0.51 (3–19)	4.3 ± 0.38 (0–10)	5.7 ± 0.4 (1–14)
Typical anemochores (TA)	6.1 ± 0.42 (1–16)	8.4 ± 0.31 (3–13)	4.2 ± 0.39 (0–11)	6.2 ± 0.49 (0–14)

These proportions changed in different ways between the first and second periods, markedly decreasing in anemochorous species and either remaining at the same level (AM, M) or slightly increasing in other groups (WD, EE).

Total number of species. According to the data obtained during the first observation period, the total number of species per group in the heavy pollution zone, compared to the light pollution zone, decreased in autochores and zoochores (by 24% in WD, 18% in

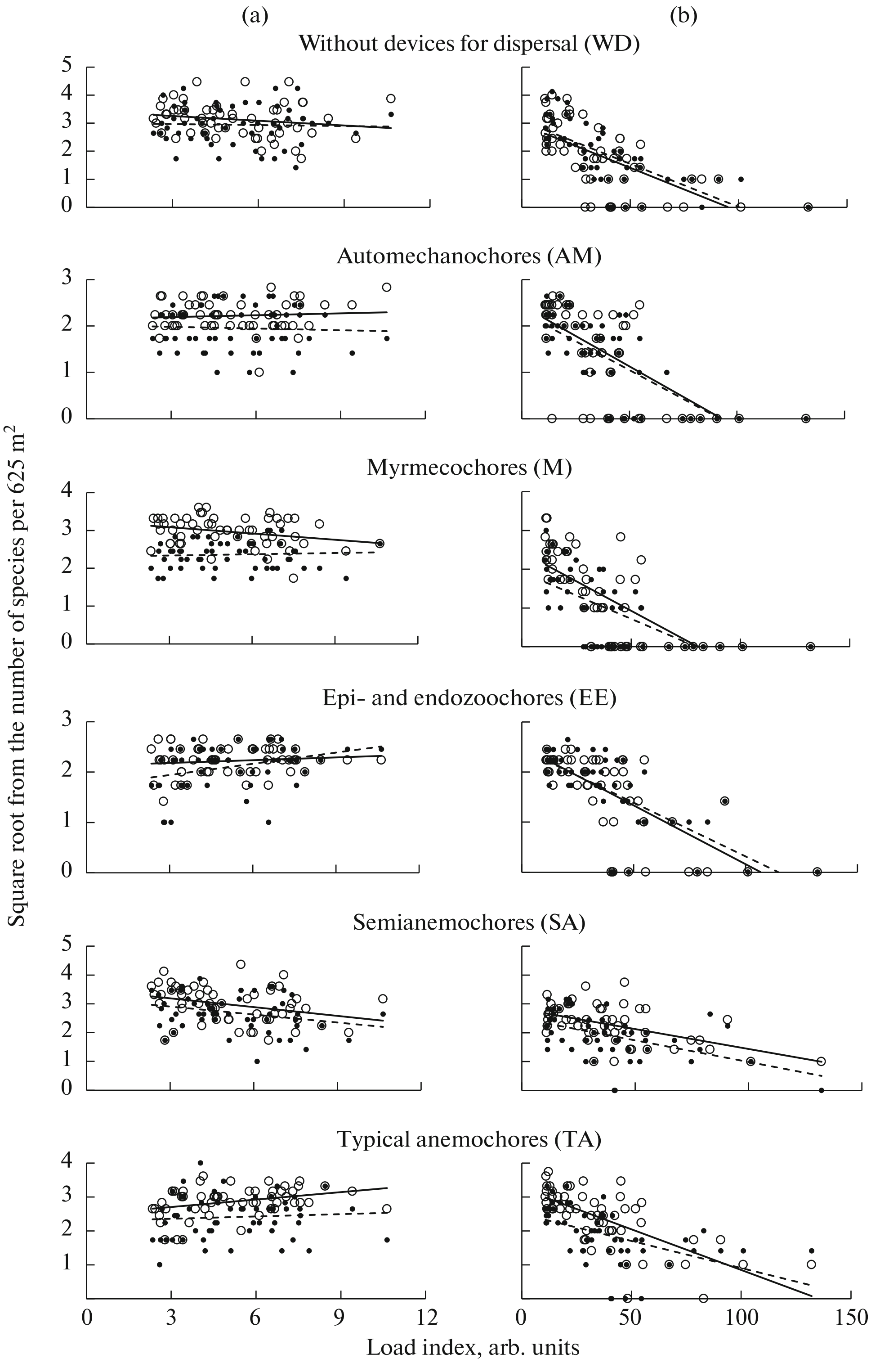

Fig. 1. Changes in species richness along the gradient of toxic load in plant groups with different types of diaspore dispersal under conditions of (a) light and (b) heavy pollution (black circles and dashed line, 1995–1998; white circles and solid line, 2014–2016).

AM, 28% in M, and 19% in EE) but increased in anemochores (by 15% in SA and 3% in TA) (Table 4). On the whole, the total number of species in the heavy pollution zone was only 9% lower than in the light pollution zone. In both zones the total numbers of species in most groups changed insignificantly between the periods: the number of typical anemochores slightly increased in the light pollution zone (there appeared

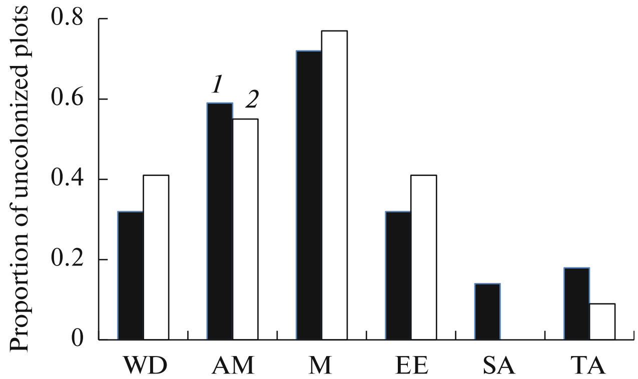

Fig. 2. Proportions of plots not colonized by species with different types of diaspore dispersal under very heavy pollution in the periods of (1) 1995–1998 and (2) 2014–2016. Groups: WD, without devices for dispersal; AM, automechanochores; M, myrmecochores; EE, epi- and endozoochores; SA, semianemochores; TA, typical anemochores.

Epipactis sp., *Senecio nemorensis*, etc.) (see Annex), and the number of myrmecochores increased in the heavy pollution zone (there appeared *Allium victorale*, *Pulmonaria obscura*, etc.), while the number of semianemochores decreased due to the disappearance of *Bupleurum aureum*, *Crepis sibirica*, and some other species.

DISCUSSION

Species with different types of diaspore dispersal proved to differ from each other both in sensitivity to pollution and in the capacity for recolonization after load reduction. However, these results only partially confirm the first hypothesis: the type of dispersal has an effect on the vulnerability of species, but the relationship between vulnerability and the distance of diaspore dispersal remains ambiguous.

Sensitivity to pollution. According to the data obtained during the first observation period, species richness decreased under high pollution levels in all groups, but adverse changes among anemochores were the least prominent (Fig. 1, Table 2). This group was also characterized by the lowest proportion of plots they failed to colonize under very heavy pollution (Fig. 2). Moreover, the total number of anemochorous species even increased in the heavy pollution zone (Table 4).

Differentiation in the response of groups may be due to various causes. In particular, a probable explanation to lower sensitivity to pollution in anemochores is that most of them produce a great amount of generative diaspores, which may spread over large distances due to very small size or the presence of specific structures (e.g., plumes) [14, 17]. This may increase the probability of their occurrence in habitat fragments with more favorable conditions, thereby making the species of this group less sensitive to fragmentation of habitats and deterioration of their quality. The dynamics of species with different types of diaspore dispersal have not been analyzed in the vicinities of other industrial plants, which makes it impossible to judge about the generality of estimates of species sensitivity obtained in this study. However, the data on plant losses in anthropogenically transformed landscapes of Europe also provide evidence that anemochorous species are less sensitive than zoochores and hydrochores [22].

Species loss in all groups was expressed more strongly on the mesoscale (species richness within communities) than on the macroscale (the total number of species per pollution zone). This is in agreement with our data on the dynamics of alpha- and gamma-diversity of plant communities in the study region [41]. Using a more detailed zoning (five pollution zones), we have found that an abrupt decrease in the total number of species occurs only in the close vicinity of the smelter, within a radius of 3 km [41]. However, the species richness of groups in certain habitats could be high even in the zone of heavy pollution (Table 3), providing evidence for an uneven spatial pattern of species elimination and the presence of localities with more favorable environmental conditions. According to our observations, these may be areas near floodplains and creeks, leeward slopes, and areas with single uprooted trees.

The difference in the expression of changes in species richness on meso- and macroscales is indicative of a significant time lag between the elimination of species in local habitats and their disappearance from the study area as a whole. The existence of such a time lag has been shown in several previous studies [2, 43]. Factors interfering with the disappearance of species include their long life span, the existence of dormant stages (seed and spores stored in the soil), and the presence of several local populations within a given area [44]. The survival of individual species under long-term pollution may also be due to inter- and intraspecific differentiation with respect to tolerance for toxicants and adaptation to their excess amount [45, 46], a highly uneven pattern of their distribution in space [41, 47], and spatial heterogeneity of environmental conditions.

Capacity for recolonization after emission reduction. A low recolonization capacity was observed not only in autochores—i.e., species with the shortest range of diaspore dispersal—but also in epi- and endozoochores, whose diaspores are dispersed over the longest distances. Unexpectedly, this capacity in the last two groups proved to be very low, which could be explained by the absence or very low abundance of dispersal vectors in polluted habitats. A significant decrease in the abundance of birds and small mammals in the zones of impact from the MUCS and other copper smelters has been observed in a number of studies [48–52]. Large mammals also contribute significantly to the dispersal of plant diaspores [31, 33, 53]. Although no data on this group of vectors in the

Table 4. Total numbers of species in groups with different types of diaspore dispersal in zones with different toxic loads in 1995–1998 and 2014–2016

Group	Years	Pollution zone (load index, arb. units)	
		light pollution (2.3–10.6)	heavy pollution (10.9–132.1)
Autochores	1995–1998	57	44
	2014–2016	52	43
including:			
without devices for dispersal (WD)	1995–1998	46	35
	2014–2016	43	35
automechanochores (AM)	1995–1998	11	9
	2014–2016	9	8
Zoochores	1995–1998	33	25
	2014–2016	34	30
including:			
myrmecochores (M)	1995–1998	18	13
	2014–2016	19	19
epi- or endozoochores (EE)	1995–1998	16	13
	2014–2016	15	12
Anemochores	1995–1998	72	78
	2014–2016	80	73
including:			
semianemochores (SA)	1995–1998	34	39
	2014–2016	36	34
typical anemochores (TA)	1995–1998	38	39
	2014–2016	44	39
Total number of species	1995–1998	163	148
	2014–2016	166	147

study area are available, it is known that the abundance of large mammals in the present-day biocenotic cover is very low because of the impact of human activities [54].

Information on the recovery of abundance of potential diaspore vectors after emission reduction is scarce. It has been found that reproductive and other parameters of bird communities improve very slowly [55, 56] and that the rate of fruit removal by birds and mammals in degraded ecosystems is still low even several decades after reduction of emissions [57], which is indirect evidence that the abundance of diaspore vectors in the vicinities of industrial plants remains at a low level for a long time.

Myrmecochores are highly sensitive to pollution, but their species richness in the light pollution zone became higher emission reduction, and the total number of species in the heavy pollution zone increased slightly. The positive dynamics of diversity in this group is more distinct than in epi-and endozoochores, which may be explained as follows. The species diversity and abundance of ants do not decrease, but rather increase as the MUCS is approached, with a slight decrease in these parameters being observed only under very heavy loads [58]. It is known that ants play a major role in the dispersal of plant diaspores [34], which is not limited to their transfer in space. Ants consume only the elaiosomes of myrmecochorous plant diaspores, while the seeds remain undamaged and are ejected from the nests. The removal of elaiosomes stimulates germination of seeds, prevents their damage by fungi, and makes them less attractive to small mammals [59]. Temporary storage of diaspores in ant nests also protects them from damage and consumption by animals,

The species richness of typical anemochores has increased in both zones over the past 20 years (Fig. 1, Table 3). Anemochores recolonize polluted habitats more rapidly than species of other groups, probably because that their proportion in the heavy pollution zone is high and that wind as a dispersal agent is ubiquitous and permanent. Large-scale windfall events that occurred in Sverdlovsk oblast in 1995 [60] could also contribute to the aforementioned increase in their species richness, since they are known to promote the abundance of plants characteristic of open and disturbed habitats, and many anemochorous species belong to this category. Although no such events occurred in the plots used in this study, windfall areas in neighboring territories could serve as an abundant source of diaspores.

Differences in recolonization between lightly and heavily polluted plots. The dynamics of species richness in most groups were dependent on pollution load: positive shifts occurred only under low loads, while species richness in the zone of high loads remained at the same level. However, the dynamics of species richness in typical anemochores showed no dependence on pollution load. Thus, our second hypothesis was also confirmed only partially.

One of possible explanation to the absence of positive changes in the species richness of most groups in heavily polluted habitats is that high concentrations of heavy metals in the soil and litter are retained for decades after emission reduction [40]. The dispersal of species over polluted habitats may also be limited by the depth of forest litter, which is increased in the zone of impact from the MUCS [61], and the adverse effect of deep litter on revegetation is well known [62, 63]. Other factors probably limiting the process of recolonization after emission reduction include pollution-induced changes in the herb–dwarf shrub layer: (1) a significant decrease in the number and abundance of species and (2) an increase in the size of the area completely unsuitable for the survival of plants, i.e., deterioration of habitat quality combined with increase in the distance to the sources of diaspores (enhancement of fragmentation). Experimental evidence has been obtained for the effect of diaspore availability and habitat quality on the dynamics of forest species after cessation of agricultural land use and for the adverse influence of habitat fragmentation on immigration of species [10, 25, 26, 37, 64]. No positive changes over decades or extremely slow recovery of species diversity of plant communities after reduction of emissions has been observed in a number of studies [39, 65–67], and our data agree well with the conclusion that plant communities remain in a degraded state for a long time after emissions were reduced.

CONCLUSIONS

Under conditions of long-term pollution with emissions from a copper smelter, an abrupt decrease in the species richness of plants, irrespective of the type of diaspore dispersal, occurs mainly in the zone of high toxic loads. The total number of species (macroscale diversity) decreases to a lesser extent than species richness (mesoscale diversity). Moreover, localities within the high-load zone where species richness remains relatively high have been revealed for all groups. The presence of such localities, combines with a considerable time lag before the extinction of a species from the study area as a whole, may have major significance for recolonization of degraded ecosystems after reduction of emissions.

Although emissions from the MUCS have been greatly reduced over the past 20 years, an increase in species richness has been revealed only in myrmecochores (in the zone of low loads) and typical anemochores (along the entire pollution gradient). In the zone of high loads, however, the species diversity of all groups remains very low, which is evidence for the stability of the degraded state of herb–dwarf shrub layer in the most heavily polluted area.

Species with different types of diaspore dispersal differ in vulnerability to changes in environmental conditions caused by long-term pollution, but the relationship between vulnerability and dispersal distance is ambiguous. Species characterized by the lowest (autochores) and the highest dispersal distance (epi- and endozoochores) show almost equally high sensitivity to pollution and very low recolonization capacity; i.e., they are extremely vulnerable. Myrmecochores are also highly sensitive to pollution, but their recolonization capacity is higher than in the above three groups; and anemochores are the least vulnerable.

The observed differences in the behavior of species with different types of diaspore dispersal are important for understanding trends in the dynamics of plant communities exposed to anthropogenic impact and evaluating the consequences this exposure. Species whose diaspores are dispersed by an abiotic agent such as wind are the least vulnerable in degraded forest ecosystems with the extremely low quality of habitats and high degree of their fragmentation [41], while the most vulnerable species are those whose diaspores either have no species devices for dispersal by external agents (autochores) or are transferred by birds and mammals (epi- and endozoochores). Changes in the contribution of vectors to diaspore dispersal in transformed ecosystems may be a factor responsible for the partial loss of relationship between the distance of diaspore dispersal and the degree of species vulnerability. Moreover, these changes may lead to a shift in the composition and structure of plant communities toward higher proportion of the east vulnerable group, i.e., anemochores (the self-enhancement effect). In such a case, the possibility for transformed communities to recover into typical forest communities of unpolluted habitats is hardly probable.

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SUPPLEMENTARY MATERIALS

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