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Species richness and resilience of forest communities: combined effects of short-term disturbance and long-term pollution

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Abstract Recovery of the species richness of plant communities after experimental disturbances of various severities were studied in spruce forests polluted by atmospheric entry of SO_2 and heavy metals from a copper smelter. In the three toxic load zones (impact, buffer, and background), 60 experimental "pit-and-mound" complexes (sized 1 m × 2 m, 20 complexes in each zone) were created. Colonization of disturbed areas by vascular plants was observed during a 6-year period after the disturbance. The results showed that the recovery processes were affected by disturbance severity and that the recovery differed significantly among the communities. In all of the zones, species richness increased rapidly after mild disturbance. In degraded communities, levelling of differences in the rate of colonization after mild and severe disturbances was observed. The highest colonization rate was found in the communities of background zone, while the lowest was found in the heavily degraded communities of impact zone. The disturbances significantly increased the species diversity of communities in all zones and caused a certain reversion of degraded communities to previous stage of anthropogenic succession. Mild disturbance promoted the greatest increase in the diversity indices. The study results indicate that recovery rate of species richness of plant communities is determined by the duration of negative effect of disturbances. Recovery also depends significantly on the magnitude and endurance of positive effect of disturbances. The studied communities differed significantly in these parameters. The study results also suggest that short-term disturbances can significantly modify the process of transformation of plant communities by atmospheric pollution. On the other hand, long-term pollution can considerably modify the response of forest communities to disturbances. The results also conclude that the resilience of communities does not exclusively depend on their species richness.

Keywords Copper smelter · Spruce forests · Species diversity · Recovery · Succession · Vascular plants

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Introduction

Short-term disturbances (windfalls, fires, eruptions, etc.) constitute an inalienable part of natural ecosystems and they play an important role in their structural organization and dynamics (Georgievsky 1992; Falinski 1978; Frelich and Reich 1999; Forest et al. 1998; Kuuluvainen 1994; Peterson and Pickett 1995; Skvortsova et al. 1983; Turner et al. 1998; Ulanova 2000). Currently, many ecosystems are subject to long-term anthropogenic stress exposure, which had led to significant decrease in biodiversity, and to changes in their composition and structure. Such changes can even modify ecosystem functions (Hooper et al. 2005; Peterson et al. 1998), e.g., their responses to natural disturbance. In this regard, questions concerning the functional after-effects of biodiversity decrease, and the changes in the composition and structure of the communities, are becoming issues of current importance.

An important component of the general stability of communities is resilience (recovery ability), in particular the time needed to return to the initial state after some perturbation. The majority of community resilience investigations have been carried out in grasslands (Lavorel 1999; McNaughton 1977; Tilman and Downing 1994; Whitford et al. 1999; see also review Hooper et al. 2005) or in forest ecosystems (Skvortsova et al. 1983; Cooper-Ellis et al. 1999; Hautala et al. 2001, 2008; Jonsson and Essen 1998; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004), which had not been affected by atmospheric pollution. Meanwhile, environmental pollution is one of the most wide-ranging types of long-term anthropogenic stresses. It has caused significant decreases in biodiversity and also changes in the composition and structure of the forest ecosystems (Vorobeichik et al. 1994; kompleksnaya ecologicheskaya 1992; lesnye ekosystemy 1990; Lukina and Nikonov 1993; Makhnev et al. 1990; Smith 1985; Trubina and Makhnev 1997; Chernenkova 2002; Bobbink et al. 1998; Freedman and Hutchinson 1980; Lee 1998; Salemaa et al. 2001).

Recovery rate of forest communities depends on their diversity, composition, and structure at the time of the disturbance (Forest et al. 1998; Jonsson and Essen 1998; Hooper et al. 2005; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004; Skvortsova et al. 1983; Turner et al. 1998). In a degraded forest ecosystems, one can expect certain changes in recovery, e.g., the decrease in colonization rate and recovery ability of species richness on the whole. On the other hand, under atmospheric pollution, short-term disturbances may also considerably modify processes of ecosystem transformation, e.g., they may accelerate or slow down the decreasing species richness.

These assumptions were examined experimentally in the vicinity of a functioning copper smelter. Spruce forests of the area have been affected by long-term emissions of heavy metals and sulfur dioxide since 1940. In 1999, 60 pit-and-mound complexes, partly imitating treefall disturbance, were created in the area. Recovery of vegetation on the plots was followed during 6 years. The objectives of this work were: (1) to describe the recovery of vascular plant species richness after different levels of disturbance severity, and (2) to evaluate the degree of modifying influences of the short-term disturbances on species richness of forest plant communities under long-term pollution.

Methods

The investigation was carried out in the vicinity of a copper smelter located near the town of Revda, 50 km west of Ekaterinburg in the Middle Urals. The area belongs to the southern taiga phytogeographical subzone with a forest cover of about 60% consisting mostly of secondary forests with mixed coniferous and deciduous trees as well as birch and aspen stands (Kolesnikov et al. 1973). The most common dominants of the overstorey include *Pinus sylvestris* L., *Picea obovata* (Ledeb.), *Betula pendula* (Roth.), *B. pubescens* (Ehrh.), *Abies sibirica* (Ledeb.), and *Populus tremula* L. Climate of the area is moderately continental, annual precipitation level is 400–600 mm on average, while depth of snow cover is 40–50 cm and more. Average annual temperature is +1°C, while during January and July temperatures are between −16°C to −17°C and +16°C to +18°C, respectively. The length of frost-free period is 90 days and the prevailing winds are westerly and southwesterly (Prokaev 1976).

The copper smelter has been operating since 1940, emitting a mass of particulate and gaseous pollutants (in a ratio of 1:8), of which sulfur dioxide makes up 98.7% of the gaseous pollutants, while copper, zinc, arsenic, and lead constitute 46.9%, 31.5%, 11.5%, and 10.1% of the particulate pollutants, respectively (Vorobeichik et al. 1994). The study sites were established in coniferous forest stands in three zones, which had been determined earlier according to the degree of forest community transformation in previous investigations (Vorobeichik et al. 1994): the impact—the zone of high load (distance from the source of emission 1 km), the buffer—the zone of intermediate load (6 km), and the background—the zone of low load (30 km). The soils of the sites are mountain forest brown soils. The tree layer has a multilayered canopy and an uneven age structure. The dominating tree species include Siberian spruce (*Picea obovata*) and Siberian fir (*Abies sibirica*), of which a few are up to 140 years old. In addition, some deciduous trees occur, of which silver birch (*Betula pendula*) is the most abundant. Detailed information on the contents of toxicants, soil characteristics, and changes in forest communities in these areas have been described earlier in the publications by Gol'dberg (1997), Kaigorodova and Vorobeichik (1996), Vorobeichik et al. (1994), and Vorobeichik and Hantemirova (1994).

Ground vegetation of the background zone consists of a mix of the following dominants and co-dominants: *Oxalis acetosella*, *Aegopodium podagraria*, *Gymnocarpium dryopteris*, *Dryopteris carthusiana*, *Asarum europaeum*, *Majanthemum bifolium*, *Cerastium pauciflorum*, and *Calamagrostis obtusata*. Ground vegetation of the buffer zone consists of *Oxalis acetosella*, *Cerastium pauciflorum*, *Majanthemum bifolium*, *Carex montana*, *Calamagrostis obtusata*, *Rubus saxatilis*, and *Rubus idaeus* and in the impact zone consists of *Equisetum sylvaticum*, *Agrostis tenuis*, *Calamagrostis arundinacea*, *Calamagrostis langsdorffii*, *Chamerion angustifolium*, and *Majanthemum bifolium*. The total cover (sum of the projective cover of all species, ± SE) of vascular plants on the undisturbed sites of the background, the buffer, and the impact zones was 152.4 ± 3.0%, 78.5 ± 5.6%, and 5.9 ± 0.8%, respectively, and the variation coefficient along the toxic gradient increased from 16% to 126%.

In the beginning of August 1999, altogether 20 complexes of disturbed plots (sized 1 m × 2 m) were created in each load zone. The distance between the complexes was 5–10 m. The experimental plots were designed to imitate the pit-and-mound complexes that tend to form after tree uprooting (Liechty et al. 1997; Peterson et al. 1990). The 1 m^2 pits were created by removing all vegetation and the topsoil from the depth of 20 cm. The disturbance was thought to represent a severe one, as it did not only destroy the vegetation, but also removed the diaspore bank and baring of the mineral soil horizons. The excavated topsoil was deposited near the pits in an area of 1 m^2. These plots imitated the mounds and represented mild disturbance (partial death of plants, preservation of soil diaspore bank, and favorable physical and chemical substrate properties).

The species richness (which was measured by counting the number of species) was recorded from 1 m × 1 m plots during the 6-year post-disturbance period (2000–2005). The species richness of the plots that had no visible signs of natural disturbances (the undisturbed plots) was measured twice, during 2000 and 2005. In the year 2000, species richness was estimated at 140 undisturbed plots (sized 1 m × 1 m). The plots were located within a radius of 500–700 m from the experimental complexes. In the year 2005, 60 similar undisturbed plots (20 plots per toxic load zone) were studied within a radius of 50 m from the experimental complexes. As species richness of the undisturbed plots was similar during the two years, their mean values were used in the further analysis.

One-way analysis of variance (ANOVA) was used to test the differences in species richness between disturbed and undisturbed plots in the each toxic load zone. Two-way mixed-effects ANOVA was used to test the importance of toxic load influence (random factor), disturbance severity (fixed factor), and their interactions during the different study years. Two-way repeated-measurements ANOVA was used to estimate the influence of toxic load zone, time, disturbance severity, and their interactions. The multiple comparisons method (Scheffe's test) was used to test the differences between means in the three toxic load zones. Before the variance analysis, square-root transformation was applied to the data.

Results

Species richness of vascular plants in the undisturbed plots of the background zone was 2 and 10 times higher compared with the buffer and the impact zones, respectively (Table 1). Besides, a significant increase in the space variation of indices along the toxic gradient was observed.

The colonization rate of disturbed plots differed between the toxic load zones ($F_{2,114} = 69.04$; $P < 0.001$). During the study period, complexes of the background zone had the highest average species richness (Fig. 1), while the lowest values were found in the impact zone. The colonization rate also significantly depended on the degree of disturbance severity ($F_{1,114} = 67.95$; $P < 0.001$). In all of the toxic load

Table 1 Mean number (±SE) of species and variation coefficient (CV) of index at the undisturbed forest floor patches in the different toxic load zones

Indices	Toxic load zone		
	Background	Buffer	Impact
Number of species per m^2	12.2 ± 0.4a	6.2 ± 0.5b	1.1 ± 0.1c
CV (%)	27.9a	58.9b	75.7c

Values followed by the same letter are not significantly different at an overall $P < 0.05$

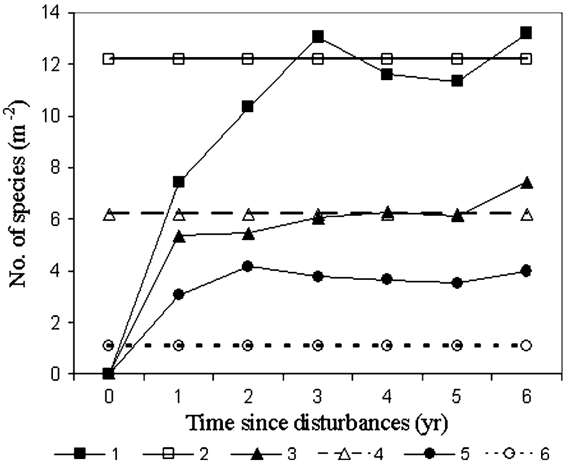

Fig. 1 Change in the number of species (mean values, m^{-2}) during the study period on the experimentally distributed complexes sited in different toxic load zones. Symbols: (1) disturbed and (2) undisturbed plots of background zone; (3) disturbed and (4) undisturbed plots of buffer zone; (5) disturbed and (6) undisturbed plots of impact zone

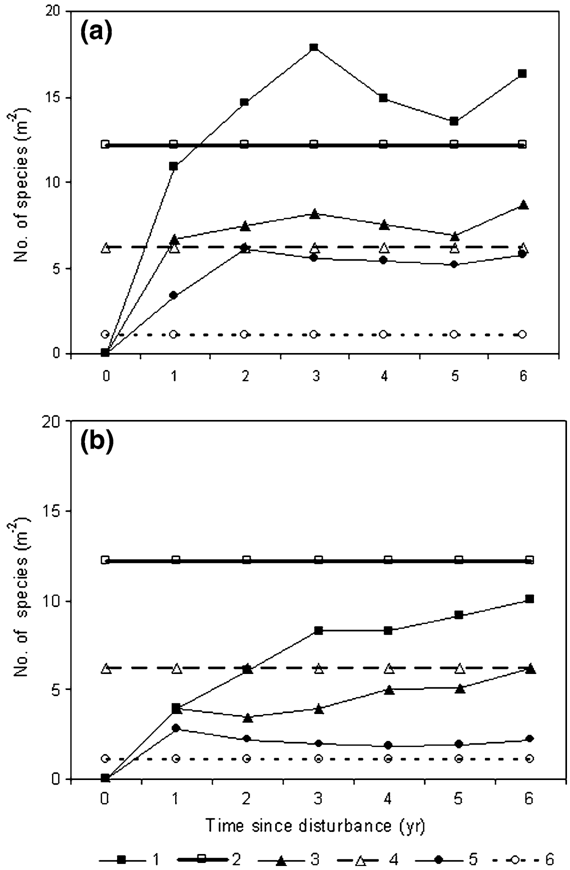

Fig. 2 Change in the number of species (mean values, m^{-2}) during the study period after **a** mild and **b** severe disturbances in the different toxic load zones. Symbols: (1) disturbed and (2) undisturbed plots of background zone; (3) disturbed and (4) undisturbed plots of buffer zone; (5) disturbed and (6) undisturbed plots of impact zone

zones, species richness increased more slowly after severe disturbance (Fig. 2b) than after mild disturbance (Fig. 2a). The successional colonization processes also differed significantly between the toxic load zones of (zone × time $F_{10,570} = 11.16$; $P < 0.001$). Maximum colonization rate was recorded in all toxic load zones within 1 year after the disturbance. In the background zone, high colonization rate was evident for three post-disturbance years, while in the buffer zone—for 1 year, and in the impact zone—for 2 years after mild disturbance and only 1 year after severe disturbance.

The toxic load zones modified significantly the colonization processes after severe and mild disturbance (zone × type of disturbances × time $F_{10,570} = 7.06$; $P < 0.001$). Levelling of the differences between the colonization rates after severe and mild disturbance was observed along the toxic gradient, especially during the first post-disturbance year. The mean (±SE) species richness after severe and mild disturbances was 3.95 ± 0.47 and 10.9 ± 0.74 in the background zone, 4.00 ± 0.54 and 6.7 ± 0.77 in the buffer zone, 2.80 ± 0.31, and 3.30 ± 0.33 species in the impact zone. Six years after the disturbance, the greatest differences between the indices of severely and mildly disturbed plots were observed in the background zone, and the lowest in the buffer zone.

One year after disturbance, species richness of the mildly disturbed plots in the background zone already did not differ from values of the undisturbed plots ($F_{1,83} = 2.12$; $P < 0.149$). In the subsequent years, the species richness of mildly disturbed plots was significantly higher than in the undisturbed ones ($P < 0.001$). Six years after the disturbance, species richness was significantly lower in severely disturbed plots than in undisturbed plots ($F_{1,83} = 6.52$; $P < 0.013$). On the whole, the species richness of the complexes in the background zone did not differ from the undisturbed areas by the third post-disturbance year ($F_{1,103} = 1.02$; $P < 0.314$).

One year after disturbance, species richness of the mildly disturbed plots in the buffer zone did not differ from the undisturbed areas ($F_{1,73} = 0.26$; $P < 0.610$). In the subsequent years, the indices were only slightly higher if compared with undisturbed plots. By the fourth post-disturbance year, the severely disturbed plots did not differ significantly in their species richness from the undisturbed ones ($F_{1,73} = 1{,}66$; $P < 0.202$). In the buffer zone, 1 year after disturbance, species richness of the complexes did not differ from that in the undisturbed areas ($F_{1,93} = 1.44$; $P < 0.233$).

One year after disturbance, the species richness of both mildly and severely disturbed plots in the impact zone was already higher than in the undisturbed ones ($F_{1,98} = 63.48$; $P < 0.001$ and $F_{1,98} = 47.92$; $P < 0.001$, respectively). The same trend continued through the subsequent years in spite of a certain decrease after the first (severe disturbances) and the second (mild disturbances) years of succession. Six years after the disturbance, complexes of the impact zone had significantly higher species richness than in the undisturbed areas ($F_{1,118} = 88.01$; $P < 0.001$).

The pattern of species richness dynamics in the total area of 20 m^2 (Fig. 3) was very similar to that in the area of 1 m^2 (Fig. 2). An important observation was that, from the second year after the disturbance onwards, species richness of the mildly disturbed buffer zone plots on the mesoscale (20 m^2) was close to the values of the undisturbed plots in the background zone (Fig. 3a). However, on the microscale (1 m^2), reversion to the previous succession state was not clearly pronounced (Fig. 2a). Species richness of the mildly disturbed impact zone plots was close to the values of the undisturbed plots in the buffer zone on both scales.

The total number of species found in the experimentally disturbed plots was considerably higher than in the undisturbed areas in all toxic load zones (Table 2). The highest number of species was registered in the mildly disturbed areas. After severe disturbance, the total number of species in the background, buffer, and impact zones increased by 13%, 45%, and 72%, respectively, and by 50%, 50%, and 85% after the mild one, respectively. The proportion of the species registered in the disturbed patches of the background, buffer, and impact zones made up 51.3%, 57.4%, and 85.3% of the total number of species in each zone, respectively. The total number of species that were found from the treated plots decreased along the toxic gradient and the species composition was different (Table 3). The disturbed plots in the background zone had mainly ruderal (e.g., *Plantago major*, *Taraxacum officinale*, *Tussilago farfara*, *Urtica dioica*), open (e.g., *Agrostis tenuis*, *Alchemilla* sp., *Coronaria flox-cuculi*, *Lathyrus*

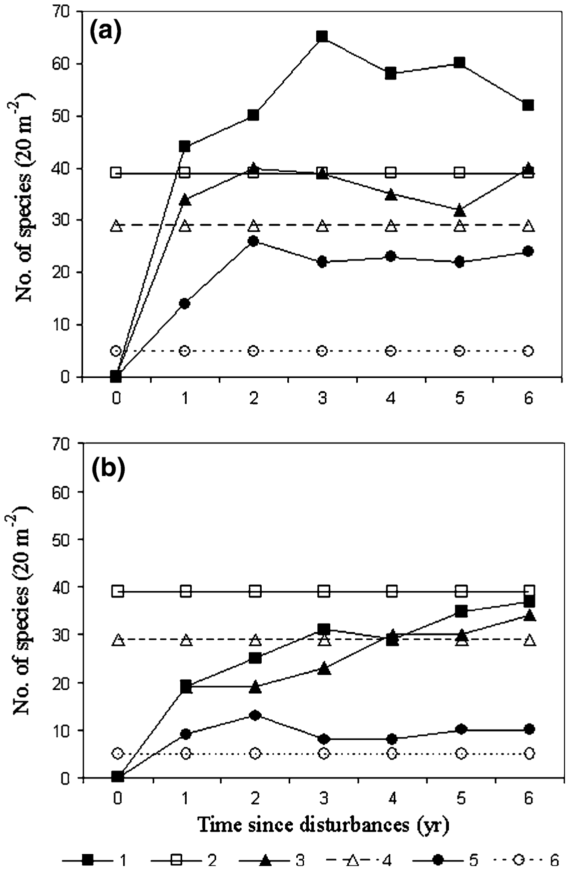

Fig. 3 Change in the total number of species on the area 20 cm^2 during the study period after **a** mild and **b** severe disturbances in the different toxic load zones. Symbols: (1) disturbed and (2) undisturbed plots of background zone: (3) disturbed and (4) undisturbed plots of buffer zone; (5) disturbed and (6) undisturbed plots of impact zone

Table 2 Total number of species observed in experimentally disturbed and undisturbed forest floor patches in the different zones of pollution

Type of site	Toxic load zone		
	Background	Buffer	Impact
Undisturbed (20 m^2)	39	29	5
Severe disturbances (20 m^2)	45	53	18
Mild disturbances (20 m^2)	78	58	33
Total (60 m^2)	80	68	34

pratensis, *Potentilla erecta*, *Prunella vulgaris*) or wet (e.g., *Calamagrostis langsdorfii*, *Crepis paludosa*, *Geum rivale*, *Filipendula ulmaria*, *Ranunculus repens*) habitat species, but also pioneer species of the initial stages of secondary succession (e.g., *Chamerion angustifolium*, *Chrysosplenium alternifolium*, *Phegopteris connectilis*) along with pine forest species (e.g., *Calamagrostis arundinaceae*, *Betonica officinalis*, *Vicia sylvatica*, *Viola canina*).

The disturbed plots of the degraded communities had species from the aforementioned groups, and also common spruce forest species, such as *Athyrium filix-femina*, *Cerastium pauciflorum*, *Dryopteris carthusiana*, *Gymnocarpium dryopteris*, *Galium odoratum*, *Luzula pilosa*, etc. The proportion of these species in the disturbed patches of buffer and impact zones made up 28% and 40% of the total number of new species in each toxic load zone, respectively.

Discussion

Peculiarities of species richness recovery after disturbance

The results of this study suggest that species richness of communities decreases under long-term atmospheric pollution by heavy metals and sulfur dioxide and that this is accompanied by a significant decrease in the colonization rate of the disturbed plots. The result is quite expectable, especially if we take into account the direct dependence of the colonization processes on the initial state of communities before disturbance (Forest et al. 1998; Hooper et al. 2005; Jonsson and Essen 1998; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004; Skvortsova et al. 1983; Turner et al. 1998).

The highest colonization rate in all of the toxic load zones was observed during the first post-disturbance year, but the investigated communities differed in the length of their intensive recovery periods. The colonization rate in the background zone decreased after 3 years of succession, which supports the view of other researches on the succession rate in unpolluted forests (Rydgren et al. 2004). The colonization rate in the degraded communities decreased already during the first (or the second) year of succession. The observed phenomenon cannot be related to the lack of colonization space, as the vegetation cover of the disturbed plots at the initial stages of succession was rather low (Trubina 2003). It is more likely caused by very fast exhaustion of the available diaspore bank in the degraded communities. The phenomenon is especially exhibited in the zone of heaviest contamination (impact zone) and under severe disturbance, i.e., when the diaspore bank (the additional resource for colonization) is absent.

Species richness increased significantly more slowly after severe disturbance than after mild disturbance. The observed data agree perfectly with results of other investigations concerning the influence of disturbance severity on colonization processes (Hautala et al. 2001, 2008; Jonsson and Essen 1998; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004; Skvortsova et al. 1983). This phenomenon is most likely induced by the almost complete destruction of the soil bank of vegetative and generative diaspores of the soil bank after a severe disturbance, as the importance of soil bank in the processes of colonization is known to be very high (Jonsson and Essen 1998; Mayer et al. 2004; Putz 1983; Rydgren et al. 2004; Turner et al. 1998). It is also possible that the removal of upper layers of soil (deterioration of the physical and chemical properties of the substrate) might have reduced colonization and survival of plants, but the importance of the latter factor can hardly be assessed within this experiment.

Increasing levels of toxic loads and degree of ecosystem degradation led to levelling of differences in the colonization rate after severe and mild disturbance. Weakening of the disturbance severity effect along the toxic load gradient may be related to several reasons. Some investigations (Komulainen et al. 1994) have proved that, even if viable seeds are present in the degraded communities, colonization may be impeded by very high levels of soil toxicity. In

Table 3 List of species found on the disturbed plots in the three toxic load zones

Zone of pollution		
Background	Buffer	Impact
Agrostis tenuis	*Adenophora lilifolia*, M	*Adenophora lilifolia*, M
Alchemilla sp., M	*Adoxa moschatellina*, M	*Ajuga reptans*, M
Angelica sylvestris, M	*Agrostis tenuis*	*Athyrium filix-femina*, M
Betonica officinalis, M	*Alchemilla* sp.	*Carduus* sp., M
Calamagrostis arundinaceae, M	*Athyrium filix-femina*	*Carex* sp.
Calamagrostis langsdorfii, M	*Cacalia hastate*, M	*Cerastium pauciflorum*
Carex montana	*Cerastium* sp., S	*Deschampsia cespitosa*
Carex sp.	*Chrysosplenium alternifolium*	*Circaea alpina*
Chamerion angustifolium, M	*Coronaria flos-cuculi*	*Coronaria flos-cuculi*
Chrysosplenium alternifolium	*Dactylis glomerata*, S	*Dryopteris carthusiana*
Cirsium sp., M	*Dryopteris filix-max*	*Fragaria vesca*, M
Coronaria flos-cuculi	*Fragaria vesca*	*Galium* sp., M
Crepis paludosa, M	*Galeopsis bifida*	*Gymnocarpium dryopteris*, M
Dryopteris filix-max, M	*Galium odoratum*	*Impatiens noli-tangere*, M
Filipendula ulmaria, M	*Galium uliginosum*	*Lathyrus pratensis*
Galeopsis bifida	*Geranium sylvaticum*, M	*Lathyrus vernus*, M
Galium uliginosum	*Gymnocarpium dryopteris*	*Luzula pilosa*
Geranium sylvaticum, M	*Juncus* sp., M	*Majanthemum bifolium*
Geum rivale	*Lathyrus pratensis*	*Melica nutans*, M
Glechoma hederacea, S	*Phegopteris connectilis*	*Phegopteris connectilis*
Goodyera repens, M	*Poa* sp., M	*Poa* sp.
Hieracium sp., M	*Prunella vulgaris*	*Ranunculus repens*, M
Lathyrus pratensis	*Pulmonaria dacica*	*Rubus idaeus*
Luzula palescens, M	*Pyrola media*, M	*Stellaria nemorum*
Orthilia secunda, M	*Silene* sp.	*Taraxacum officinale*
Phegopteris connectilis	*Solidago virgaurea*	*Thalictrum minus*, M
Plantago major, M	*Stellaria* sp., S	*Tussilago farfara*
Poa nemoralis	*Stellaria nemorum*	*Urtica dioica*, M
Poa sp., M	*Taraxacum officinale*	*Veratrum lobelianum*, M
Potentilla erecta, M	*Thalictrum minus*	*Viola* sp.
Prunella vulgaris	*Trientalis europaea*	
Ranunculus borealis, M	*Tussilago farfara*	
Ranunculus cassubicus, M	*Urtica dioica,* M	
Ranunculus repens, M	*Valeriana wolgensis*	
Stachys sylvatica	*Veratrum lobelianum*, M	
Taraxacum officinale	*Veronica chamaedrys*	
Tussilago farfara	*Vicia sylvatica*	
Urtica dioica	*Viola canina*, S	
Veronica chamaedrys	*Viola selkirkii*	
Vicia sylvatica, M		
Viola canina, M		

Species occurring at mildly disturbed plots are marked with M; S marks species of severely disturbed plots; the rest of the species occurred at both types of disturbance high-toxicity areas, colonization of vacant areas may also be impeded by a very thick layer of forest litter (more than 5 cm), which is typical for the degraded forest ecosystems near this particular copper smelter (Vorobeichik 1995). The negative influence of litter on regeneration and survival of plants, composition, and species richness of communities has been shown in a range of studies (Peterson and Campbell 1993; Sydes and Grime 1981a, b; Xiong and Nilsson 1999; Weltzin et al. 2005; Sannikov 1992). Apparently, disturbance of the thick and highly toxic forest litter and exposure of the less contaminated soil lessens the negative effect of the disturbance severity and led to its weakening. The levelling of differences may also result from a significant decrease of soil seed bank diversity in the degraded communities, which often takes place under long-term pollution (Ginocchio 2000; Meerts and Grommesch 2001; Salemaa and Uotila 2001). The low number of post-disturbance species in the heavily degraded communities (Table 3) also confirms indirectly this supposition. Another reason for the observed phenomenon may be in the composition of these communities, e.g., the high proportion of eurytopic species that are quite indifferent to unfavorable conditions of the substrate, but these questions would require a special study.

In the course of the recovery period, species richness of the disturbed areas at certain stages was significantly higher than in the undisturbed area. This phenomenon is quite typical for post-disturbance successions after disturbances in most forest communities (Barik et al. 1992; Cooper-Ellis et al. 1999; Goldblum 1997; Mayer et al. 2004; Peterson and Campbell 1993; Skvortsova et al. 1983) and implies the presence of at least two time points during which disturbed and undisturbed areas of communities will not differ significantly in their species richness. The first of these time points characterizes the duration of the negative effects of the disturbances and is a very important component of the resilience of communities, in addition to the period of positive effects and the time of the final return (T_R) to the initial state. The negative-effect period, as a rule, seems to be shorter after mild disturbance than after severe disturbance, which is not unexpected, as severity of disturbance largely defines colonization rate. Differences in the duration of the negative effect after severe and mild disturbance were greatest in the background zone and were not observed in the impact zone. The possible reasons for levelling of the differences between the effects of severe and mild disturbances along the toxic load gradient have been discussed above. However, the following important points should be emphasized.

The duration of the negative effect of mild disturbance was equal in the investigated communities. After severe disturbance, this period was significantly longer in the background zone than in the intermediately and heavily degraded communities, despite the highest species richness and colonization rates in the background zone. The results prove that it is not only the species richness of communities that determines the duration of the negative effects. It is quite possible that the composition of communities or functional diversity (Hooper et al. 2005) also plays a decisive role in the rate of recovery. In the degraded communities, the prevalence of pioneer species and clonal plants (see above) with high colonization abilities could have promoted faster overcoming of the negative effects of disturbance.

Data from a few studies (e.g., Skvortsova et al. 1983) provide evidence that high species richness can be preserved in disturbed areas for several decades. Therefore, longer-term data is needed to determine the time of the final return to the initial state. Nevertheless, some suppositions about recovery of species richness after disturbance can be made from the given index rate of recovery changes and its degree of deviation from the indices measured from the undisturbed areas. After the 6 years of recovery from mild disturbance, the greatest positive deviation and the lowest rate of recovery were found in the communities of the impact zone. One can suppose that, after mild disturbance, communities of this zone will return to the initial state more slowly than communities of less contaminated habitats. However, on the basis of the present data, hardly any suppositions can be made for the communities in the buffer and background zones. However, if we consider the complexes of the disturbed areas in general, and suppose that the species richness of disturbed plots will not increase significantly in the course of further succession, we may conclude that the highest recovery rate of the initial species richness prevails in the buffer-zone communities ($T_R = 1$ year on observed time interval), a lower rate prevails in the background-zone communities ($T_R = 3$ years), and the lowest rate prevails in the communities in the impact zone ($T_R \gg 6$ years).

In general, the results suggest that the period of final return to the initial state depends on the duration of the negative effects of disturbance. It also depends on the magnitude and duration of the positive effects. The heavily degraded communities were characterized by the shortest period of negative effects of disturbance, the greatest magnitude and duration of positive effects, and as a result the greatest deviation of species richness from the indices of the undisturbed areas after 6 years of recovery. The intermediately degraded communities were characterized by an average duration of negative effect of disturbances, the lowest magnitude and duration of positive effects, and the highest recovery rate of species richness on the whole. Recovery of the least degraded communities occurred at an intermediate rate owing to the longest period of negative effects after severe disturbance. This fact once again confirms that resilience of communities is not determined merely by their species richness.

Influence of short-term disturbances of various severity levels on species richness of communities under long-term pollution

In this study experimental disturbance promoted a considerable increase in the total number of species in the investigated communities. The observed results coincide especially with the study results on the influence of windfall disturbances to diversity of forest communities (Barik et al. 1992; Cooper-Ellis et al. 1999; Goldblum 1997; Kuuluvainen 1994; Peterson and Campbell 1993; Skvortsova et al. 1983; Ulanova 2000). At the same time, the degree of modifying influence of disturbances depended on their severity, as well as on the community degradation level.

The increase in species richness in the background-zone communities derived from the emergence of open and wet habitat species, ruderals, pioneer species of initial stages of secondary successions or species of other forest communities. The composition of species growing in the disturbed sites of the background zone is in agreement with data cited for the initial stages of succession after treefalls in unpolluted areas (Skvortsova et al. 1983; Ulanova 2000). The positive effects of disturbance increased considerably along the gradient of toxic load. In the impact zone, the total number of species in the communities after the disturbances became seven times higher than in undisturbed areas. Moreover, species richness increases at the expense of both the characteristic species of disturbed patches in the unpolluted forest and of the most common unpolluted spruce forest species that disappear from the communities as a result of long-term pollution. Interestingly, a similar phenomenon was observed in the studied communities after treefalls (unpublished data).

Such a large increase in the diversity of degraded communities may be related to the preservation of sufficiently diverse and viable diaspore bank in the degraded communities, as well as to dispersal of diaspores from outside. However, the role of the latter factor may be small, as diversity and total cover of vegetation were extremely low in this load zone.

It has been proved earlier that diaspore bank can remain viable under long-term pollution by copper-smelter emissions (Ginocchio 2000; Huopalainen et al. 2001; Komulainen et al. 1994; Meerts and Grommesch 2001; Salemaa and Uotila 2001). Increased species richness after mild disturbances proves indirectly that the diaspore bank can preserve certain diversity in heavily polluted zone. The results also suggest that, after 60 years of copper smelter functioning, only partial recovery of species richness from the diaspore bank is possible in highly degraded communities.

Mild disturbances decreased diversity differences between the studied communities on both micro- and mesoscale, and caused a certain reversion of the degraded communities to the earlier state of anthropogenic succession. Particularly, after the second post-disturbance year, species richness of mildly disturbed plots in the impact zone was close to the level observed in undisturbed plots of the buffer zone on both scales. In the buffer zone, reversion to the indices of undisturbed plots of the background zone was observed only on the mesoscale. This is most likely due to the different species elimination rates from the communities on the micro- and mesoscale. Particularly, the number of species in undisturbed 1 m^2 plots (microscale) in the buffer zone was 2 times lower compared with the background zone, whereas in the area 20 m^2 (mesoscale) was lower only 1.3 times. It was remarkable that severe disturbance only slightly modified species richness of the communities on the micro- and mesoscale and increased only the total number of species. Moreover, the positive effect of severe disturbance on the total number of species was less pronounced than that of mild disturbance, which again emphasizes the importance of diaspore bank in the maintenance of high community diversity.

Thus, our results suggest that short-term small-scale disturbance promotes species richness in plant communities and that, under strong long-term pollution, it slows down the decline in species richness and may also lead to certain reversion of degraded communities to the previous state of succession. However, the following important points should be emphasized. Short-term disturbances, e.g., treefalls, at the initial pollution stages can promote elimination of typical forest species, because during the first years of succession disturbed plots are actively occupied by untypical species (Kuuluvainen 1994; Nakashizuka 1989; Rydgren et al. 2004; Skvortsova et al. 1983; Ulanova 2000). The duration of negative effects after severe disturbance in the background zone proves that severe disturbance of vegetation and soil, such as tree uprooting, could have led to the significant and long-term decrease in species richness of communities on both micro- and mesoscales. In other words, severe disturbance can accelerate the processes of diversity decline in communities during the initial stages of environmental contamination. The positive effect of disturbance that is currently observed in the degraded communities may subsequently decrease or disappear due to the continuing input of toxicants. In particular, germination of spores and seeds of species intolerant to contamination and their subsequent elimination because of persisting toxic influence will lead to the exhaustion of the diaspore bank and to the further decrease in diversity and recovery abilities of the degraded communities as a whole.

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