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Significant Shifts in Predominant Plant Dispersal Modes in Pine Forests of the Southern Urals (Russia): Responses to Technogenic Pollution and Ground Fires

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Abstract: The purpose of this work was to assess the functional diversity of herb–shrub layer communities determined by their dispersal mode in pine boreal forests depending on two factors: (i) the degree of technogenic heavy metal pollution and (ii) the time passed since the last fire. We tested two hypotheses: (1) the functional diversity of communities determined by their diaspore dispersal mode decreases in polluted forests and in forests disturbed by recent fires; (2) the abundance, i.e., participation of anemochorous species in communities, is relatively greater in polluted forests and in forests disturbed by recent fires than in unpolluted or in forests that have not burned for a long time. We analyzed 77 vegetation relevés made in polluted and unpolluted pine forests to obtain the impact gradient of the Karabash copper smelter (South Urals, Russia). The studied forests also had different durations of time since the last ground fire—from 1 to 60 years. Two classifications of the diaspore dispersal modes were used. We found that community functional diversity and predominant dispersal modes changed significantly in response to technogenic pollution and, to a lesser extent, in response to ground fires. In polluted forests, the importance of species with a long diaspore dispersal distance—anemochores and zoochore—increased. This result suggests conducting a specific study of long-distance diaspore migration as a possibly underestimated factor of community formation under severe technogenic disturbances. The importance of zoochore in a broad sense, including species with diaspores dispersed by vertebrates and invertebrates, increased in post-fire succession. This result coincides with the known pattern of increasing abundance of zoochorous plants in regenerative successions in tropical forests. Therefore, the data on plant–animal interactions can possibly provide valuable information on succession mechanisms in taiga forests.

Keywords: diversity of plant communities; functional diversity; seed dispersal mode; types of dissemination; technogenic pollution; heavy metals; ground forest fires; anemochory; zoochory; successions



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1. Introduction

Reproduction, including diaspore production and dispersal, is a key ontogenesis stage of all organisms. The number, mass, range and seed dispersal mode are important traits, according to which the composition of specific communities is formed from species pools through a system of environmental filters [1–3]. The most important characteristic of dispersal success is the dispersal distance of seeds or other diaspores [4], which is clearly related to the dispersal mode [5,6].

Successional changes in the properties of seeds, their mass, and dispersal mode were studied mainly using the example of trees [7–12], rather than herbaceous plants. Another specific feature of the research array on changes in seed properties, their mass, and dispersal modes in successions is that such studies have often been conducted in tropical

forests [12–16]. The results of studying tree successions in tropical forests suggested the relative predominance of anemochorous species at the initial stages of succession and an increase in the abundance of zoochorous species as succession progresses [3,12].

In taiga (boreal forests), the variety of tree species is generally low, and the diversity of plant communities is mainly influenced by the variety of herbs, subshrubs, and shrubs. The ontogenesis of many groundcover forest plant species is shorter than the ontogenesis of woody plants. Therefore, consideration of different adaptations to diaspore dispersal may be as important for understanding the mechanisms of plant community assemblage, mechanisms of herb and shrub species persistence in specific habitats as a similar consideration for woody plants. In the Southern Urals region, the suboptimal conditions for forest vegetation in the zonal forest-steppe ecotone combined with intensive industrial development of the territory result in increased vulnerability of forests to ongoing and expected climate change. The region near the South Urals city of Karabash is a geographically extensive contrasting ecosystem impact region formed by emissions from a large copper smelter (Karabash copper smelter) that has been operating for more than 100 years [17]. The main toxicants are metals from atmospheric emissions [17]. Another constant factor determining the region's vegetation is periodic forest fires [18,19]. Thus, the state of forest communities in this region may be determined not only by the technogenic impact, but also by regular fire disturbances, and different forest areas are at different stages of secondary post-fire succession. As pollution increases, species richness usually decreases, although the effects are not the same across studies (meta-analysis [20–23]). The consequences of forest fires are less predictable and depend on fire intensity and fire frequency [24–26]. The diversity of plant communities after fires can either decrease [24,26,27], or remain unchanged [25,28,29].

The features of biology and dispersal of seeds and diaspores have often been studied in connection with habitat fragmentation [4,30,31]. However, information about the specifics of the herbaceous plant dissemination in forests under the influence of pollution and fires is limited. The study [32] shows that the least vulnerable species to technogenic transformation of habitats are anemochores, whose diaspores can spread far and wide even in the absence of specialized carriers. The abundance of annual species may increase immediately following fires, which may be related to the short maturation time, small size, and easy dispersal of seeds [33]. The abundance of some species with a short ontogenesis after ground, i.e., not total, fires may also be caused by the development of individuals from the soil seed bank [34]. Fire disturbances can affect the number of seed produced by perennial species [35,36].

The purpose of this work is to assess the functional diversity of herb–shrub layer communities determined by the seed dispersal mode in forests that have been polluted by the Karabash copper smelter emissions and have different durations of time since the last fire disturbance. We tested two hypotheses: (1) the functional diversity of communities determined by their diaspore dispersal mode decreases in polluted forests and in forests disturbed by recent fires; (2) the abundance, i.e., participation of anemochorous species in communities, is relatively greater in polluted forests and in forests disturbed by recent fires than in unpolluted or in forests that have not burned for a long time. As can be seen, we assumed similar community responses to different types of disturbances. Hypotheses were formulated as the most probable based on the analysis of known data.

2. Materials and Methods

2.1. Study Area

The study area belongs to the subzone of southern taiga pine–birch forests of the eastern macro-slope of the Southern Urals (Chelyabinsk Region; the vicinity of the city of Karabash and the Ilmensky State Reserve UB RAS; abbreviation—ISR). Typical heights of the uplands are 250–600 m a.s.l. Albic Luvisols and Luvisols soils predominate. According to the Köppen–Geiger classification [37], the climate is cold with short warm summers (code—Dfb). The growing season is 160–170 days; precipitation is about 430 mm per year;

snow cover height is up to 40 cm. Predominant vegetation types are forb pine forests and secondary grass-forb birch forests.

The ISR was established in 1920 and is categorized as IA, Strict Nature Reserve, state nature reserve, according to the International Union for Conservation of Nature classification. The ISR area is 30.4 thousand ha. The average age of the main generation trees in coniferous forests is 80–180 years. On average, 14–16 forest fires are registered in the territory of the ISR per year. The complete fire cycle for the entire reserve is 360 years. Between 1948 and 2014, the number of fires increased [18] and fire localizations changed in the peripheral, border areas of the reserve [19].

The Karabash copper smelter (KCS, Karabashmed JSC, Karabash) is a major source of emissions, the main of which are SO₂ and dust containing mainly Cu, Zn, Pb and Cd. The zone of disturbed ecosystems extends up to 15–25 km from the KCS [17]. Chemical pollution of ecosystems results in a decrease in phytomass and forest productivity [38], a decrease in microbial diversity and biomass in soils [39,40] and changes in the conditions of mineral nutrition of plants [41,42].

2.2. Sample Plots

We studied 77 sample plots (SPs) in maturing, mature and overmature natural pine forests on the middle and lower parts of slopes on Albic Luvisols and Luvisols soils in the absence of waterlogging. Forty-one plots were located at distances of 3.5–12 km from the KCS (impact zone); thirty-six plots were located 25–50 km south of the KCS in the ISR forests (Figure 1). The sample plots were not selected randomly. They were selected in such a way as to cover as wide a range of fire ages as possible. Within the burned forest areas, specific locations for performing vegetation relevés were selected randomly. In the study area, the transfer of air masses from the southwest to the northeast predominates; therefore, the Ilmensky State Nature Reserve, which is located south of the smelter, can be considered a background (control) area by pollution level. The time since the last fire disturbance was represented as the number of years passed between the last recorded fire and the time when the vegetation relevé was performed. Years of fires were established from the Fire Record Books of the Ilmensky Reserve and the Karabash Forestry. The SPs with ground stable medium fires were considered burned; plots with crown fires were not considered. If there were no information about fires in the study area and no visual consequences of fires, such areas were considered unburned for 60 years. The designation for characterizing the duration of the post-fire period is $N_{\text{years no fire}}$.

2.3. Characteristics of Plant Species and Plant Communities

Geobotanical relevés were performed in a 10 × 10 m area in July and the first half of August: 2017—24 SP; 2018—33 SP; 2019—18 SP; 2021—2 SP. The number of herb–shrub species per 100 m² was recorded and the total projective cover (%) of the aerial portions and projective cover (%) of each species of herb–shrub layers were visually assessed. No devices were used to determine the projective cover. The total cover of epigeic mosses on the SPs was determined (%). Names of vascular plant species were given according to the Plants of the World Online [43]. The Shannon diversity index was calculated based on field relevés.

In total, 167 species of the herb–shrub layer were recorded in 77 vegetation relevés. For these species, two approaches were used to determine their dispersal mode.

First, the traditional dispersal mode classification was used. In accordance with this classification, species are divided into groups by their seed dispersal modes with the identification of “dispersal syndromes”, including anemochores, autochores, zoochores and others. We used the following sources: [44–46]. A total of 158 (95%) species were identified as having distribution syndromes according to the traditional classification. Four syndromes were analyzed: anemochores, autochores (including ballistochores), zoochores (including epizoochores and endozoochores), and myrmecochores (Table 1).

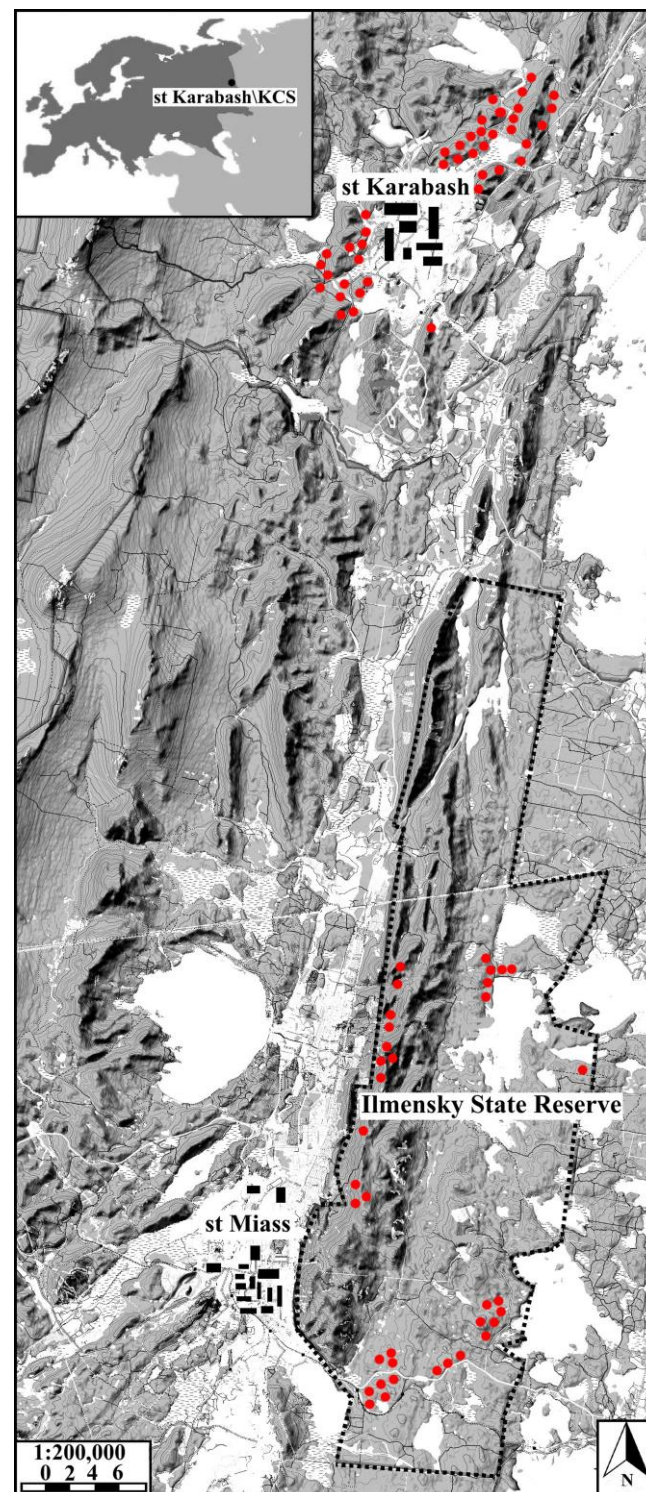


Figure 1. The area of research with locations of sample plots. Note: Red dots—sample plots, dotted boxed—ISR borders.

The second dispersal mode classification is chronologically more recent [47]. The classification is based on the assumption that one species can be adapted to different diaspore dispersal modes, and in accordance with it, so-called “dispersal strategies” are distinguished. To clearly distinguish between the two classification options of seed dispersal modes, we used the terms “traditional classification” and “new classification”. Dispersal strategies for 136 (81%) species according to the new classification were determined on

the basis of information in the Pladias—Database of the Czech Flora and Vegetation [48]. Five strategies were analyzed: *Allium*-type, *Bidens*-type, *Cornus*-type, *Epilobium*-type and *Lycopodium*-type strategies.

Table 1. Number of species, average projective cover and examples of species with different dispersal syndromes according to the traditional classification and with different dispersal strategies according to the new classification.

Dispersal Syndrome/Strategy	Total Number of Species	Mean Value per Relevé in the Entire Set of 77 Relevés (±SE)		Typical Representatives
		Cover	CWM	
Dispersal syndromes according to traditional classification				
Anemochores	58	17.6 ± 1.8	0.32 ± 0.02	<i>Calamagrostis arundinacea</i> (L.) Roth, <i>Sanguisorba officinalis</i> L., <i>Orthilia secunda</i> (L.) House, <i>Lilium pilosiusculum</i> (Frey) Misch.
Autochores	71	16.9 ± 2.1	0.16 ± 0.01	<i>Brachypodium pinnatum</i> (L.) Beauv., <i>Stachys officinalis</i> (L.) Trevis., <i>Lathyrus pisiformis</i> L., <i>Trifolium medium</i> L., <i>Seseli libanotis</i> (L.) Koch, <i>Vicia cracca</i> L., <i>Geranium pseudosibiricum</i> J. Mayer.
Zoochores	16	18.7 ± 1.6	0.41 ± 0.03	<i>Galium boreale</i> L., <i>Vaccinium myrtillus</i> L., <i>Polygonatum odoratum</i> (Mill.) Druce, <i>Rubus saxatilis</i> L., <i>Vaccinium vitis-idaea</i> L.
Myrmecochores	13	8.3 ± 1.3	0.08 ± 0.01	<i>Luzula pilosa</i> (L.) Willd., <i>Carex montana</i> L., <i>Pulmonaria mollis</i> Wulfen ex Hornem.
Dispersal strategies under the new classification				
<i>Allium</i> -type	91	28.9 ± 3.6	0.33 ± 0.03	<i>Adenophora lilifolia</i> (L.) A. DC., <i>Brachypodium pinnatum</i> (L.) Beauv., <i>Galium boreale</i> L., <i>Sanguisorba officinalis</i> L.
<i>Bidens</i> -type	3	0.2 ± 0.1	0.002 ± 0.001	<i>Agrimonia pilosa</i> Ledeb., <i>Geum rivale</i> L., <i>Geum urbanum</i> L.
<i>Cornus</i> -type	8	16.1 ± 1.3	0.39 ± 0.03	<i>Polygonatum odoratum</i> (Mill.) Druce, <i>Rubus saxatilis</i> L., <i>Vaccinium vitis-idaea</i> L.
<i>Epilobium</i> -type	15	9.2 ± 1.2	0.19 ± 0.02	<i>Calamagrostis arundinacea</i> (L.) Roth, <i>Hieracium umbellatum</i> L., <i>Trommsdorffia maculata</i> (L.) Bernh.
<i>Lycopodium</i> -type	19	4.8 ± 0.7	0.09 ± 0.01	<i>Orthilia secunda</i> (L.) House, <i>Pyrola rotundifolia</i> L., <i>Chimaphila umbellata</i> (L.) W.P.C. Barton, <i>Pteridium aquilinum</i> (L.) Kuhn.

Using the F Diversity program [49] and considering dispersal modes as a functional trait, we calculated the community functional diversity characteristics—the FAD and Rao index. The FAD index (functional attribute diversity) is the number of trait combinations occurring in a community; it is always less than or equal to the number of community species. The Rao parameter combines information about species richness and differences in functional characteristics between pairs of species. The community weighted mean (CWM) of plants with different dispersal modes was calculated using estimates of projective cover of species as weights, as shown below:

$$CWM = \sum_{i=1}^S w_i \quad (1)$$

where S is the number of species with this dispersal mode and w_i is the proportion of the i -th species projective cover in the sum of projective covers of all species in the vegetation relevé.

2.4. Determination of Technogenic Impact

Concentrations of Cu, Zn, Pb and Cd were measured in samples from the middle layer of the forest floor. For each SP, sampling was performed at three sites located 5–6 m from each other. At each site, samples were collected using the envelope method from an area of 1 m². One mixed sample was formed from the material collected from the three plots. Decomposition with a mixture of concentrated nitric acid and hydrogen peroxide

was used. This method determined almost all forms of metals present in the forest floor (pseudo total concentrations) [50]. Concentrations of elements were determined with a VARIAN-720-ES atomic emission spectrometer (ICP-OES method) (Agilent Technologies Inc., Santa Clara, USA). Measurements were carried out at the South Ural Collective Center for the Study of Mineral Raw Materials of the Institute of Mineralogy of the Ural Branch of the Russian Academy of Sciences (accreditation certificate No. AAS.A.00330, valid until 3 November 2026). The pollution index was calculated characterizing the average excess (arbitrary units—number of times) of Cu, Zn, Pb, Cd concentrations for four elements in each area compared to the least polluted area [51]. The decimal logarithm ($\text{Log}(\text{PI})$) of the pollution index was used.

The concentrations of Cu varied from 14 to 74 mg/kg in the forest floors of the ISR and from 293 to 6143 mg/kg in forest floors from the KCS; the concentrations of Zn ranged from 78 to 339 mg/kg and from 666 to 4514 mg/kg; the concentrations of Pb ranged from 19 to 76 mg/kg and from 385 to 2952 mg/kg; the concentrations of Cd ranged from 0.62 to 1.91 mg/kg and from 5.35 to 37.70 mg/kg, respectively. That is, on average, the content of metals in the impact zone exceeded their content in the background forests by tens and sometimes hundreds of times. The values of the pollution index in the ISR were from 1 to 4 rel. units, and near the KCS, the values ranged from 15 to 175 rel. units.

2.5. Data Analysis

Pearson's correlation coefficient (r) was used to assess the relationship between variables. The dendrogram was constructed using the distance $(1 - r)$ and the single linkage method. To select the optimal combination of explanatory predictors and to determine the further method of statistical analysis, the AIC calculation was used. We compared the information content of two predictors— $N_{\text{years no fire}}$ and $\text{Log}(\text{PI})$ —and two of their combinations, respectively, including and not including the interaction between the following predictors: (i) $N_{\text{years no fire}} + \text{Log}(\text{PI})$; (ii) $N_{\text{years no fire}} + \text{Log}(\text{PI}) + N_{\text{years no fire}} \times \text{Log}(\text{PI})$. Community characteristic variation patterns depending on $\text{Log}(\text{PI})$ and $N_{\text{years no fire}}$ were analyzed using multiple linear regression. The statistical unit was the sample plot. The arithmetic mean was used as the characteristic of the central tendency; the error of the arithmetic mean or, where appropriate, the error of the standardized partial coefficient of multiple regression is given through the $\pm$ symbol.

3. Results

3.1. The Ratio of Results Obtained Using Traditional and New Classifications

Using estimates of the absolute projective cover of species groups with different dispersal modes, we investigated how the results of the two classifications correlate with each other (Figure 2). Similar variability was observed in projective covers of plants of the following groups (in all cases $n = 77$ and $p < 0.0001$): anemochores and *Epilobium*-type ($r = 0.85$); autochores and *Allium*-type ($r = 0.97$); zoochores and *Cornus*-type ($r = 0.96$); myrmecochores and *Allium*-type ($r = 0.88$).

3.2. Selection of a Combination of Predictors Explaining the Variability of Herb–Shrub Layer Diversity Estimates

We found that the parameter “Number of years since the last fire” was not the best predictor for the diversity characteristics of the herb–shrub layer (Table 2). For the majority of traits, the minimum AIC values were found for the pollution degree predictor. Therefore, $\text{Log}(\text{PI})$ is the optimal predictor in terms of quality/complexity to explain variability in many community diversity characteristics. However, for some of the functional diversity characteristics, the minimum AIC values were found for the combination of predictors $N_{\text{years no fire}} + \text{Log}(\text{PI})$. For a small number of characteristics, minimum AIC values were found for the following combination including interaction between the predictors: $N_{\text{years no fire}} + \text{Log}(\text{PI}) + N_{\text{years no fire}} \times \text{Log}(\text{PI})$.

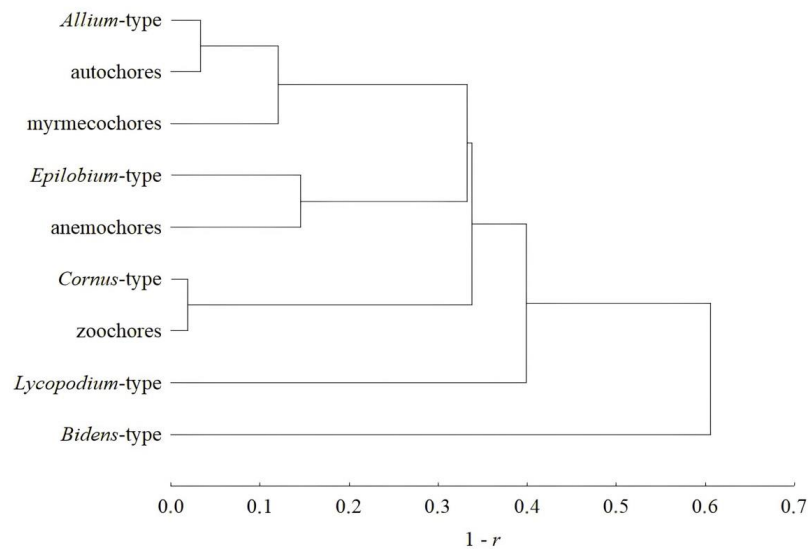


Figure 2. Similarity dendrogram of projective cover variability of species groups with different dispersal syndromes/strategies.

Table 2. AIC values for different combinations of predictors explaining the variability of herb–shrub and moss layer state characteristics, as well as functional diversity characteristics of herb–shrub layer determined by dispersal modes. Gray-blue shading indicates minimum AIC values in each row.

Characteristics	Number of Years Since the Last Fire— N years no fire	Pollution Index— $\text{Log}(\text{PI})$	Predictor Combination	
			Without Interaction: N years no fire + $\text{Log}(\text{PI})$	with Interaction: N years no fire + $\text{Log}(\text{PI})$ + N years no fire $\times$ $\text{Log}(\text{PI})$
State characteristics of the herb–shrub and moss layers				
Number of species of the herb–shrub layer per 400 m ²	624.81	560.84	562.83	564.81
Shannon index	193.57	120.47	122.39	123.99
Projective cover of				
Herb–shrub layer	709.98	646.13	648.13	650.12
epigeic mosses	754.96	710.67	705.72	706.91
Functional diversity: dispersal syndromes according to the traditional classification				
Projective cover of species groups				
Anemochores	648.16	624.16	623.75	623.93
Autochores	669.34	608.86	609.06	607.81
Zoochores	624.68	540.41	541.23	542.68
Myrmecochores	589.15	534.79	536.35	538.29
CWM				
Anemochores	−30.41	−31.48	−33.24	−31.28
Autochores	−91.60	−110.74	−109.01	−111.90
Zoochores	9.72	0.55	−3.06	−1.42
Myrmecochores	−148.42	−208.07	−206.09	−204.13
FAD	233.57	199.86	200.10	200.63
Rao's quadratic entropy	−33.15	−68.71	−67.87	−67.72
Functional diversity: dispersal strategies according to the new classification				
Projective cover of species groups				
<i>Allium</i> -type	753.03	683.76	684.76	684.88
<i>Bidens</i> -type	241.53	243.38	236.97	236.97
<i>Cornus</i> -type	596.04	531.02	532.13	533.26
<i>Epilobium</i> -type	573.61	568.95	566.38	548.30
<i>Lycopodium</i> -type	508.26	495.18	497.12	498.31
CWM				
<i>Allium</i> -type	7.54	−45.84	−43.88	−47.16
<i>Bidens</i> -type	−495.24	−493.16	−499.06	−499.06
<i>Cornus</i> -type	16.56	2.27	−1.94	−0.31
<i>Epilobium</i> -type	−42.00	−42.75	−44.21	−42.26
<i>Lycopodium</i> -type	−113.66	−115.00	−113.28	−112.69
FAD	151.23	132.24	133.87	135.55
Rao's quadratic entropy	−31.48	−43.90	−41.91	−41.89

Thus, the parameter “Number of years since the last fire” should not be completely excluded from the analysis when explaining the functional diversity of communities. It seems optimal to use the following combination of both predictors, but not including their interaction: $N_{\text{years no fire}} + \text{Log(PI)}$. This approach allowed us to use multiple regression to assess the direction and strength of the predictors’ influence.

3.3. Direction and Strength of Influence of $N_{\text{years no fire}}$ and Log(PI) on Diversity Parameters

The direction and strength of influence of the predictors $N_{\text{years no fire}}$ and Log(PI) on the community diversity parameters were judged by the values of the standardized partial coefficients of multiple regression (β). The overall quality of multiple regressions was judged by the value of R^2_{adj} (Table 3).

Table 3. Parameters of multiple linear regression equations describing the dependence of herb–shrub and moss layer state characteristics, as well as functional diversity characteristics of herb–shrub layer according to the time since the last fire and pollution level. Gray shading indicates cases of significant influence of predictors.

Characteristics	Number of Years Since the Last Fire— $N_{\text{years no fire}}$		Pollution Index— Log(PI)		R^2_{adj}
	$\beta \pm SE$	p	$\beta \pm SE$	p	
State characteristics of the herb–shrub and moss layers					
Number of species of the herb–shrub layer per 400 m ²	−0.016 ± 0.076	0.8361	−0.764 ± 0.076	<0.0001	0.57
Shannon index	−0.035 ± 0.072	0.6271	−0.790 ± 0.072	<0.0001	0.61
Projective cover of					
Herb–shrub layer	−0.020 ± 0.074	0.7841	−0.776 ± 0.074	<0.0001	0.59
epigeic mosses	0.146 ± 0.086	0.0937	−0.647 ± 0.086	<0.0001	0.45
Functional diversity: dispersal syndromes according to the traditional classification					
Projective cover of species groups					
Anemochores	−0.193 ± 0.096	0.0475	−0.571 ± 0.096	<0.0001	0.32
Autochores	−0.015 ± 0.077	0.8497	−0.759 ± 0.077	<0.0001	0.56
Zoochores	0.078 ± 0.065	0.2351	−0.818 ± 0.065	<0.0001	0.68
Myrmecochores	0.012 ± 0.080	0.8795	−0.733 ± 0.080	<0.0001	0.53
CWM					
Anemochores	−0.215 ± 0.110	0.0542	0.244 ± 0.110	0.0297	0.10
Autochores	−0.130 ± 0.102	0.2070	−0.491 ± 0.102	<0.0001	0.22
Zoochores	0.222 ± 0.106	0.0391	0.403 ± 0.106	0.0003	0.17
Myrmecochores	−0.001 ± 0.076	0.9942	−0.763 ± 0.076	<0.0001	0.57
FAD	0.129 ± 0.090	0.1579	−0.609 ± 0.090	<0.0001	0.39
Rao’s quadratic entropy	0.115 ± 0.090	0.2039	−0.615 ± 0.090	<0.0001	0.39
Functional diversity: dispersal strategies according to the new classification					
Projective cover of species groups					
<i>Allium</i> -type	−0.024 ± 0.072	0.7410	−0.795 ± 0.072	<0.0001	0.62
<i>Bidens</i> -type	0.175 ± 0.112	0.1233	−0.201 ± 0.112	0.0773	0.06
<i>Cornus</i> -type	0.089 ± 0.074	0.2325	−0.758 ± 0.074	<0.0001	0.59
<i>Epilobium</i> -type	−0.264 ± 0.106	0.0151	−0.368 ± 0.106	0.0009	0.16
<i>Lycopodium</i> -type	0.012 ± 0.106	0.9077	−0.416 ± 0.106	0.0002	0.15
CWM					
<i>Allium</i> -type	−0.109 ± 0.081	0.1852	−0.725 ± 0.081	<0.0001	0.50
<i>Bidens</i> -type	0.172 ± 0.113	0.1304	−0.195 ± 0.113	0.0870	0.05
<i>Cornus</i> -type	0.218 ± 0.102	0.0357	0.496 ± 0.102	<0.0001	0.22
<i>Epilobium</i> -type	−0.198 ± 0.111	0.0784	0.227 ± 0.111	0.0442	0.08
<i>Lycopodium</i> -type	0.036 ± 0.116	0.7553	0.133 ± 0.116	0.2561	0.01
FAD	0.064 ± 0.102	0.5308	−0.474 ± 0.102	<0.0001	0.22
Rao’s quadratic entropy	0.010 ± 0.108	0.9279	−0.391 ± 0.108	0.0005	0.13

Standard characteristics of the herb–shrub and moss layers state—number of species, Shannon index and projective cover—depended only on the pollution level. The effects

associated with pollution were significant at a high statistical level (in all cases $p < 0.0001$). The effects associated with the parameter “Number of years since the last fire” were not statistically significant. Pollution was associated with more than a half (58%–62%) of the total variability in the herb–shrub layer state characteristics and slightly less than a half (44%; this value of the coefficient of determination indicates a weak effect) of the variability in projective cover of epigeic mosses (Figure 3). As the heavy metal content in the forest floor increased, all characteristics of the herb–shrub and moss layers decreased, including the species richness and Shannon index value by 2–3 times; herb–shrub layer projective cover by 3–5 times; mosses projective cover by more than an order of magnitude, which is explained by the almost complete disappearance of ground mosses in the forests near the plant. Also, as pollution increased, the absolute projective cover of all groups of species distinguished by dispersal mode decreased.

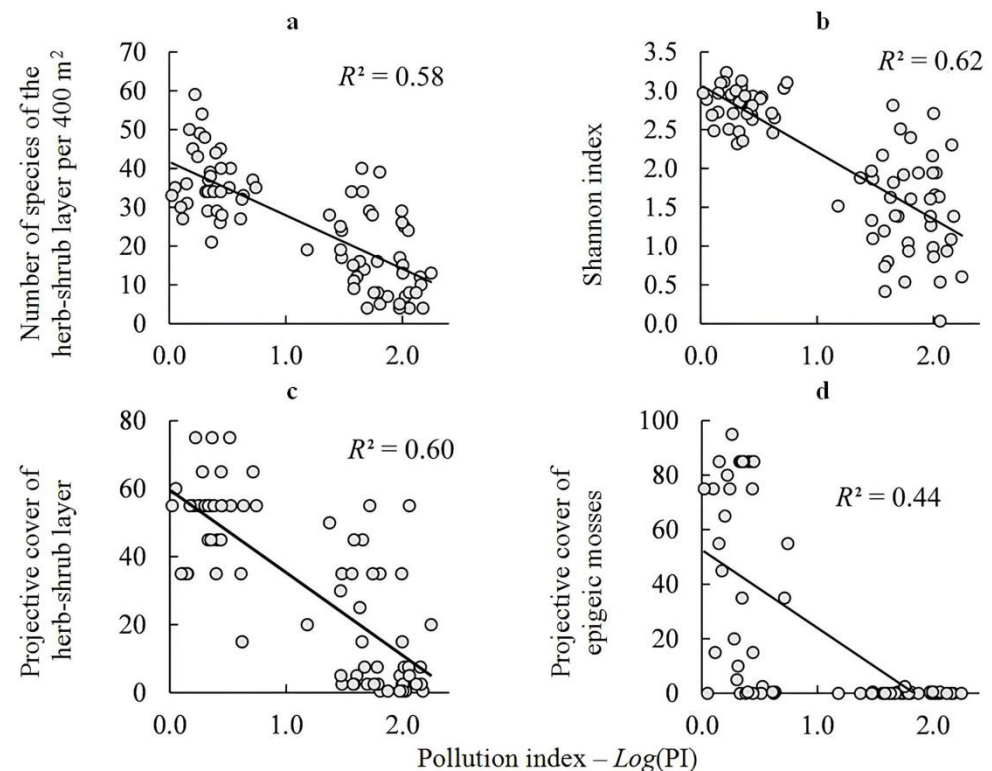


Figure 3. Changes in species richness (a), diversity (b) and projective cover (c) of the herb–shrub layer and projective cover of epigeic mosses (d) with increasing pollution. The determination coefficient values are shown for straight line approximation.

The characteristics of functional diversity and the proportions of functional groups of species depended either solely on the pollution level or more strongly on the pollution level rather than on the time since the last fire. Species groups with different dispersal modes were sensitive to pollution to different extents. This is evident from the dynamics of CWM values. Using the traditional classification, a significant effect of pollution level dependence was found for CWM myrmecochores, but weak effects were found for CWM anemochores, CWM autochores, and CWM zoochores (Figure 4). However, even the weakest effects were statistically significant at the level of $p < 0.05$. As pollution increased, the participation of autochores (by 2–2.5 times) and myrmecochores (by contrast, by tens of times) in community formation decreased. At the same time, the participation of anemochores and zoochores increased by approximately 1.5 times. Using the new classification, statistically significant dynamics of CWM values were established for *Allium*-type, *Cornus*-type, and *Epilobium*-type species; however, for *Cornus*-type and *Epilobium*-type species, the effects were weak. (Figure 5). As pollution increased, the participation of *Allium*-type species in community formation decreased (by 3–4 times). At the same time, the participation of *Cornus*-type and

Epilobium-type species increased by 1.7–2 times. The dynamics of CWM values for *Bidens*-type and *Lycopodium*-type species depending on the level of pollution were insignificant.

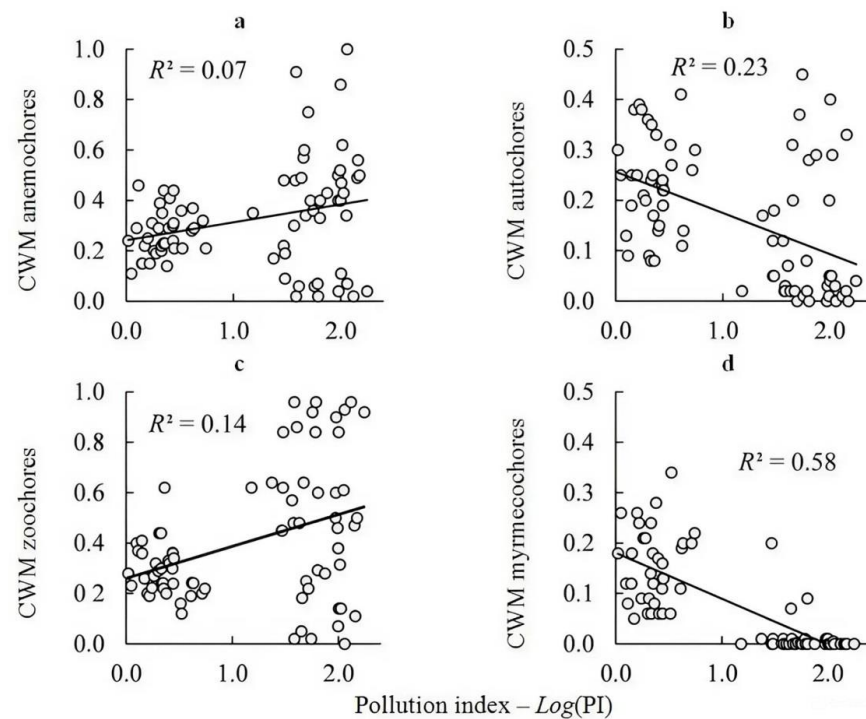


Figure 4. Changes in CWM of species groups with different dispersal syndromes according to the traditional classification: anemochores (a), autochores (b), zoochores (c) and myrmecochores (d) with increasing pollution. The determination coefficient values are shown for straight line approximation.

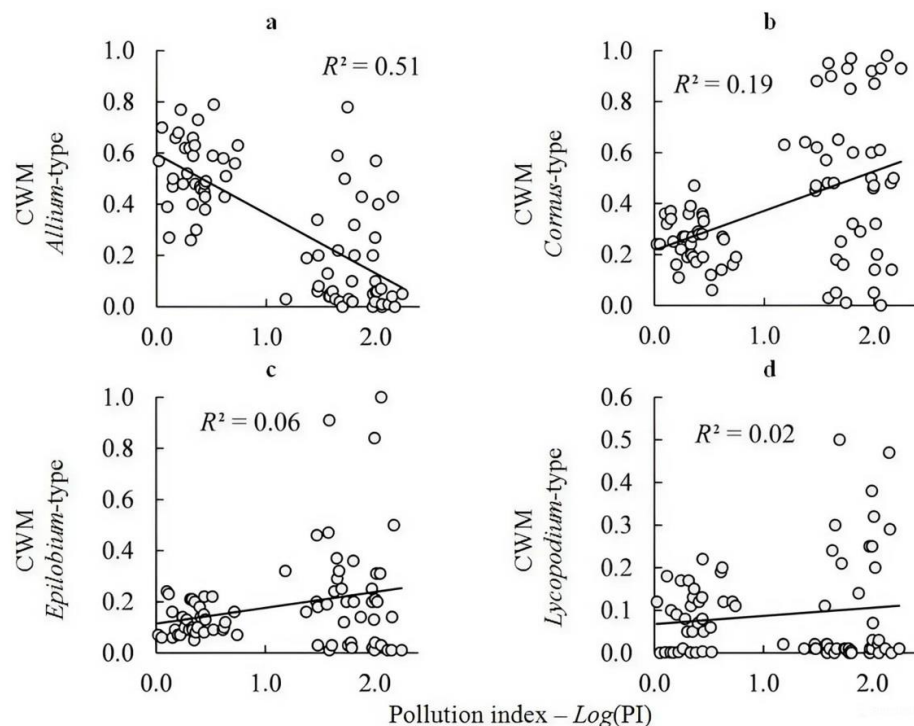


Figure 5. Changes in CWM of species groups with different dispersal strategies according to the new classification: *Allium*-type (a), *Cornus*-type (b), *Epilobium*-type (c) and *Lycopodium*-type (d) with increasing pollution. The determination coefficient values are shown for straight line approximation.

The effects on functional diversity characteristics associated with the time since the last fire were rare and statistically weak ($p \approx 0.04$). Using the traditional classification, we found that the participation of zoochores in community formation increased during post-pyrogenic recovery. Using the new classification, as the post-fire period increased, the CWM of *Cornus*-type species increased as well.

The FAD and Rao's quadratic entropy decreased with pollution and did not depend on the time since the last fire disturbance. At the same time, FAD and Rao were less determined by the predictors included in the multiple regression than species-based characteristics. The range of R^2_{adj} values for the FAD and Rao parameters was $R^2_{\text{adj}} = 0.13\text{--}0.39$, and for the number of species and the Shannon index, $R^2_{\text{adj}} = 0.57\text{--}0.61$.

3.4. The Ratio of Species Groups with Different Diaspore Dispersal Distances in Connection with Pollution

Dispersal syndromes identified according to the traditional classification can be ranked by diaspore dispersal distance. Although there is a controversy about the actual seed dispersal distances in forests [6], we assumed that different syndromes can be characterized by the following approximate dispersal distances for most seeds [5,6]:

- Autochores and myrmecochores—seeds disperse not far, from tens of centimeters to tens of meters;
- Anemochores and zoochores—seeds disperse far, from tens to hundreds of meters, possibly further.

The type of dependencies in Figure 4 suggests that under pollution conditions, the contribution to community formation of species dispersing over long distances increases while the total CWM of species dispersing over short distances decreases. We tested this hypothesis by running multiple regression analyses for the “autochores + myrmecochores” and “anemochores + zoochores” groups (Table 4). Our assumption was confirmed: the CWM of the “anemochores + zoochores” group increased as pollution increased (Figure 6a), while the CWM of the “autochores + myrmecochores” group decreased.

Table 4. Parameters of multiple linear regression equations describing the dependence of the CWM of functional species groups with different distances and seed dispersal agents by the time since the last fire and pollution level. Gray shading indicates cases of significant influence of predictors.

Characteristics	Number of Years Since the Last Fire— $N_{\text{years no fire}}$		Pollution Index— $\text{Log}(\text{PI})$		R^2_{adj}
	$\beta \pm SE$	p	$\beta \pm SE$	p	
CWM of functional groups with different seed dispersal distances					
Autochores + myrmecochores	-0.090 ± 0.084	0.2872	-0.704 ± 0.084	<0.0001	0.47
Anemochores + zoochores	0.064 ± 0.082	0.4377	0.717 ± 0.082	<0.0001	0.49
CWM of functional groups with different seed dispersal agents					
Autochores + anemochores	-0.265 ± 0.113	0.0219	-0.068 ± 0.113	0.5513	0.05
Myrmecochores + zoochores	0.244 ± 0.113	0.0342	0.146 ± 0.113	0.2007	0.05

It should be noted that simultaneous analysis of the combined groups “anemochores + zoochores” and “autochores + myrmecochores” is redundant since theoretically, their CWM is related by the following ratio:

$$\text{CWM (anemochores + zoochores)} = 1 - \text{CWM (autochores + myrmecochores)}. \quad (2)$$

But this relationship is not fulfilled exactly because dispersal syndromes are not known for all species. Since the syndromes for some species are unknown, the multiple regression results for these groups are not completely symmetrical.

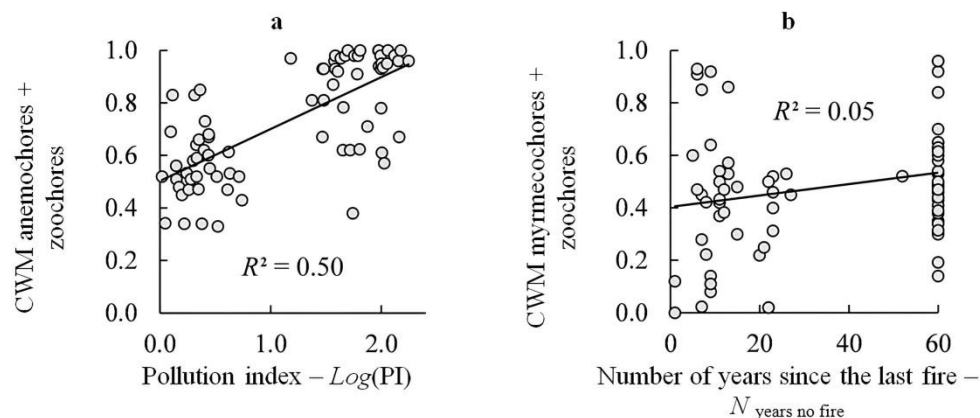


Figure 6. Change in the CWM of the “anemochores + zoochores” group depending on pollution level (a) and change in the CWM of the “myrmecochores + zoochores” group depending on the time since the last fire (b). The determination coefficient values are shown for straight line approximation.

3.5. The Ratio of Species Groups with Different Diaspore Dispersal Agents in Relation to the Time Since the Last Fire Disturbances

Using traditional classification, dispersal syndromes can be ranked not only by the seed dispersal distance but also by the agents responsible for it. We identified two groups of dispersal mechanisms as shown below:

- Seeds are dispersed without animals—anemochores and autochores;
- Seeds are dispersed by invertebrates and vertebrates—myrmecochores and zoochores.

The analysis of β -coefficients characterizing the dependence of the CWM of species groups in connection with the time since the last fire suggested that during post-pyrogenic recovery, the CWM of anemochores and autochores decreases, while the CWM of myrmecochores and zoochores, respectively, increases. We tested this hypothesis using multiple regression (see Table 4). Our assumption was confirmed. The CWM groups allocated by seed dispersal agents did not depend on pollution but were related to the time since the last fire. The CWM of the “anemochores + autochores” group decreased during post-fire recovery (Figure 6b), while the CWM of the “myrmecochores + zoochores” group increased accordingly. Judging by the determination coefficient values, the pyrogenic dynamics of the CWM of species groups dispersing with different agents was very weak, although statistically significant.

4. Discussion

Both working hypotheses were only partially confirmed. The aspects related to the effects of technogenic pollution were found to be correct. In polluted forests, the functional diversity of the herb–shrub layer was lower compared to unpolluted forests, while the presence of anemochoric species was higher. General diversity characteristics did not depend on the time since the last fire, but we found a slight increase in the participation of animal-dispersed species as post-fire recovery progressed. According to our estimates, traditional diversity measures that do not take into account species heterogeneity—the number of species and the Shannon index—were more sensitive and changed significantly as pollution increased compared to the parameters that take into account species heterogeneity in dispersal modes. This is explained by the functional duplication of taxa. A similar pattern of functional diversity relative stability was found when studying the drought effects [52]. However, sometimes, functional diversity is as sensitive as traditional diversity measures [53,54].

4.1. Impact of Pollution

Under the influence of heavy metal pollution, the herb–shrub layer communities changed significantly. This is evident from the sharp decrease in taxonomic diversity near

the factory similar to what is usually observed near industrial enterprises [17,20–23]. It is important to consider that technogenic changes in functional diversity and ratios of groups of species with different diaspore dispersal modes occurred along with a drastic decrease in plant abundance. Therefore, we tend to explain the increase in the contribution of anemochore and zoochore species to the community formation observed under pollution by the fact that autochores and myrmecochores are more sensitive to pollution impact, while anemochores and zoochores are less sensitive, i.e., relatively more resistant. The similar resistance of anemochores in forests under polymetallic pollution was demonstrated in the vicinity of another factory in the Urals [32].

The response of some groups identified by their dispersal mode is partly understandable. For example, ant diversity and abundance decrease in forests near the KCS [55]. Although the study [55] was conducted in birch forests and included observations in areas with heavily damaged vegetation, it can be assumed that the deteriorated state of ant communities due to pollution may be one of the reasons for the lower distribution of myrmecochorous herbs. The increased CWM of anemochores in polluted forests may reflect not only changes in the forest environment, but also the transformation of adjacent non-forest areas. In the KCS area, fragments of forest ecosystems alternate with heavily anthropogenically transformed industrial, agricultural and residential areas. This environment is a likely source of seeds of edge species capable of long-range dispersal [4]. In general, high abundance of species with long seed dispersal distances, including anemochores, may be a sign of disturbance of the ecosystems themselves or their environment [4,32,33].

The established relative resistance of anemochores and zoochores to pollution allowed us to suggest that species survival near the KCS may be related to the diaspore dispersal distance. It is possible that under pollution, when survival of individuals is hampered by toxic substrates, the maintenance of local populations depends on a constant flow of diaspores from less disturbed habitats. A strong decrease in the number of seedlings from soil seed banks was found earlier in this pollution gradient [56]. In this study [56], it was found that the number of seedlings from the soil seed bank decreased by 5–8 times under conditions of severe pollution, while the proportion of dicotyledons in the total number of seedlings increased. However, connection between the number of seedlings and the parameter “Number of years since the last fire” could not be established. This supports the hypothesis that a constant influx of seeds from distant habitats is important for the stable existence of species under pollution.

4.2. Impact of Fires

The direction and strength of fire impact on plant communities depend on the severity of fires and, accordingly, on the degree of post-fire disturbances [24–26]. We assessed the consequences of low-intensity ground fires in which trees and forest stands did not die. The consequences of such fires were not detected by standard geobotanical characteristics. We found no relationship between the time since the last fire disturbances and community diversity and the overall abundance of the herb–shrub layer. Similar conclusions of no change in plant diversity in response to fire disturbance have been observed in some studies [25,28,29], although a decrease in plant diversity was observed about as often after fires [24,26,27].

It is therefore unexpected that the ratio of species groups dispersed by different agents, although not strongly, changed in a direction depending on the time since the last fire. During post-fire succession, the CWM of zoochores in the broad sense increased including species with diaspores dispersed by vertebrates and invertebrates. In general, different plant species are known to be differentially resistant to fire disturbance and therefore affected by fire in different ways [28,29]. This is the basis for distinguishing such groups as pyrophytic, early- and late-successional species. Our data showed that one of the traits differentiating herbs in post-fire succession may be the degree of adaptation to seed dispersal by animals. The established increase in the importance of zoochory is a common feature in post-fire succession of the herb–shrub layer of pine forests and in restoration

successions of tropical forests [3,12]. This similarity allows us to cautiously suggest that the pattern of successional strengthening of zoochorous plants is a general pattern reproduced in different biomes and in different succession types.

4.3. The Correspondence Between “Dispersal Syndromes” and “Dispersal Strategies”

The four dispersal syndromes used according to the traditional classification had closely varying analogs among the six dispersal strategies identified according to the new classification. This is understandable since we have classified the same set of species using two approaches. The list of partial flora species of pine forests is rather small. The basis of a particular syndrome/strategy’s projective cover is often created by one, two or several abundant species. For example, common abundant anemochores and *Epilobium*-type species were *Calamagrostis arundinacea* (L.) Roth (the most common species of the herb–shrub layer) and *Chamaenerion angustifolium* (L.) Scop. (a typical and sometimes common species in areas disturbed by fire). A common abundant species of autochora and *Allium*-type is *Brachypodium pinnatum* (L.) Beauv. Commonly abundant zoochoric and *Cornus*-type species are the dominant or common species *Polygonatum odoratum* (Mill.) Druce, *Rubus saxatilis* L. and *Vaccinium vitis-idaea* L. Close coincidence of the different functional groups’ dynamics can be shown not only by calculating the correlation coefficients, as shown above. We can see that similarly varying groups had similar changes in value in the condition gradient. For example, as pollution increased, the CWM of both anemochores and *Epilobium*-type, as well as zoochores and *Cornus*-type, increased as well. On the contrary, the CWM of both autochores and *Allium*-type decreased significantly as pollution increased.

5. Conclusions

We used elements of functional diversity analysis and two classifications of plant dispersal modes to understand whether the characteristics of diaspore dispersal are associated with technogenic and fire disturbances of the herb–shrub layer of pine forests in the Southern Urals. We found strong changes in the contributions of species with different seed dispersal modes depending on heavy metal pollution. In polluted forests, the importance of species with a long-distance diaspore dispersal—anemochores and zoochores—increased. This result suggests the need for a special study of the significance of long-distance diaspore dispersal as a probably underestimated factor in the community structure formation under severe technogenic disturbances.

The effects associated with fire disturbances were weaker than those associated with pollution. However, we found that zoochores in the broad sense, including species with diaspores dispersed by vertebrates and invertebrates, increased in importance during post-fire succession. This result seems important to us for two reasons. First, we found no relation with the time since the last fire for traditional community diversity characteristics not considering functional differences between species. We also found no relation with the time since the last fire for soil seed bank parameters [56] and for functional diversity parameters based on Grime’s ecological strategies [57]. But the dispersal modes, although not by much, changed with the time passed since the last fire. Consequently, the characteristics of seed dispersal probably determine the positions of herb species in the post-fire habitat mosaic in the Southern Urals taiga. Second, the increase in the importance of animals in seed dispersal in the post-fire succession of the herb–shrub layer in pine forests closely coincides with the well-known pattern of the increase in the abundance of zoochorous plants in restoration successions in tropical forests. Therefore, it is possible that the information on plant–animal interactions can provide valuable data about the succession mechanisms in taiga forests, which have been studied less than succession in tropical and subtropical regions.

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