

Long-term passive restoration following fluvial deposition of sulphidic copper tailings: nature filters out the solutions

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Abstract Despite the growing popularity of ecological restoration approach, data on primary succession on toxic post-mining substrates, under site environmental conditions which considerably differ from the surrounding environment, are still scarce. Here, we studied the spontaneous vegetation development on an unusual locality created by long-term and large-scale fluvial deposition of sulphidic tailings from a copper mine in a pronouncedly xerothermic, calcareous surrounding. We performed multivariate analyses of soil samples (20 physical and chemical parameters) and vegetation samples (floristic and structural parameters in three types of occurring forests), collected along the pollution gradients throughout the affected floodplain. The nature can cope with two types of imposed constraints: (a) excessive Cu concentrations and (b) very low pH, combined with nutrient deficiency. The former will still allow convergence to the original vegetation, while the latter will result in novel, depauperate assemblages of species typical for cooler and moister climate. Our results for the first time demonstrate that with the increasing severity of environmental filtering, the relative importance of the surrounding vegetation for primary succession strongly decreases.

Keywords Alluvial forests · Cu toxicity · Ecological restoration · Environmental filtering · Novel ecosystem · Nutrient deficiency · Post-mining land · Primary vegetation succession · Soil acidity · Spontaneous restoration

Introduction

Barren land where plant growth is constrained by different soil factors and (re)creation of vegetation cover and ecosystem functioning starts de novo is a common post-mining legacy, often posing a challenge for efficient and cheap restoration of the productive use of these substrates (Bradshaw 1997; Hüttl and Weber 2001). There is growing evidence that ecological restoration can yield a much higher conservation value of post-mining sites for a much lower price compared to technical reclamation (Prach et al. 2011). However, ecological restoration of barren land heavily relies on thorough understanding of the processes of primary succession of vegetation and soil, which is highly site-specific with a low possibility for extrapolations of the findings to different sites, what actually reflects a broader problem of finding general principles in community ecology (see McGill et al. 2006). Post-mining primary succession has been thoroughly studied on non-toxic, nutrient-poor, acidic substrates created by open cast mining of coal with high amounts of sulphides in Central Europe; conceptual models of vegetation development have been proposed (e.g. Pietsch 1996; Schulz and Wiegler 2000; Tischew and Kirmer 2007), but clear and generally valid correlations of environmental gradients with vegetation patterns are difficult to establish.

There is a pronounced scarcity of data concerning the principles of spontaneous vegetation development on toxic post-mining substrates in different environmental conditions (Prach 2003). For instance, the most intractable issue on

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post-mining land is caused by tailings waste of sulphidic metal ores (combination of high soil acidity and high concentrations of heavy metals, Bradshaw 1997). Failures of tailings dams reported worldwide have degraded considerable floodplain areas (Macklin et al. 2006). Due to strict legal regulations, however, such potential research sites where no reclamation has been undertaken and de novo vegetation establishment proceeds under severe environmental constraints have become extremely scarce in Europe. Moreover, on severely degraded post-mining sites, spontaneous restoration might not be feasible (Prach and Hobbs 2008); although this is increasingly recognised in the concept of “novel ecosystems” which arise as a consequence of anthropogenic disturbance (Hobbs et al. 2009), case studies from such localities are still scarce.

The present work investigates a spontaneous development of vegetation on an exceptional locality where strongly acidic, nutrient-poor and Cu-enriched substrates were anthropogenically created in a continental climate and calcareous surrounding. The study addresses a question of how would nature, if left to its own, recover from this long-term and large-scale pollution which has completely transformed the landscape. The aim of this research was to provide a “would be” scenario to indicate the potentials and constraints of spontaneous restoration under extreme environmental filtering and offer new insights into assembly processes on the post-mining land.

Material and methods

Research locality

The research locality in Eastern Serbia (satellite view available at: <http://goo.gl/maps/U4C51>) has been created during over 50 years of uncontrolled discharge of highly sulphidic Cu tailings from the Bor Copper Mines into the local river system. The tailings slurry had been received by the two smaller tributaries of the Timok River and further carried by Timok to the Danube, creating thus a transboundary environmental issue, affecting Bulgaria and Romania as well. In the Timok watershed, the mining waste had been deposited by regular uncontrolled floods over the alluvial fields; the pollution ceased allegedly about 30 years ago, while mass spontaneous revegetation started about 20 years ago, under the unchanged flooding regime. Our unpublished results indicate that elimination of flooding after pollution deposition strongly impedes the revegetation process. The depth of deposited tailings waste in the floodplain ranged from about 10 cm to over 1 m. Due to complex historic socio-political circumstances, no systematic reclamation of the polluted area has been undertaken. The true extent of the degraded land has never been published; so far, about 10,000 ha of the floodplain are still barren, and far larger area

is severely degraded. The major process on these polluted soils is oxidative weathering of sulphides, which leads to strong acidification and leaching of most mineral elements (Nikolic and Nikolic 2012). Our previous research showed clear spatial gradients in properties of polluted soils along the transects, <1 km long, perpendicular to the river channel; the concentration of total soil sulphur was a good indicator of pollution load, which regularly decreased with the distance from the river (for more details, see Nikolic et al. 2011, 2014; Nikolic and Nikolic 2012).

The research area is under both sub-continental and sub-Mediterranean climatic influences, with annual precipitation below 600 mm (Online Resource 1). The former natural vegetation of the floodplain had been azonal alluvial poplar forests (*Populion albae* alliance). In the immediate surroundings of the polluted floodplain, agricultural land uses are being increasingly abandoned (socio-economic reasons), and the landscape is now dominated by a matrix of different successional stages of fallow vegetation. The zonal vegetation of the region are xerothermic oak forests (association *Quercetum frainetto-cerridis* Rudski (1940) 1949), while in the immediate surroundings of the research locality, the carstic geology, shallow calcareous soils and dissected topography favour the mosaic vegetation dominated by light, xerothermic calcicole forests and scrubs with many sub-(Pontic) and sub-Mediterranean species (Mišić 1997). Unpolluted acidic soils do not occur outside of the floodplain research area within the distance of at least 10 km.

Vegetation sampling

This study investigated 50 km of the Timok River floodplain affected by the slurry mine discharge; major sampling locations (approximate position centered around N 44° 04', E22° 31'; see <http://goo.gl/maps/U4C51>) were at the meandering position, where large tracts of barren polluted soils are still easy to find. Pioneer forests were surveyed along the transects perpendicular to the river channel through the polluted floodplain; sampling design was based on the flexible systematic sampling according to the visual appearance of the vegetation (Smartt 1978). As a control, alluvial poplar forests with as little as possible anthropogenic disturbance were sampled shortly upstream before the polluted tributaries join the Timok. The selection of forest localities was opportunistic, with the main criteria being the absence of the visible anthropogenic influence (logging, burning, waste/garbage deposition and bank fortification for flooding control). The selection of sampling units (relevées) for vegetation survey in each locality was random. Vegetation was surveyed in the standardized 25 m×25 m quadrates in each forest sample (total of 63 samples) in the period May–July during 2010 and 2011 year, when most of the herbaceous species of poplar forests was in flowering. Cover-abundance

value of each species (summary cover-abundance in all the three forest vegetation layers) was estimated on the extended nine-grade Braun-Blanquet scale (van der Maarel 2007). For the subsequent multivariate analyses, species not achieving the frequency of at least 15 % in one forest type were excluded. Tiny species with very low abundance and/or only few small individuals (“r” class on the Braun-Blanquet scale) were not excluded. Forest structure parameters (diameter at breast height (DBH), total dominance and absolute density) were assessed by a plotless sampling the point-centred quarter method (Cottam and Curtis 1956).

Soil sampling and analyses

A composite soil sample was obtained by sampling a soil core (40 cm depth) at three locations in each forest relevée (approximately 1 kg soil per relevée). Barren tailings deposits, where no plant growth occurs, were sampled as described by Nikolic and Nikolic (2012). Soil samples were analyzed in fine earth fraction (for methodological details, see Nikolic et al. 2014). In brief, the pH was measured in water and the concentrations of total C, N and S by the CHNS elemental analyzer (Vario Micro Cube, Elementar Analysensysteme GmbH, Hanau, Germany). Organic carbon (C_{org}) was calculated from total C and soluble $CaCO_3$, which was determined by calcimetry. Different extraction procedures were applied to determine plant-available concentrations of elements: ammonium lactate-ammonium acetate (AL) for P and K, ammonium acetate (NH_4 -Ac) for Mg and Ca, KCl-extraction for exchangeable Al and hot water (70 °C) for B. Plant-available fractions of other metals (Fe, Cu, Zn, Mn, Cd, Ni and Pb) were extracted by the DTPA-TEA solution and respective pseudototal concentration by microwave digestion with conc. HNO_3 . The concentrations of chemical elements in soil samples subjected to different extraction procedures were determined by ICP-OES (SpectroGenesis EOP II, Spectro Analytical Instruments GmbH, Kleve, Germany), with the exception of the P concentrations, which were determined colorimetrically. Potential cation exchange capacity (CEC) was determined by ammonium acetate extraction buffered at pH 7.

Statistical analysis

The abundance-dominance data recorded on nine-grade Braun-Blanquet scale were transformed to a quasi-metric 1–9 ordinal transform scale of ordinal transform values (OTVs; van der Maarel 2007) for further analyses. Normal ordination was performed by indirect gradient analysis: non-metric multidimensional scaling (NMS): Sørensen distance; and detrended correspondence analysis (DCA): Hill’s scaling, downweighting of rare species and rescaling of the axes with 26 segments. Variation in vegetation data accounted for by the key soil parameters was done with canonical correspondence analysis (CCA): Hill’s scaling, optimizing samples, the hypothesis “no relationship

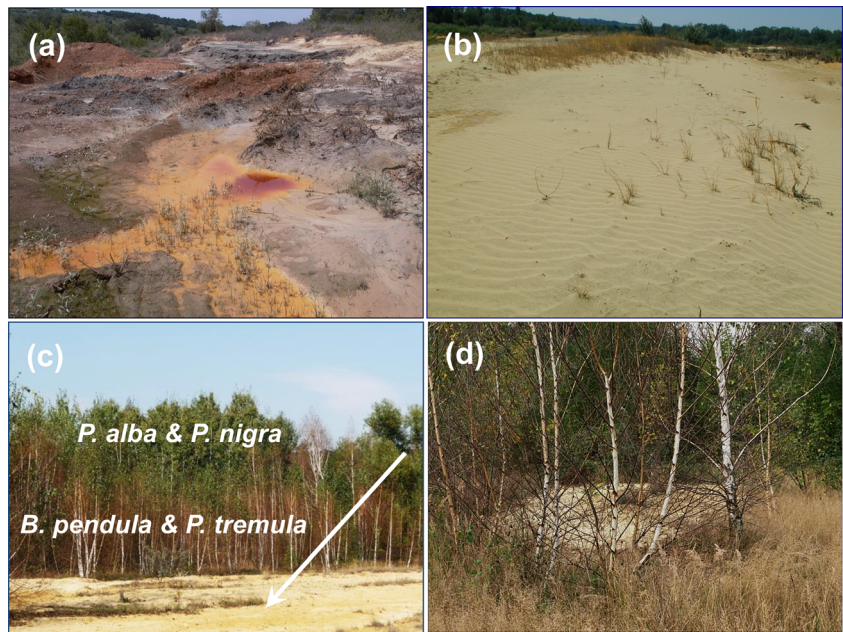
between species and environmental matrices” was tested. The number of significant ordination axes to be interpreted was determined by Monte Carlo randomization test. Plexus values (ϕ coefficient) were calculated as a standardized χ^2 statistic for species association; Yates’ correction was applied. All the multivariate analyses were done with the PC-ORD 6 software (MjM Software Design, Gleneden Beach, USA). A posteriori comparison of means was done by Tukey’s test, with $\alpha=0.05$. Ellenberg indicator values (Ellenberg et al. 1991) and chorological spectra (chorotype, i.e. species distribution patterns follow Obratov et al. 1990) for each sample were calculated as averages weighted by the species cover-abundance (OTV).

Results

The major soil constraints for spontaneous revegetation on this complexly polluted area change as a consequence of oxidative weathering of sulphides (predominantly pyrite, FeS_2) in the deposited tailings waste (Fig. 1a, b; Table 1). In brief, two extreme types of conditions: very fresh and highly weathered tailings sediments prevent the establishment of vegetation (Table 1). On the polluted soils between these two extremes, two distinct types of pioneer forests have spontaneously developed on the barren land (Fig. 1c, Table 2). The estimated age difference between the two types of pioneer forests is about 20–25 years (participatory surveys with local land users). The occurrence of these pioneer forests is spatially explicit along the transects (Fig. 1c): Older forests dominated by poplars (*Populus alba* and *Populus nigra*) at the outer edge of the polluted floodplain, and younger forests, closer to the river channel, dominated by birch (*Betula pendula*) and aspen (*Populus tremula*; see also Table 2). The properties of the polluted soils show two clear gradients (Fig. 2). The major gradient (axis 1, Fig. 2) corresponds to the amount of mining waste deposited along the transects, which is clearly indicated by soil concentrations of S_{tot} . High concentrations of Cu (axis 2, Fig. 2) were found at the longest distance from the pollution source, where pioneer poplar forests have developed.

The details on soil properties are presented in Fig. 3. Compared to unpolluted alluvial soils covered by natural vegetation (forest type 1), soils of forests developing on most severely degraded parts of floodplain (forest type 3, dominated by birch and aspen) are drastically altered: pH lower by 4 units, strongly deteriorated soil C_{org} and CEC and 20–40 times increased exchangeable Al (Fig. 3), while all macronutrients and micronutrients are severely deficient (Fig. 3). The process of oxidative weathering has been very intensive on these soils (clearly indicated by a very high ratio of sulphates in total soil S, Fig. 3) and presumably historically very high amounts of deposited Cu (indicated by high concentrations of S_{tot} , Fig. 3, and Cu is co-deposited with S, see “fresh deposits” in Table 1) have been leached to background levels (Fig. 3). On the other

Fig. 1 Spontaneous restoration of alluvial land polluted by sulphidic Cu mine tailings. **a** Fresh fluvial deposits of mining waste, 50 km from the tailings lake; **b** highly weathered tailings transform the landscape into a nutrient-poor “desert”; **c** pioneer forests colonize the barren polluted land in a spatially explicit manner along the transects perpendicular to the river channel (direction indicated by the arrow tip); **d** novel type of forests, whose key species cannot survive in the surrounding of the polluted area gradually re-green the large barren area



side, pioneer poplar forests (Table 2, forest type 2) developing at the outer edge of the polluted floodplain were initially constrained by a lower amounts of deposited mine tailings (lower S_{tot} , Fig. 3).

The pioneer formations developing on the barren land differ from the reference alluvial forest in structural parameters,

species richness and floristic homogeneity, and all three types of forests considerably differ in ground layer vegetation (Table 2). The details of differences in vegetation properties are shown in Fig. 4. Indirect gradient analysis shows that the soil properties are highly correlated with the major vegetation gradient (axis 1, Fig. 4a). The strongest distinction of all the

Table 1 Selected chemical characteristics of the two extreme stages in the aging process of fluvially deposited pyritic Cu tailings where no plant growth occurs

Parameter	“Fresh” tailings deposits (n=16)	“Weathered” tailings deposits (n=18)
pH (in H ₂ O)	6.3±1.2 b	3.1±0.5 a
S_{tot} (%)	3±1 b	2.3±0.6 a
Soluble salts (%)	0.4±0.3 a	0.4±0.3 a
C_{org} (%)	0.6±0.5 a	0.3±0.2 a
N_{tot} (%)	0.18±0.04 b	0.04±0.01 a
P_{AL} (mg kg ⁻¹)	92±53 b	0.9±1.1 a
K_{AL} (mg kg ⁻¹)	230±119 b	36±14 a
Ca_{NH_4-Ac} (mg kg ⁻¹)	179±70 b	62±13 a
Mg_{NH_4-Ac} (mg kg ⁻¹)	15.8±0.6 b	11±2 a
$B_{hot\ H_2O}$ (mg kg ⁻¹)	0.2±0.2 a	0.6±0.7 a
Cu_{HNO_3} (mg kg ⁻¹)	1941±171 b	207±30 a
Cu_{DTPA} (mg kg ⁻¹)	532±41 b	22±16 a
Zn_{HNO_3} (mg kg ⁻¹)	337±83 b	7.5±4.1 a
Zn_{DTPA} (mg kg ⁻¹)	60±47 b	0.83±0.81 a
Cd_{HNO_3} (mg kg ⁻¹)	1.7±0.3 b	0.4±0.1a
Ni_{HNO_3} (mg kg ⁻¹)	28±6 b	4±2 a
Cr_{HNO_3} (mg kg ⁻¹)	34±7 b	9±2 a
Pb_{HNO_3} (mg kg ⁻¹)	52±13 b	21±9 a
Al_{KCl} (mg kg ⁻¹)	0.6±0.5 a	74±40 b
As_{HNO_3} (mg kg ⁻¹)	73±41 b	33±15 a

Plant-available concentrations of elements (obtained by different extractions) and pseudototal (HNO₃-extractable) are shown. Mean values ± SD followed by the same letter in a row are not different ($p < 0.05$, Tukey’s test)

Table 2 Comparison of pioneer forests which colonize the barren alluvial land polluted by sulphidic Cu mining waste with the original alluvial forests on unpolluted soil

Forest type Dominant species	Reference forests on unpolluted soil	Pioneer forests	
	1 <i>Populus alba</i> and <i>Populus nigra</i>	2 <i>Populus alba</i> and <i>Populus nigra</i>	3 <i>Betula pendula</i> and <i>Populus tremula</i>
No. of samples	15	23	25
Average species number per sample	26.1	33.7	18.9
Estimated species richness ^a	66	79	63
Average within-group distance (Sørensen) ^b	0.40	0.54	0.31
Median DBH (cm)	61.4 c	43.7 b	14.5 a
Total density (trees ha ⁻¹)	320±41 a	424±38 b	1402±281 c
Absolute dominance (m ² trunks ha ⁻¹)	84.1±21.2 c	61.9±8.8 b	21.8±5.2 a
Species prevailing in ground layer vegetation	Non-ruderal, eutrophic	Ruderal	Non-ruderal, oligotrophic
Major soil constraint ^c	None	High Cu	Low pH, nutrient deficiency
Rel. position on the transect ^d	Random	Outer edge	Middle portions

^a First-order jackknife estimate

^b Group is defined by the forest type

^c See Fig. 3

^d Transects run perpendicularly from the river channel through the floodplain

Mean values ± SD followed by the same letter in a row are not different ($p < 0.05$; Tukey's test)

forest types coincides with the gradient of decreased pH and increased nutrients and CEC (see also Fig. 2). Multiple linear regression (CCA, not shown) indicates that soil pH accounts for about 20 % of the total variance in vegetation data. Soil pH is strongly correlated with other major constraints, namely with deficiency of P and Ca, and excessive concentrations of Al (Figs. 2 and 3), whose effect is thus not accounted for by CCA.

The spontaneous vegetation sampled along the spatial transects shorter than 1 km exhibited very high beta diversity (DCA gradient length of 3.56 SD units). Pioneer poplar forests on the polluted soils (type 2) converge to reference poplar forests (type 1, Fig. 4a). The main differences are (a) structure and density (Table 2) and (b) ruderal and segetal species instead of true forest species (Fig. 4b; see also the relative increase of adventive and cosmopolitan species in type 2 forests, Fig. 5b). On the other hand, pioneer forests dominated by birch and aspen (type 3, Fig. 1d) are clearly set apart from both poplar forests (Fig. 4a, c). Vegetation of pioneer forests is ordered along only one exceptionally strong gradient (Fig. 4c); this vegetation gradient (NMS axis 1, Fig. 4c) is highly correlated with the gradient of soil constraints. Out of the 92 species included in the ordination (see Online Resource 2), 48 were found to occur in both pioneer forest types, albeit with very different abundances. The dominant species however are clearly confined to either forest type (Fig. 4c). Out of nine species confined to birch-aspen forests (Fig. 4c, see also Online Resource 2), four of them (*B. pendula*, *P. tremula*, *Agrostis capillaris* and *Rumex acetosella*) consistently occur

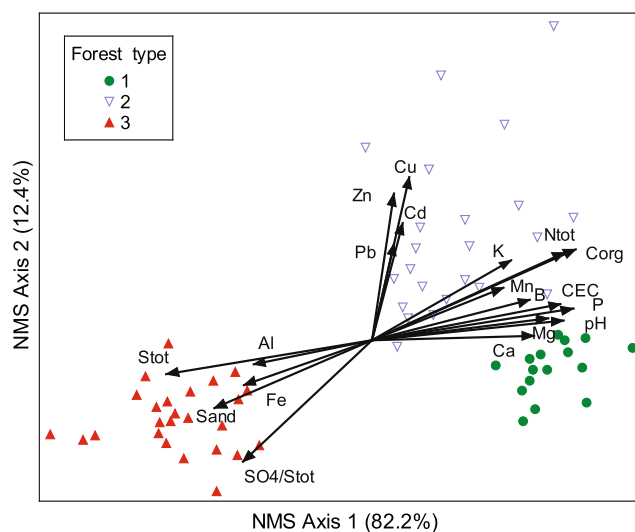
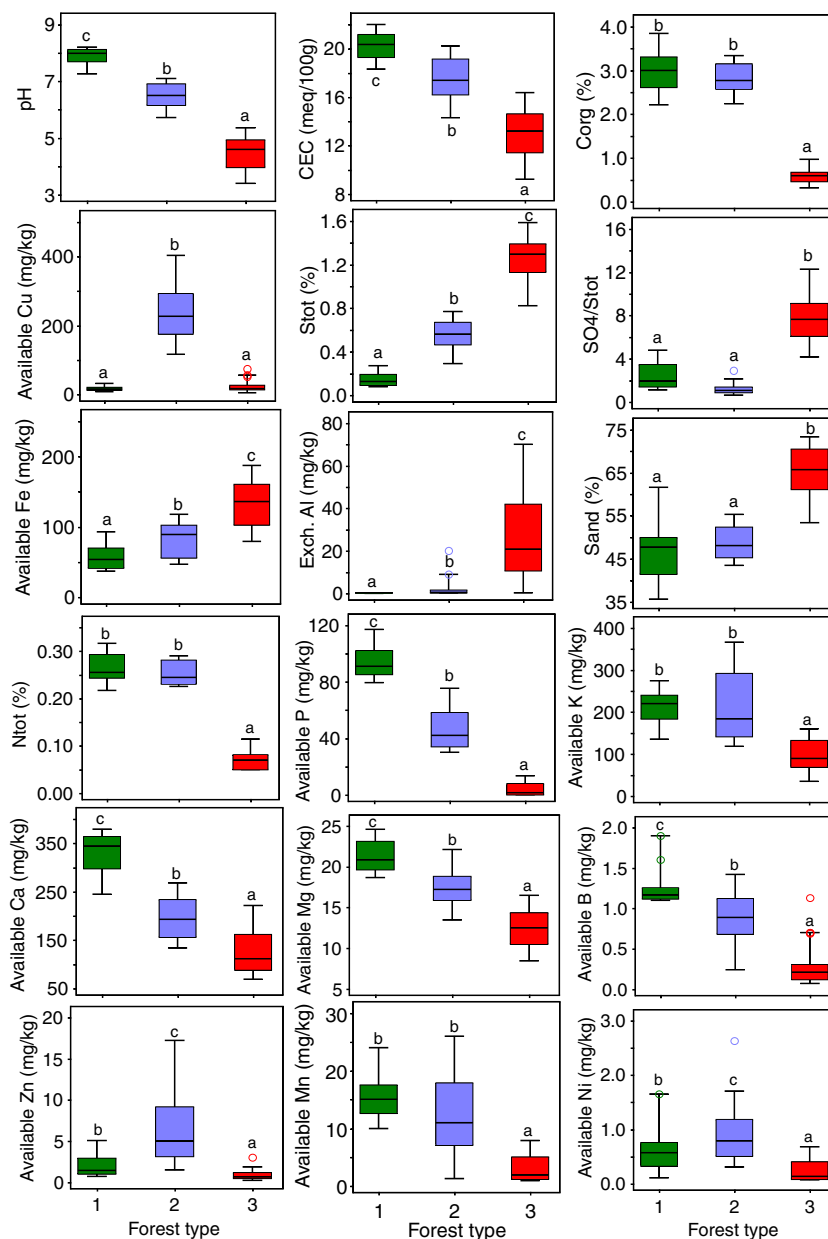


Fig. 2 Major gradients (NMS ordination) in soil properties of the forests spontaneously developing after vegetation destruction by fluvial deposition of sulphidic Cu tailings. 1 Soils of the poplar forests on the unpolluted alluvium (reference community); 2 soils of the older pioneer forests dominated by poplars, developing at the outer edge of the polluter alluvium; 3 soils of the younger pioneer forests dominated by birch and aspen, developing on severely polluted alluvium closer to the river channel. Data matrix: 64 soil samples, 22 soil chemical parameters (relativized by adjusting to standard deviate), Euclidean distance, varimax rotation; final stress for 2-D solution 8.95; ordination rotated by -55° . Parameters presented are correlated with the ordination scores by more than 35 %; plant-available concentrations of all the elements except S_{tot} , N_{tot} and C_{org} are shown

Fig. 3 Selected physico-chemical parameters of the forest soils in the polluted Timok floodplain: 1 poplar forests on the unpolluted alluvium (reference community); 2 older pioneer forests dominated by poplars, developing at the outer edge of the polluter floodplain; 3 younger pioneer forests dominated by birch and aspen, developing on severely polluted floodplain closer to the river channel. Box-plots (scaled in percentiles) outline the frequency distribution of each soil variable in the samples. Values deviating by more than 1.5 times interquartile range are marked as outliers. For each presented soil parameter, mean values marked by the same letter are not different among the forest types ($p < 0.05$; Tukey's test)



together (φ coefficient $> +0.84$) and make up more than 80 % of the total vegetation cover in these forests. Overall, the vegetation of pioneer birch-aspen forests possesses significantly different adaptations than both the original (type 1) and spontaneously restored (type 2) alluvial forests dominated by *P. alba* and *P. nigra* (Fig. 5). The species of the type 3 forests (birch-aspen) are adapted to acidic, nutrient-poor soils and have lower continentality index (Fig. 5a). Surprisingly, though dominant species are not pronouncedly drought-tolerant, the presence of particular xerophytic species from the surrounding gives this forest type a significantly drier character (Fig. 5a). Finally, these novel forests are clearly set apart by the forest floor vegetation, composed of species of broad geographical

distribution (circumpolar and sub-circumpolar chorotype, Fig. 5b).

Discussion

Imposed constraints bring different outcomes of spontaneous revegetation

The complex soil pollution by sulphidic Cu tailings has posed a challenge for the nature to cope with two different types of constraints over very short (less than 1 km) distances: (a) extremely high concentrations of available Cu and (b)

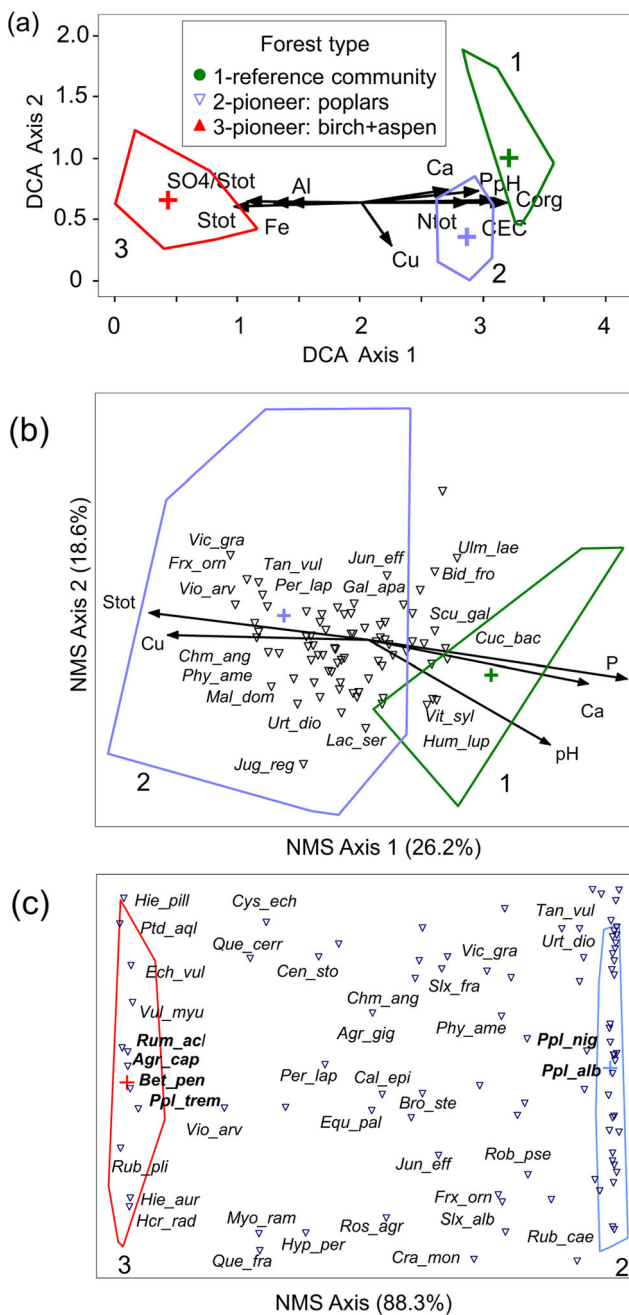


Fig. 4 Unconstrained ordination of spontaneous forest vegetation occurring in the polluted Timok floodplain. Convex hulls and group centroids are shown, and soil properties correlated with ordination scores by more than 35 % are passively overlaid. Data matrix: ordinal transformed values of species abundance (OTV). Species are abbreviated as in Online Resource 2. **a** DCA (Hill's scaling in SD units, eigenvalues 0.661 and 0.148 for axes 1 and 2 respectively; some highly correlated soil parameters are omitted); **b** NMS of poplar forests (38 samples, 79 species, Sørensen distance). **c** NMS of pioneer forests (Sørensen distance, 48 samples, 92 species)

extremely low pH combined with nutrient deficiency (Fig. 3). When the severity of these constraints was below an apparent critical “threshold” (Table 1), spontaneous revegetation did occur, resulting in two different types of pioneer forests

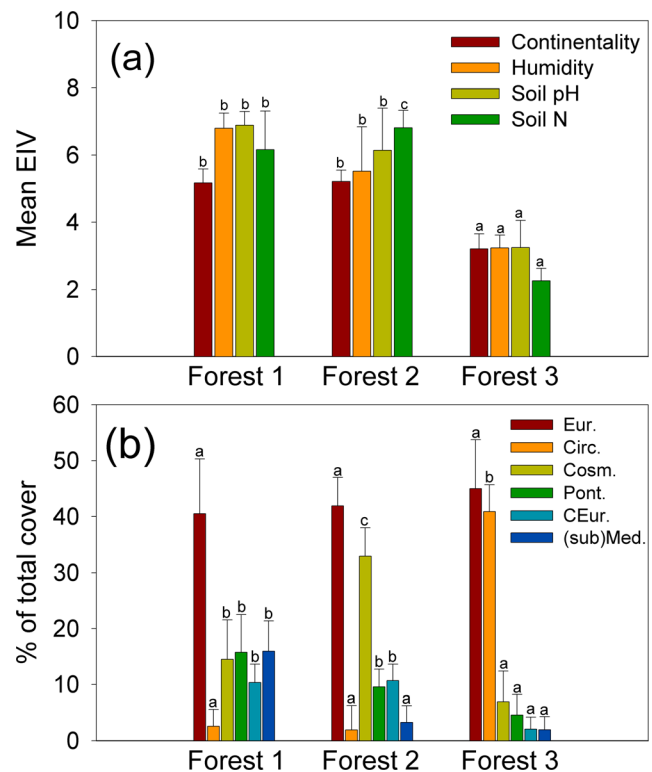


Fig. 5 Major ecological adaptations of forest vegetation in the floodplain polluted by sulphidic Cu tailings. **a** Ellenberg indicator values and **b** chorological spectra. Parameters are weighted by the species cover-abundance (OTV). Weighted mean values + SD marked by the same letter in each colour-coded category are not different ($p < 0.05$; Tukey's test). Forest 1 reference poplar forests on unpolluted alluvium. Forest 2 pioneer poplar forests at low level of pollution deposition; forest 3 pioneer birch-aspen forests at high level of intensively weathered tailings deposits. *Eur.* (sub-)Eurasian, *Circ.* (sub-)Circumpolar, *Cosm.* adventive + cosmopolitan, *Pont.* (sub-)Pontic, *CEur.* (sub-)Central European, *(sub)Med.* sub-Atlantic + sub-Mediterranean

strongly correlated with soil constraints (Table 2; Fig. 4). The surrounding vegetation had different importance in overcoming these two imposed environmental filters.

Overcoming Cu toxicity is easier; the surrounding vegetation matters

Very high concentrations of plant-available Cu (well over 200 mg kg^{-1} , Fig. 3) did not prevent spontaneous restoration of forests which converge to the reference poplar community (Fig. 4a, b). The major differences with respect to the original vegetation (sparser structure, Table 2; remnant species from pre-pollution agricultural land use like fruit trees, Fig. 4b; and increase of adventive species, Fig. 5b) can be partly explained by a pioneer character of spontaneously restored poplar forests. Apart from very prominent difference in the availability of Cu, P and Ca, the differences in other soil properties of the two types of poplar forests are relatively moderate (Fig. 3). Though an overriding effect of metals on vegetation patterns is usually assumed (e.g. Becker and Brändel 2007), studies

have shown that metals can have minor effect compared to other soil constraints (e.g. Smith and Bradshaw 1979; Thompson and Proctor 1983; Nikolic et al. 2014). In the present work, an important share of adventive and cosmopolitan species which increase the abundance in the pioneer poplar forests (Fig. 5b) is pseudometallophytes (see also Online Resource 2). Pseudometallophytes are species which commonly possess certain tolerance to metals, mostly based on metal exclusion (Baker 1987), and in our study they apparently constitute a part of vegetation response to the elevated soil Cu concentrations. Pioneer poplar forests (*P. alba*-*P. nigra*) were established by the species from the immediate surroundings, i.e. by vegetative lateral spread from the remnants of the riparian forests/groves out of reach of the major floods; these forests are however strictly limited to the outer edge of the polluted zone (Fig. 1c). Likewise, as a consequence of this particular setup, the available Cu concentrations, 80 years after the onset of the long-term tailings deposition, were higher in soils farthest from the river (i.e. farthest from the pollution source, Fig. 2). The restored soil organic matter (Fig. 3) exerts a key role in preventing further sulphide oxidation and Cu leaching, as well as in decreasing Cu phytotoxicity; moreover, a process of mutual protection of plant debris from degradation and heavy metals from leaching (Balabane et al. 1999) apparently occurs in these soils.

Drastically lower pH: no effect of the surrounding vegetation

On the other hand, spontaneous revegetation of severely acidified, nutrient-poor tailings deposits was considerably slower: The pioneer birch-aspen forest were sparser, composed of smaller individuals, less diverse (Table 2) and floristically very different from both the pioneer poplar forests developing under Cu toxicity and the original poplar forests on unpolluted soils (Fig. 4a, c). Without the four key species of pioneer birch-aspen forests (*R. acetosella*, *A. capillaris*, *B. pendula* and *P. tremula*, Fig. 4c), primary succession on the highly weathered tailings deposits does not start, not even after several decades. The occurrence of these species per se is not unusual; they are able to tolerate metal (particularly Cu) toxicity, low pH and nutrient deficiency (e.g. Smith and Bradshaw 1979; Thompson and Proctor 1983; Prach 2003; Marguí et al. 2007; Guerra et al. 2011). Two phenomena, however, are rather interesting: (a) These four species do not occur in the adjacent vegetation, and (b) these four species support assemblages which are highly atypical for natural birch-aspen forests.

The importance of *B. pendula* and the occurrence of *P. tremula*, *R. acetosella* and *A. capillaris* in post-mining successions have been established in German and Czech acidic coal spoils (e.g. Pietsch 1996; Hüttl and Weber 2001; Prach 2003; Tischew and Kirmer 2007; Kirmer et al. 2008) and also in the non-acidic metal pits in Poland (Szarek-Lukaszewska

and Grodzinska 2007). Contrary to the situation described in the present study, these four species were also able to grow in the immediate vicinity on non-degraded soils in all the aforementioned papers; the pH of these soils usually differed by up to 2 pH units from the non-affected surrounding. Moreover, though species arriving from a distance of more than 17 km were shown to have a role in post-mining succession (Lusatian coal-mining area, Germany, Kirmer et al. 2008), more than 50 % of the species from a relatively small surrounding area were able to colonize the acidic spoils (Tischew and Kirmer 2007). In Serbia, however, *B. pendula* is at the southern border of its distribution range, and in the xerothermic, carstic research area in the east of the country birch does not occur in the zonal forest vegetation of xerothermic oaks (Dinić 2006). Overall, all the four mentioned key species naturally occur in Serbia on non-calcareous soils, moister climate and higher altitudes in the western part of the country, at least 300 km away from the research locality (Tomić 2004). Likewise, some of the accompanying species of the type 3 forests (*Rubus plicatus*, *Hieracium pilosella* and *Pteridium aquilinum*, Fig. 4c) are as well commonly found in the birch-aspen vegetation, but not in the vegetation adjacent to the research locality (Dinić 2006). On the other hand, the presence of some of the common species of the surrounding vegetation, in particular, species of sub-mediterranean and (sub-)Pontic provenance (Fig. 5b), such as *Echium vulgare*, *Centaurea stoebe*, *Cynosurus echinatus*, *Hordeum bulbosum*, *Vicia grandiflora*, *Quercus cerris*, see Online Resource 2), is highly atypical for birch-aspen forests described so far.

Thus, lowering of soil pH of a large area by more than 4 units (Fig. 3) acted as the severe environmental filter which has not allowed successional convergence to the original vegetation; surrounding vegetation had negligible effect on spontaneous restoration (Fig. 4). A remarkable feature of spontaneous vegetation developing on post-mining land is the occurrence of “novel ecosystems”, characterized by new, non-historic combinations of species that bear little resemblance to the assemblages on non-affected soils; they are assembled primarily by environmental filtering (Walker and del Moral 2003; Hobbs et al. 2009). The underlying physiological drivers of “novelty” are however still widely unknown (but see Nikolic et al. 2014).

Management implications

This “would be” scenario, though providing interesting ecological insights into the principles of primary succession, is a case where spontaneous restoration is not an option. The enormous amounts of weathering-induced leaching of Cu (about 10 t ha⁻¹ leached at least below 40 cm, calculated from Table 1) implies the necessity for fast establishment of vegetative cover. Soil covering by allochthonous material might not be feasible because of the pronounced fluvial dynamics of the

Timok River and the large area affected. Neither would planting of local species be an option, as restoration of vegetation cover or land use resembling the pre-pollution one is deemed impossible. On the contrary, this is the case where assisted establishment of a community very different from the original one, by planting well known but locally absent keystone species, would be a socially and economically acceptable necessity.

Conclusions

If left to its own, the nature will, in the same environmental setup, cope differently with the stresses of Cu toxicity and with low pH combined with nutrient deficiency. While excessive soil pollution by Cu will still allow convergence to the reference community, the extreme induced acidity (more than 4 pH units difference from the surroundings) will result in novel, depauperate assemblages of species typical for cooler and moister areas. The presented results for the first time provide evidence that with the increasing severity of environmental filtering the relative importance of the surrounding vegetation for primary succession decreases and might even become irrelevant. When induced soil change is drastic enough, its filtering effect overrides the hierarchically higher filters of regional flora and climate which normally have a primary effect on plant communities.

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