Preslia 96: 223–246, 2024
doi: 10.23855/preslia.2024.223

Preslia

Environmental factors shape the relationship between seed bank and vegetation on periodically emerged alluvial gravel bars of the Elbe river

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Abstract: Riparian ecosystems are among the most valuable natural ecosystems in terms of their diversity and ecosystem functions, but their intensive use by humans has led to their degradation and reduction in extent. One of the last free-flowing rivers in central Europe is the Elbe, with more than 600 km of water course without weirs. Thanks to the relatively natural fluvial regime, exposed gravel bars hosting specific vegetation including several endangered species have been preserved. In this study, we examined how factors that are related to fluvial dynamics influence plant communities, above and belowground, on gravel bars that are periodically exposed along the Elbe in the Czech Republic. This study was carried out along a 40 km long stretch of the river between Ústí nad Labem and the Czech-German border. There, 10 localities were selected where 60 plots 1 × 1 m in size were established that were arranged in transects perpendicular to the river. Plant communities were recorded in terms of their composition and richness of both the standing vegetation and the soil seed bank, which provides information on the regeneration potential of these communities. All vascular plant species were identified at the peak of vegetation development and the soil seed bank cultivated from sediment sampled next to the plots. Of the environmental factors, the texture and chemical properties of the sediment were analysed, and hydrological modelling was used to determine the duration of plot exposure. The composition of the vegetation was most influenced by the duration of plot exposure, which separated the species of long- and short-flooded sites. In contrast, the composition of the seed bank was not significantly influenced by the environmental factors studied, but by functional species traits, with stress-tolerant species capable of clonal spread clearly different from light- and moisture-demanding species with a ruderal life-strategy. It is concluded that fluctuations in water level are essential for maintaining species richness on gravel bars because they create a strong gradient, which promotes the coexistence of species with different requirements in small areas.

Received: 19 Apr 2024; Revised: 19 May 2024; Accepted: 23 Jun 2024; Published: 20 Sep 2024

Keywords: disturbance, endangered habitat, endangered species, flooding, fluvial dynamics, invasive species, moisture, plant community composition, plant traits, riparian vegetation, sediment texture

Introduction

Riparian ecosystems are among the most valuable natural ecosystems because they are rich in species, diverse in natural conditions and provide many ecosystem services (Naiman & Décamps 1997). However, the morphology of rivers has been severely altered by human-related activities, such as those associated with transport by water, flood protection, agricultural land acquisition and energy production (Nilsson & Berggren 2000, Tockner et al. 2010). Intensive human use, combined with the specific nature of these ecosystems in terms of their linearity, interconnectivity and limited size, has made riparian habitats one of the most threatened ecosystems worldwide (Richardson et al. 2007, Jones et al. 2020).

The Elbe river is one of the last free-flowing rivers in central Europe, with more than 600 km without weirs or similar types of barrier, 40 km of which are in the Czech Republic (Härtel 2019). Due to the fluctuating water level, alluvial gravel bars (hereafter referred to as gravel bars) with specific plant communities have been preserved (Rottenborn et al. 2018, Kalníková et al. 2019). These gravel bars typically form along the inner concave banks, where sediments carried by the flow are deposited. The vegetation that develops on these gravel bars when the water level drops is characterized by high diversity, which is a consequence of the high stand heterogeneity maintained by regular disturbance by the river, and the type of vegetation differs depending on time for which the gravel bar is exposed (Šumberová 2010, Surian et al. 2015). Dominance of annual species is typical at sites that are submerged for long periods (Tabacchi et al. 1998) and succession towards perennial and woody species is expected when they are submerged for very short periods or only shallowly with low disturbance intensity (Šumberová & Lososová 2011, Prach & Walker 2020). The duration of gravel bar exposure/submergence depends on runoff, which is highly variable between years in the Elbe (Rottenborn et al. 2018). This also changes with increasing distance from the river, so that during the vegetation season there is a strong gradient from newly exposed to higher sites further from the river.

The seed bank is very important for survival when submerged and for dispersal in highly dynamic riparian habitats (Pettit & Froend 2001), although its role may be less at sites where periodic flooding precludes seed storage and where species survival largely depends on the import of seed (Pettit & Froend 2001). Connectivity is thus essential for the resilience of plant communities and the maintenance of other processes (Lytle & Poff 2004), such as transport of sediment (Galia et al. 2021). Sedimentation and seed deposition by rivers are closely related processes (Goodson et al. 2003) and sedimentation is therefore linked to both seed transport (Gurnell et al. 2008) and plant establishment and growth (Richardson et al. 2007, Šumberová 2010, Šumberová & Lososová 2011).

The vegetation on gravel bars in the Czech Elbe is well studied (e.g. Kubát 1995, Chvojková & Marková 2009, Bejček & Mandák 2018), because it is a unique example of this habitat with several endangered species, namely *Corrigiola litoralis* and *Pulicaria vulgaris* (Kubát 1977, Machová & Kubát 2004, Rottenborn et al. 2018, Havlíček et al.

2024). It is also an important migration corridor for alien species (Jehlík & Hejný 1974), which might benefit from regular disturbances and flooding (Čuda et al. 2017). However, there is a lack of information on the most important factors affecting plant species composition and species richness.

To address this gap in our knowledge, the focus here is on factors that affect plant growth and seed germination and are related to the river's fluvial regime, which determines the period for which the gravel bars are exposed, sediment texture and chemistry. Specifically, the questions addressed were: (i) What are the effects of flooding, sediment texture and chemistry, and location of a gravel bar on the species composition of the vegetation and seed bank? (ii) How do these environmental factors affect plant species richness and how they relate to plant traits? (iii) Do the seed banks and the species compositions of the vegetation differ and if so, why? The expectation is that the species composition of the vegetation is driven mainly by flooding and available nutrients, and its richness by flooding and the species richness of the seed bank. In contrast, the expectation is seed-bank species composition is predominantly determined by sedimentation, which depends on the position on the gravel bar and texture of the sediment. There are likely to be greater differences in the species composition of the seed bank and the vegetation close to the river, as diaspores are often carried by water flow and the seed of some species may be buried and therefore are not present in the vegetation. These findings will contribute to a better understanding of the key processes driving the species composition and richness of the vegetation on the threatened habitat of gravel bars in rivers.

Material and methods

Study sites and sampling

This study was done on periodically flooded gravel bars in the Elbe river between Ústí nad Labem and the Czech-German border (Fig. 1). The exposure of the gravel bars usually starts in summer and the duration of exposure depends on the discharge. The minimum duration of exposure of a gravel bar necessary for the development of vegetation is 8–10 weeks (Šumberová 2010, Šumberová & Lososová 2011), however, in some years with high rainfall gravel bars remain under water all year round. In addition, fluctuations in the level of the river during a year are currently significantly influenced by the dams of the Vltava cascade and the Střekov weir. It is assumed that the maximum flow during seasonal floods was originally higher, and conversely the minimum flow during dry periods in summer was lower. Furthermore, sediment quality probably changed due to the increased unit flow energy (Škarpich et al. 2016) caused by the narrowing of the channel over the last 200 years (Galia et al. 2024). This resulted in reduced accumulation and potential degradation of the existing gravel bars due to increased fluvial erosion. All of these changes have had a significant role in the potential for the formation of gravel bars.

Gravel bars are characterized by frequent disturbances and are extreme environments even when exposed: the bare surface overheats, dries out and can be repeatedly cooled by rising water level. The above factors affect succession, which is impeded by disturbances and the plant community is composed of light-demanding, low-competitive species that survive long periods of flooding mostly in the form of seeds. The habitat is classified as European Habitat 3270 "Rivers with muddy banks with *Chenopodion rubri* p.p. and

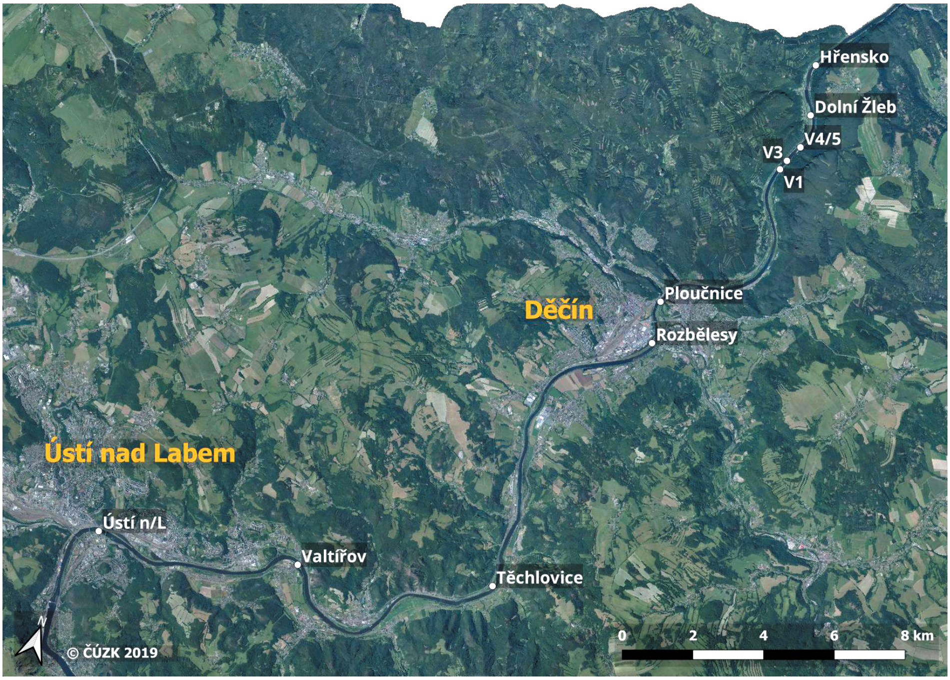

Fig. 1. Overview of the localities studied on the Elbe river between Ústí nad Labem and the Czech-German border. Artificial localities are marked with the letter V, the names were adopted from previous studies. Map base – orthophoto ČÚZK 2019.

Bidention p.p. vegetation" (https://eunis.eea.europa.eu/habitats/10078). The European Red List of Habitats (Janssen et al. 2016) distinguishes two types of this habitat, one which is near threatened (C3.5a Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation) and the other is vulnerable (C3.5.b Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation). Gravel bars have been affected by various human activities aimed at preventing flooding and facilitating transport by water. Despite these interventions, the typical gravel-sandy river sediments with characteristic vegetation including critically endangered species, such as *Corrigiola litoralis*, can still be seen there.

To study the relationships between standing vegetation, seed bank and environmental conditions, seven natural sites representing the largest and best preserved gravel bars, and three artificial sites (groynes V1, V3 and V4/5) that were originally constructed to concentrate flow in the river channel, and some of which were restored to provide a more suitable natural habitat were established (Supplementary Table S1). Sixty 1 × 1 m plots that were arranged in transects perpendicular and parallel to the river were established. The five largest localities had nine plots with three transverse transects at the beginning, centre and end of each gravel bar, five smaller localities had three plots with one transverse transect in the central part of the locality. Transverse transects were used to determine differences in plant species composition in a direction perpendicular to the river, which differed in height above water level and duration of exposure of the gravel bars (Fig. 2A). Each transverse transect started at the point adjusted to the water level of 150 cm at the water level gauge in Děčín

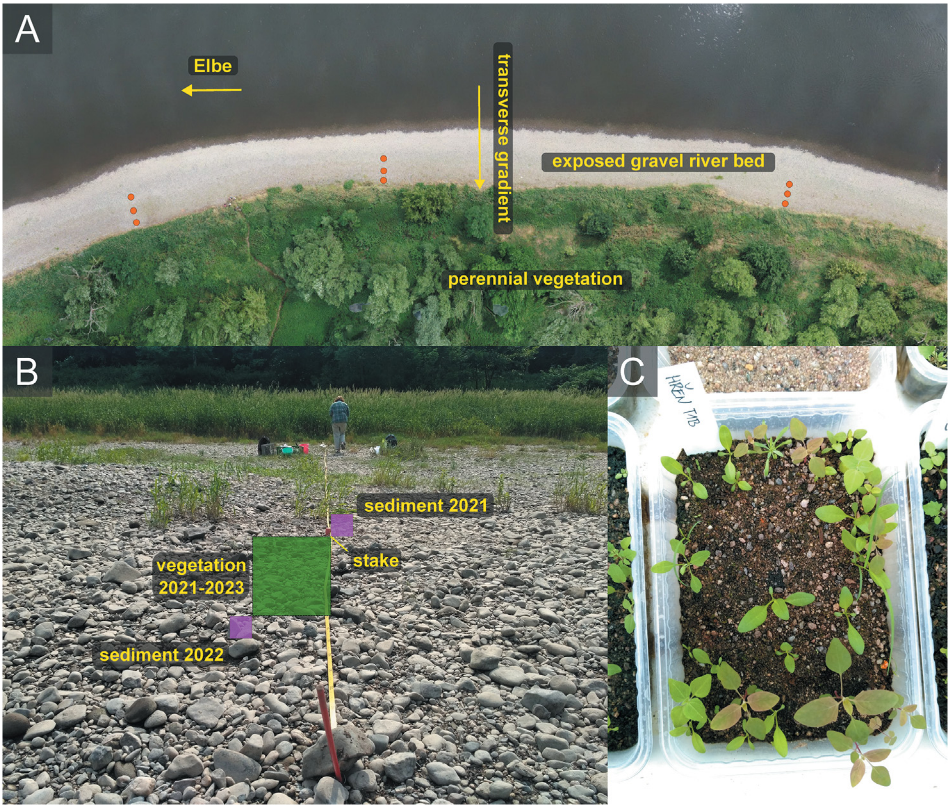

Fig. 2. (A) Arrangement of study plots (orange dots) in transverse transects at Těchlovice. The map is based on a georeferenced aerial image taken by a drone. (B) The transect in the central part of the Hřensko locality showing 1 × 1 m plots for recording vegetation (green) and 20 × 20 cm plots for sediment sampling for seed-bank cultivation (purple). Photograph taken on 16 June 2021 during the establishment of the plots. (C) Emergence of seedlings in a cultivation pot of sediment from Hřensko. Both the critically endangered species *Corrigiola litoralis* and the invasive species *Eragrostis albensis* and *Galinsoga quadriradiata* are present.

(https://hydro.chmi.cz/hppsoldv/popup_hpps_prfdyn.php?seq=2497644) and ended in front of the perennial vegetation (Fig. 2B).

Vegetation sampling and data on plant species characteristics

In each 1 × 1 m plot, the percentage covers of all the species of vascular plants were recorded at the time of maximum development of vegetation, once a year, during three growing seasons: 2021 (4–6 October), 2022 (15–16 September, 28–29 September, 3–4 October, 6 October) and 2023 (10–12 July). In 2022, the botanical survey was interrupted by a rise in water level that flooded the plots and was completed as soon as possible after the water level dropped. In 2023, the botanical survey was done in July as the vegetation then was already well developed.

Data on plant species characteristics were obtained from the Pladias database (Chytrý et al. 2021), specifically, maximum plant height (Kaplan et al. 2019), CRS life strategy

(Pierce et al. 2017), clonal dispersal distance (Klimešová et al. 2017), Ellenberg-type indicator values for light, temperature, soil reaction, moisture, nutrients and salinity (Chytrý et al. 2018), herbaceous plant layer indicator values for frequency and severity of disturbance (Herben et al. 2016), residence time and invasion status (Pyšek et al. 2022) and Czech Red List status (Grulich et al. 2017) and IUCN threat level (IUCN 2014). Data on seed mass were obtained from Lososová et al. (2023). Nomenclature of plant species follows Kaplan et al. (2019).

Seed-bank sampling

To assess the seed bank, sediment was collected with a garden trowel from a 20 × 20 cm area to a depth of 5 cm next to each of the 1 × 1 m plots (Fig. 2B). Sediment was sampled approximately one week after gravel bar exposure, in 2021 during the plot establishment on June 15–17 and in 2022 on May 23–24. The sediment was further sieved through two coarse sieves (1.0 cm and 0.5 cm) and a thin layer of sediment (~1 cm) was spread on a 3 cm layer of sterilized clean sand in 18 × 13 × 5 cm plastic pots (Fig. 2C). These pots were placed in a glasshouse in cages covered with fine mesh to prevent seed contamination from outside and their surfaces kept permanently moist.

Emerging seedlings were checked every two to three weeks, determined to species, counted, and identified seedlings were removed. Some of the seedlings that could not be identified were transplanted and grown until maturity when the plants had all the critical features needed for identification. Two individuals could not be identified to species level, because plants died during cultivation/transplantation (they were *Poa* sp. and *Euphorbia* sp.) and five other individuals could not be identified because they did not flower in cultivation (*Oenothera* sp. and *Melilotus* sp.). At the beginning of November, the pots still covered with mesh were moved outside and overwintered in the experimental garden. The following spring, the pots were returned to the glasshouse and the sediment was cultivated under the same conditions as before, in order to determine whether any seed germinated after cold stratification in the experimental garden. Germination was recorded for each of the samples in two consecutive years; during 23 June – 15 November 2021 and 17 May – 1 November 2022 for sediment collected in 2021, and during 6 June – 9 November 2022 and 3 May – 30 October 2023 for sediment collected in 2022.

Data on flooding of sites

The time of flooding of the 1 × 1 m plots between 2020 and 2023 was determined using their GPS coordinates and the modelling of the water level in the Elbe. First, a polygon of the flooded area was determined based on the daily flow of the Elbe. The extents of the flooded areas were determined using the HEC-RAS hydrodynamic model (Brunner 2016) and exported from the HEC-RAS environment as georeferenced polygons. If there was no intersection between the polygon of the flooded area and the polygon of a plot, or if there was an intersection, but the permanent plot was less than half flooded, it was considered unflooded. Otherwise, it was considered as flooded. Spatial data were processed using the packages rgdal (shapefile loading), raster (intersect of plot and flood polygons) and anytime (date format). This analysis was done in the R 4.3.1 (R Core Team 2023).

Texture and chemistry of the substrate

Texture of the top 5 cm of the substrate collected from a 20 × 20 cm area near the 1 × 1 m plots was measured (seed-bank germination substrate was collected elsewhere as it was sometimes completely used in the germination experiments). The weights of the fresh sample and the sample after drying at 60 °C were used to calculate the water content. Texture was analysed using the whole dry sample, when the fractions > 200 mm, 200–50 mm, and 50–20 mm were separated manually; fractions 20–5 mm, 5–2 mm, 2–0.5 mm by dry sieving and the particles below 0.5 mm were analysed in suspension using the MasterSizer 2000 MU (Malvern Instruments, England). The finest fraction of particles below 0.5 mm was used for loss on ignition (550 °C /2 h) and all other chemical analyses. For the statistical analyses, only the percentage of fine sediment (sand) obtained by summing the fractions 2–0.063 mm was used. This was because the percentage of the finest fraction below 0.063 mm (clay) was negligible and the correlation between percentage sand and the 200–2 mm coarse fraction (gravel and stones) was therefore high (Supplementary Fig. S1).

For the determination of plant-available nutrients and selected metals (P, K, Ca, Mg, Fe, Mn, Al, Cr, As), the Mehlich III extraction solution (Mehlich 1984) was used, where 1 g of sample was extracted with 10 ml of solution for 5 min. The samples were centrifuged and filtered (0.4 µm GF filters) before analyses by ICP-QQQ (Agilent, Japan). A semi-micro modification of the perchloric acid digestion method for the determination of total P in soils, sediments and organic materials (Kopáček et al. 2001) was used to analyse the composition of the particles smaller than 0.5 mm. Samples were digested for 30 minutes in nitric acid at 115 °C and then for 2 hours in perchloric acid at 170 °C in an aluminium heating block before analyses by ICP-QQQ. Values for the environment, seed bank and characteristics of the vegetation are summarized and presented in Supplementary Table S2.

Statistical analyses

Multivariate analyses

The relationships between the species compositions of the vegetation or seed bank and environmental factors were explored in two steps. First, the main gradients in the species composition data using non-metric multidimensional scaling (NMDS) with the function metaMDS was used (Oksanen et al. 2024). Bray-Curtis dissimilarity was used to calculate differences between plots (Legendre & Legendre 2012). Second, a multiple regression of the environmental variables on the ordination axes of the NMDS was done using the envfit function and the significance of this regression was determined using a permutation test. The aim was to determine whether the gradients revealed by NMDS are associated with environmental variables. The advantages of NMDS are that it works on more general compositional data, such as count data and does not rely on assumptions of multivariate normality, because it uses non-parametric permutation methods (Legendre & Anderson 1999).

For species composition of the vegetation, plant species percentage covers were used as response values that were square-root transformed prior to analysis. The position of a plot on the transverse transect, the number of days in a vegetation season (1 April – 31 October) for which the gravel bar was exposed, the percentage of sand in sediment and the available phosphorus in the sediment were used as environmental variables. All environmental variables were standardized using the scale function in R, that is, the mean was subtracted from each value and then divided by the standard deviation in order to unify the range of all variables.

Available phosphorus and percentage sand were chosen because most of the soil parameters were highly correlated with each other (see Supplementary Fig. S1 for mutual correlations) and these parameters are considered important for plant growth. Permutations were restricted by blocks defined by the year of the botanical survey and transect code, within which the records were permuted. Significance was tested using a Monte-Carlo test with 999 permutations (Lepš & Šmilauer 2003).To explore the environmental conditions important for plants, the mean Ellenberg-type values (light, temperature, soil reaction, moisture, nutrients, salinity) unweighted by the percentage cover of each species (Käfer & Witte 2004) in the relevé was used and the same procedure was followed for other ecological indicator values and selected plant traits (maximum height, clonal spread, life strategy, frequency and intensity of disturbance). Taxa that were assigned only to a genus, e.g. *Oenothera* sp. and *Euphorbia* sp., were excluded from the calculations of ecological indicator values.

For the species composition of the seed bank, the total number of seedlings of each species were response values, which were square-root transformed prior to analysis. The setting of the analysis and environmental variables were the same as for the analysis of the species composition of vegetation, except that the number of days in a vegetation season in the preceding year for which the gravel bar was exposed was used to express the effect of flooding on seed banks.

Differences between species compositions of the vegetation and seed bank were determined similarly as for individual analyses of vegetation and seed bank using two types of analyses, NMDS followed by multiple regression of environmental variables using the envfit function. The presence or absence of species in particular plots were response variables in the NMDS. The NMDS was used to assess the similarity of the seed bank and vegetation records by plotting their scores on the ordination diagram. In a second step, differences between species compositions of the vegetation and seed bank were analysed by multiple regression via the envfit function. The response variable was record type (seed bank or vegetation), with year and plot ID set as block-defining covariables, and the first two NMDS axes were predictors. This ensured that the seed bank and vegetation records were compared within pairs originating from the same year and same plot.

Univariate analyses

To determine the effect of the percentage of sand, plot position on the transverse transect and duration of gravel bar exposure on mean seed mass, a generalized linear mixed model (GLMM) with gamma distribution was used. Mean seed mass was calculated as the mean of the seed mass of all species present in a sample weighted by the number of seedlings that germinated. Locality, transect (nested in locality) and year were random factors used to account for spatial and temporal autocorrelation of plots. To account for possible non-linear effects of the predictors (percentage of sand and duration of gravel bar exposure) their quadratic term was included in the model. The significance of the terms in the GLMM was determined using the Anova function in the car package (Fox & Weisberg 2019).

Differences between species composition of seed bank and vegetation within each plot and year was expressed by the Bray-Curtis dissimilarity index, calculated using the vegdist function in the vegan package (Oksanen et al. 2024). Dissimilarity values were used as a response variable in the linear mixed model (LMM) and duration of gravel bar exposure, position on the transverse transect, species richness of vegetation and seedbank were predictors. Random factors were locality, transect (nested in locality) and year. The R code for all multivariate and univariate analyses are in the Supplementary Data S1.

All analyses and data visualization were done in R 4.3.1 (R Core Team 2023), graphs were plotted using the tidyverse packages (Wickham et al. 2019) and correlation heatmap with corrplot package (Wei & Simko 2021). Package lme4 was used to fit linear mixed models (Bates et al. 2015) and the explained variance was calculated using the r.squaredGLMM function in the MuMIn package (Bartoń 2023).

Results

Vegetation

A total of 109 plant taxa were recorded in the plots, with the highest number of species (76) in 2021, and lower numbers in the following years, 67 and 68 in 2022 and 2023, respectively. Only 38% of the species were recorded in all three years (Fig. 3A). The most frequent species in all three years were *Rorippa sylvestris*, which occurred in 100% of plots, *Agrostis stolonifera* (90%) and *Plantago uliginosa* (88%) (see Table 1).

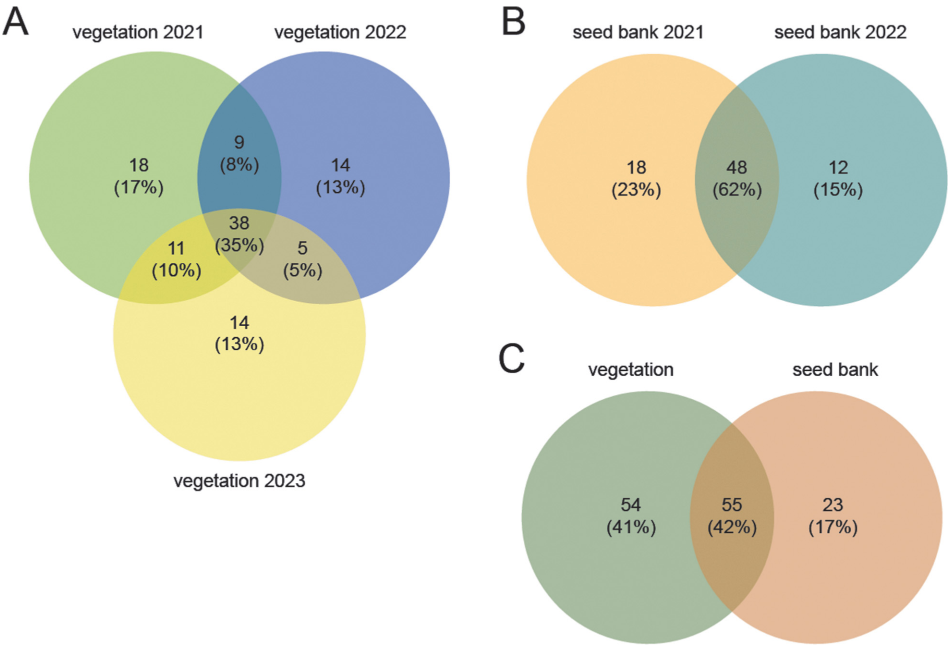

Fig. 3. The number and percentage of species shared between (A) vegetation in 2021, 2022 and 2023, (B) seed banks from 2021 and 2022, (C) all vegetation and seed-bank records.

Table 1. The most frequent and abundant species in the seed bank (2021–2022) and in the vegetation (2021–2023). Species frequency is expressed as percentage of plots occupied (% plots), abundance as percentage of total number of seedlings (% seedlings) and percentage cover as a percentage of total cover (% cover). Plots were considered occupied if the species occurred at least once during the sampling period.

	Vegetation			Seed bank	
Species	% plots	% cover	Species	% plots	% seedlings
Rorippa sylvestris	100	10.6	*Rorippa sylvestris*	97	43.0
Agrostis stolonifera	90	3.6	*Lythrum salicaria*	92	21.2
Plantago uliginosa	88	0.6	*Cyperus fuscus*	88	2.8
Urtica dioica	80	0.2	*Plantago uliginosa*	82	6.2
Eragrostis albensis	77	0.9	*Eragrostis albensis*	78	10.4
Lythrum salicaria	75	0.6	*Chenopodium polyspermum*	72	3.7
Chenopodium polyspermum	73	0.4	*Portulaca oleracea*	40	0.8
Persicaria lapathifolia	65	0.3	*Galinsoga quadriradiata*	38	0.9
Phalaris arundinacea	62	1.4	*Galinsoga parviflora*	33	0.6
Polygonum aviculare agg.	62	0.4	*Chenopodium album* agg.	32	0.6
			Inula britannica	32	0.9

Table 2. The relationship between vegetation or seed-bank species composition and environmental factors analysed using multiple regression with the envfit function. Variables abbreviations: unflooded – duration of exposure of gravel bar in the growth season (vegetation) or in the previous growth season (seed bank); transverse – position of plot on transverse gradient; available phosphorus – plant available phosphorus in sediment; sand – percentage of sand in sediment. Explained variance (EV) is shown for significant predictors.

	Vegetation community composition		Seed-bank community composition	
Variable	EV (%)	P	EV (%)	P
Unflooded	44.1	0.001	–	0.142
Transverse	26.7	0.001	–	0.603
Available phosphorus	8.0	0.001	–	0.462
Sand	–	0.126	–	0.273

Species composition varied significantly with the duration of plot exposure (multiple regression with the envfit function, P = 0.001), available phosphorus (P = 0.001) and transverse position of the plot (P = 0.001, see Table 2). The duration of plot exposure was the most important factor influencing the species composition in plots (Fig. 4A); *Rorippa sylvestris*, *Agrostis stolonifera*, *Inula britannica* were typical species in plots submerged for short periods, whereas *Chenopodium polyspermum*, *Lythrum salicaria* and *Persicaria hydropiper* were more typical of plots submerged for long periods.

The relationship between the aggregate plant species characteristics and environmental variables is shown in Fig. 4B. Communities submerged for long periods were typically represented by nutrient- and moisture-demanding species with a ruderal life strategy. In contrast, stress-tolerant species occurred further away from the river.

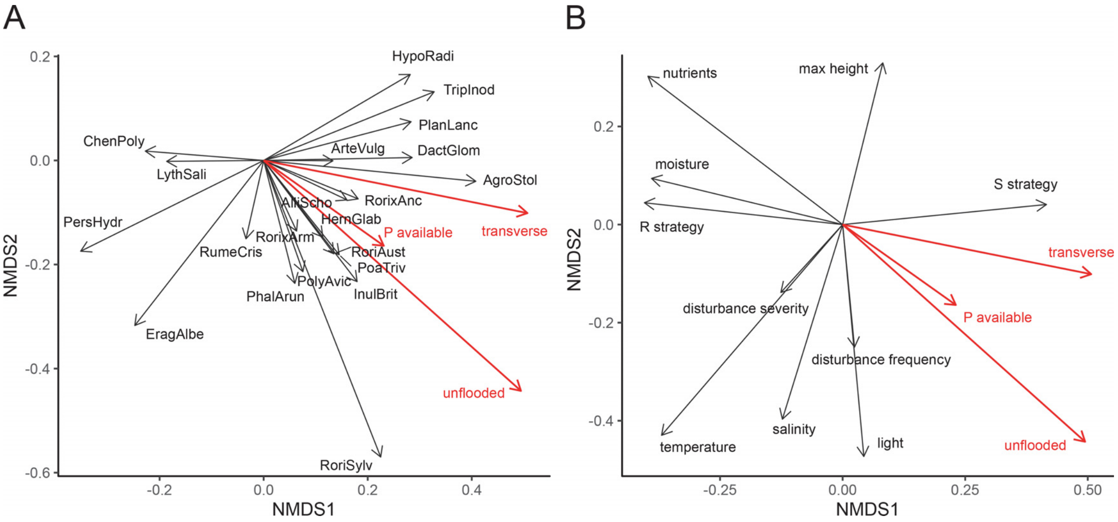

Fig. 4. (A) Relationship between species composition of vegetation (black) and environmental variables (red) presented as NMDS ordination diagram with projected species and environmental variables based on a multiple regression with the envfit function. Environmental variables explained 44.1% (unflooded), 26.7% (transverse), and 8.0% (available phosphorus) of the variance. (B) Ordination diagram based on the same analysis; environmental and aggregate plant characteristics derived from species occurrence in permanent plots are shown instead of plant species. Environmental variable abbreviations: unflooded = duration of gravel bar exposure during the growth season, transverse = position of the plot on the transverse transect, available phosphorus = plant available phosphorus in sediment. Only significant (P < 0.05) species, environmental variables and plant characteristics are shown. Species abbreviations: AgroStol = *Agrostis stolonifera*, AlliScho = *Allium schoenoprasum*, ArteVulg = *Artemisia vulgaris*, ChenPoly = *Chenopodium polyspermum*, DactGlom = *Dactylis glomerata*, EragAlbe = *Eragrostis albensis*, HernGlab = *Herniaria glabra*, HypoRadi = *Hypochaeris radicata*, InulBrit = *Inula britannica*, LythSali = *Lythrum salicaria*, PersHydr = *Persicaria hydropiper*, PhalArun = *Phalaris arundinacea*, PlanLanc = *Plantago lanceolata*, PoaTriv = *Poa trivialis*, PolyAvic = *Polygonum aviculare* agg., RoriAust = *Rorippa austriaca*, RoriSylv = *Rorippa sylvestris*, RorixAnc = *Rorippa ×anceps*, RorixArm = *Rorippa ×armoracioides*, RumeCris = *Rumex crispus*, TripInod = *Tripleurospermum inodorum*.

Seed bank

A total of 7,681 seeds of 78 species germinated from the seed bank; 4,114 seeds of 66 species in sediment collected in 2021 and 3,567 seeds of 60 species in sediment collected in 2022. The majority of species (62%) occurred in both years (Fig. 3B), the species that occurred in most plots in both years were *Rorippa sylvestris* (97%), *Lythrum salicaria* (92%) and *Cyperus fuscus* (88%) (see Table 1 for the most common species). Forty-two percent of the species in the vegetation were in the seed bank (Fig. 3C).

Species composition of the seed bank was not significantly related to any of the environmental variables (Table 2, Fig. 5A). Of the aggregate plant characteristics, total and alien richness was related; these species-rich communities typically contain stress-tolerant species capable of long-distance vegetative dispersal (Fig. 5B).

Mean seed mass, which reflects the sedimentation characteristics of a species, increased along the transverse transect away from the river (GLMM, P = 0.004). It also initially increased with the percentage of sand in the substrate and then slightly decreased (P < 0.001; Fig. 6, Table 3), but the reason for the weak association with the high percentage of sand is unclear because of the wide confidence interval.

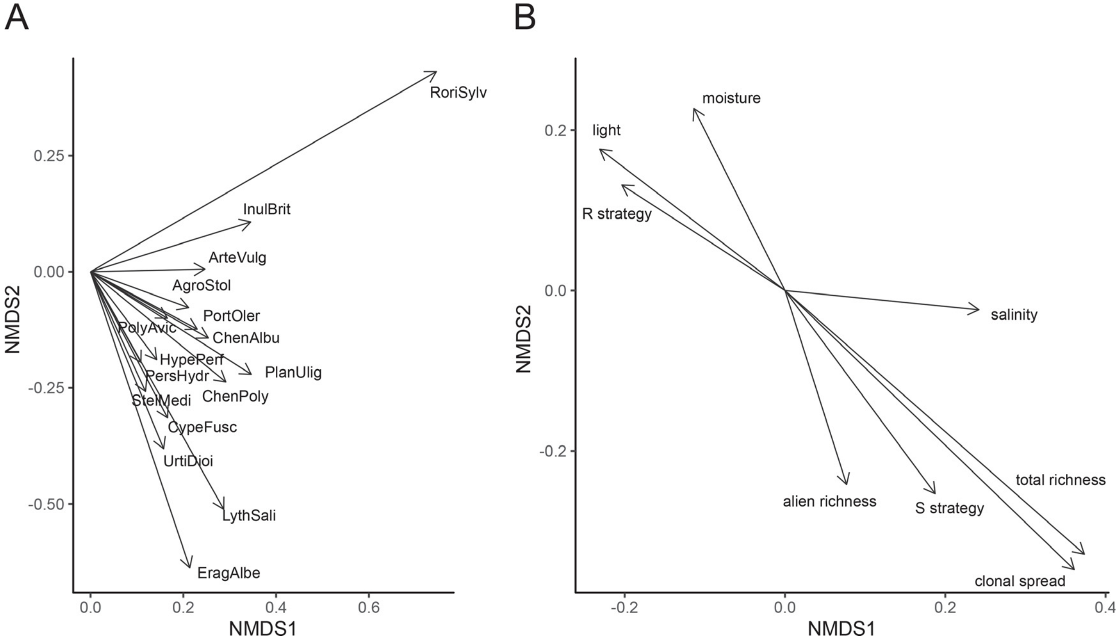

Fig. 5. (A) Relationship between species in the seed bank presented as NMDS ordination diagram with projected species by a multiple regression with the envfit function. No environmental predictors were significant. (B) Ordination diagram based on the same analysis, with environmental and aggregate plant characteristics derived from species occurrence in the plots are shown instead of plant species. Only significant ($P < 0.05$) species and plant characteristics are shown. Species abbreviations: AgroStol = *Agrostis stolonifera*, ArteVulg = *Artemisia vulgaris*, CypeFusc = *Cyperus fuscus*, EragAlbe = *Eragrostis albensis*, HypePerf = *Hypericum perforatum*, ChenAlbu = *Chenopodium album* agg., ChenPoly = *Chenopodium polyspermum*, InulBrit = *Inula britannica*, LythSali = *Lythrum salicaria*, PersHydr = *Persicaria hydropiper*, PlanUlig = *Plantago uliginosa*, PolyAvic = *Polygonum aviculare* agg., PortOler = *Portulaca oleracea*, RoriSylv = *Rorippa sylvestris*, StelMedi = *Stellaria media*, UrtiDioi = *Urtica dioica*.

Endangered and alien plants

In total, nine endangered species on the Red List of vascular plants of the Czech Republic (Grulich et al. 2017) were recorded, seven in vegetation and five in the seed bank (Table 4). Three of them belong to the highest protection level and were classified as critically endangered taxa: *Corrigiola litoralis*, *Populus nigra* and *Pulicaria vulgaris*. The rarest species, *Corrigiola litoralis*, was recorded at all three localities, where it had been recorded in the past. At these three localities they were recorded in 64% of the plots in the vegetation and in 55% of plots in the seed bank. *Cyperus fuscus*, an endangered species typical of periodically flooded stands, was recorded in 25% of plots in the vegetation, but in 89% of plots in the seed bank, indicating its high dispersal ability.

Forty-nine alien species were recorded in both the vegetation and seed bank, of which 21 species were common (see Table 5 for details of all alien species); 15 species were recorded only in vegetation, and 13 only in the seed bank. Neophytes and archaeophytes were similarly represented (22 and 25 species, respectively), with one species (*Weigela florida*), which germinated from the seed bank known only from cultivation. The most

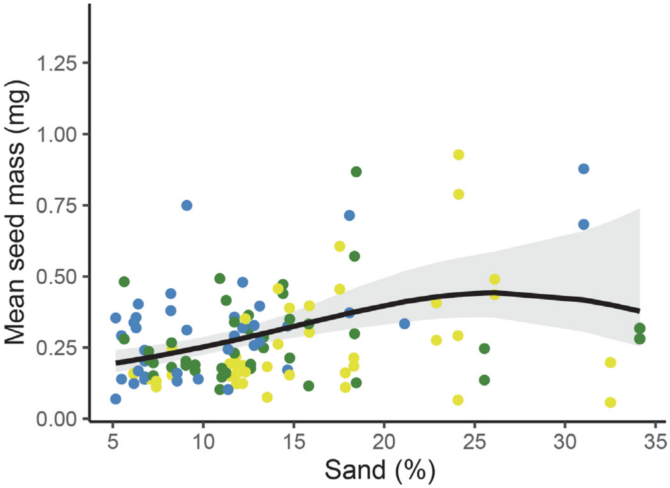

Fig. 6. Relationship between mean seed mass and percentage sand in the sediment. Points show the mean seed mass weighted by the species abundance in 60 plots over two years (n = 120), colours give information on their position on the transverse transect: ● plots nearest the river, ● plots in the middle, ● plots on the top of gravel bars. Regression line shows fit of a generalized linear model (GLM) where the predictors were percentage sand and its quadratic function and the dependent variable was mean seed weight; the grey area shows the 95% confidence interval. Data on seed mass of individual species were obtained from Lososová et al. (2023).

Table 3. The effect of position on the transect (transverse), duration of gravel bar exposure and its quadratic function (unflooded, unflooded^2), percentage sand and its quadratic function (sand, sand^2) on mean seed mass tested using generalized linear mixed model with gamma distribution. Full model with random effects (locality, transect and year) explained 84.7% of the variance, fixed effects explained 43.3% of the variance (EV).

Model	χ^2	Df	EV (%)	Effect	P
Full model			84.7		
Transverse	8.46	1	13.7	+	0.004
Unflooded	0.06	1	–		0.814
Unflooded^2	0.36		–		0.549
Sand	13.00	1	18.7	+	< 0.001
Sand^2	11.33	1	10.9	–	< 0.001

Table 4. Frequency of occurrence of the Czech Red List species in 60 plots and in the seed bank. Degree of endangerment was taken from Grulich et al. (2017): C1t – critically threatened taxon, declining; C2b – endangered taxon, rare and declining; C3 – vulnerable taxon, C4a – near threatened taxon. IUCN categories: CR – critically endangered, VU – vulnerable, NT – near threatened, LC – least concern, DD – data deficient (IUCN 2012, 2014). The mean percentage cover in all vegetation plots in which the species occurred is given in the % cover column.

			Vegetation		Seed bank	
Species	Red List CZ	IUCN	Plots	% cover	Plots	Seedlings/m^2
Allium schoenoprasum	C3	NT	3	1.6		
Atriplex prostrata	C4a	NT	2	0.1	1	1 (25)
Corrigiola litoralis	C1t	CR	14	0.9	12	88 (2200)
Cyperus fuscus	C3	NT	15	0.5	54	212 (5300)
Epilobium parviflorum	C3	NT			1	1 (25)
Limosella aquatica	C4a	LC			1	10 (250)
Nasturtium officinale	C2b	VU	1	0.1		
Populus nigra	C1t	DD	1	0.1		
Pulicaria vulgaris	C1t	CR	1	0.5		

Table 5. Overview of 49 alien taxa occurring in the vegetation and the seed bank. Residence time (neo – neophyte, arch – archaeophyte, cult – cultivated only) and invasion status (inv – invasive, nat – naturalized, cas – casual, NA – not available) in the Czech Republic were obtained from Pyšek et al. (2022). The number of plots is shown in which the species occurred in the seed bank and vegetation in 2021–2022 and 2021–2023, respectively. The total number of seedlings is in terms of the number of seedlings per square meter. The mean percentage cover in all vegetation plots in which the species occurred is given in the % cover column.

Species	Residence time	Invasion status	Vegetation		Seed bank	
			Plots	% cover	Plots	Seedlings/m^2
Amaranthus powellii	neo	inv	6	0.6	6	7 (175)
Amaranthus retroflexus	neo	inv			3	3 (75)
Ambrosia artemisiifolia	neo	inv	9	0.7	3	4 (100)
Atriplex patula	arch	nat	4	0.4		
Ballota nigra	arch	nat			1	2 (50)
Bidens frondosa	neo	inv	10	0.9		
Bromus sterilis	arch	inv	2	2.0		
Capsella bursa-pastoris	arch	nat			1	1 (25)
Cirsium arvense	arch	inv	2	0.3		
Convolvulus arvensis	arch	nat	1	0.3		
Conyza canadensis	neo	inv	1	1.0	4	5 (125)
Digitaria ischaemum	arch	inv			3	4 (100)
Digitaria sanguinalis	arch	inv	22	0.7	14	18 (450)
Echinochloa crus-galli	arch	inv	18	0.3		
Eragrostis albensis	neo	nat	46	2.2	47	796 (19900)
Eragrostis minor	arch	inv	1	1.0	5	5 (125)
Erigeron annuus	neo	inv	28	0.5	9	30 (750)
Erysimum cheiranthoides	arch	nat	8	0.5	6	12 (300)
Galinsoga parviflora	neo	inv	16	0.7	20	43 (1075)
Galinsoga quadriradiata	neo	inv	20	0.6	23	66 (1650)
Geranium pusillum	arch	nat	1	0.1		
Impatiens glandulifera	neo	inv	1	1.0		
Juncus tenuis	neo	nat			2	2 (50)
Melilotus albus	arch	nat	1	0.1	1	1 (25)
Mentha spicata	arch/neo	cas			1	1 (25)
Microrrhinum minus	arch	nat	3	0.4	2	2 (50)
Oxalis corniculata	neo	inv	5	0.5	14	25 (625)
Oxalis dillenii	neo	inv			3	4 (100)
Oxalis stricta	neo	nat	8	0.4	3	6 (150)
Panicum capillare	neo	nat			1	1 (25)
Physalis pubescens	neo	cas	1	0.1		
Portulaca oleracea	arch	inv	21	0.5	24	64 (1600)
Raphanus raphanistrum	arch	nat	1	0.1		
Robinia pseudoacacia	neo	inv			1	1 (25)
Rumex thyrsiflorus	neo	nat	9	0.4	2	2 (50)
Salvia hispanica	neo	cas	1	0.5		
Senecio vulgaris	arch	nat	2	0.7	4	5 (125)
Setaria pumila	arch	inv	1	0.1		
Setaria verticillata	arch	inv			1	1 (25)
Setaria viridis	arch	inv			1	1 (25)
Solanum lycopersicum	neo	nat	16	0.7		
Sonchus asper	arch	nat			4	4 (100)
Sonchus oleraceus	arch	nat	4	0.3	1	1 (25)
Symphyotrichum novi-belgii agg.	neo	nat	2	1.1	2	3 (75)
Tanacetum vulgare	arch	nat	5	0.4	3	5 (125)
Tripleurospermum inodorum	arch	nat	7	0.8	2	3 (75)
Vicia sativa	arch	nat	1	0.1		
Weigela florida	cult	NA			1	1 (25)
Xanthium albinum	neo	nat	2	2.0		

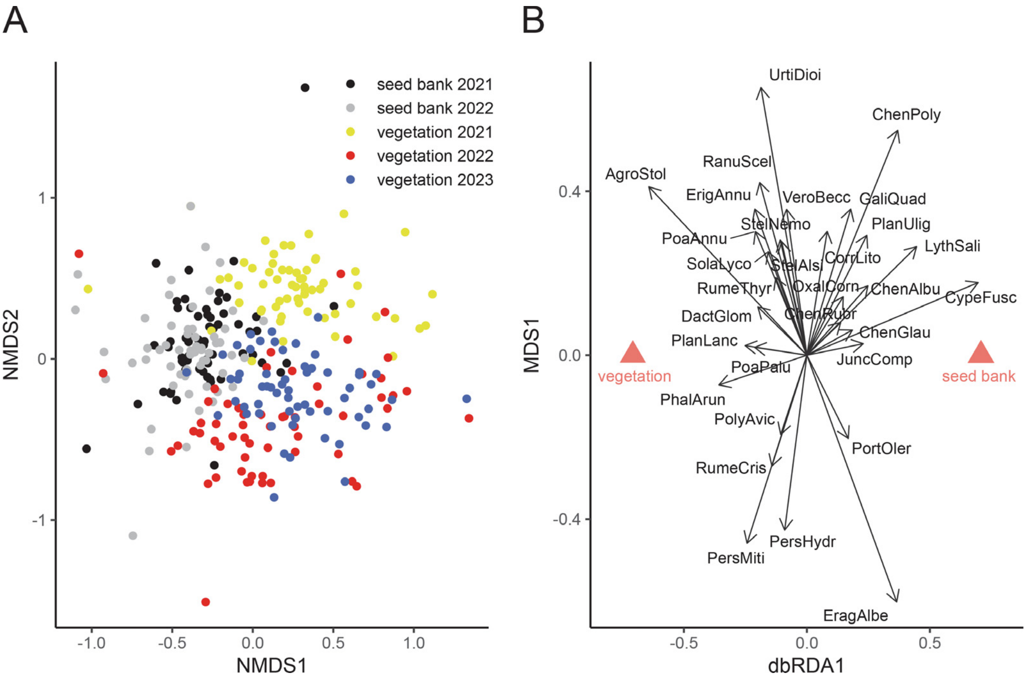

Fig. 7. (A) NMDS ordination diagram showing plot scores of species composition in the seed bank and vegetation. Species presences or absences were used as response values in the analysis. First two axes explained 11.6% and 8.7% of the variance, respectively. (B) dbRDA ordination diagram showing differences in species composition (black) of the seed bank and vegetation. Record type (seed bank or vegetation) was used as an explanatory variable (red). Record type explained 9.2% of the variance. Species that significantly differed ($P < 0.001$) between vegetation and seed bank are shown. Species abbreviations: AgroStol = *Agrostis stolonifera*, CorrLito = *Corrigiola litoralis*, CypeFusc = *Cyperus fuscus*, DactGlom = *Dactylis glomerata*, EragAlbe = *Eragrostis albensis*, ErigAnnu = *Erigeron annuus*, GaliQuad = *Galinsoga quadriradiata*, ChenAlbu = *Chenopodium album* agg., ChenGlau = *Chenopodium glaucum*, ChenPoly = *Chenopodium polyspermum*, ChenRubr = *Chenopodium rubrum*, JuncComp = *Juncus compressus*, LythSali = *Lythrum salicaria*, OxalCorn = *Oxalis corniculata*, PersHydr = *Persicaria hydropiper*, PersMiti = *Persicaria mitis*, PhalArun = *Phalaris arundinacea*, PlanLanc = *Plantago lanceolata*, PlanUlig = *Plantago uliginosa*, PoaAnnu = *Poa annua*, PoaPalu = *Poa palustris*, PolyAvic = *Polygonum aviculare* agg., PortOler = *Portulaca oleracea*, RanuScel = *Ranunculus sceleratus*, RumeCris = *Rumex crispus*, RumeThyr = *Rumex thyrsiflorus*, SolaLyco = *Solanum lycopersicum*, StelAlsi = *Stellaria alsine*, StelNemo = *Stellaria nemorum*, UrtiDioi = *Urtica dioica*, VeroBecc = *Veronica beccabunga*.

common and abundant species was the invasive neophyte *Eragrostis albensis*, which occurred in 78% of the seed banks of plots and 77% of the vegetation of plots and whose seedlings accounted for 10% of the total number of seedlings.

Relationship between seed bank and vegetation, and the effect of environmental conditions

The species composition of the vegetation was more diverse than that of the seed bank as indicated by less clustered plots showing species composition of vegetation in individual years compared to more aggregated plots of the seed bank (NMDS, Fig. 7A). Vegetation and seed-bank species composition differed significantly (multiple regression with the envfit function, P = 0.001). Species that were over-represented in vegetation were *Agrostis stolonifera* and *Phalaris arundinacea*, whereas *Chenopodium polyspermum* and *Cyperus fuscus* were more common in the seed bank than in vegetation (Fig. 7B, see also Supplementary Table S3 for full comparison of vegetation and seed bank).

The results of univariate regression indicate that the difference between vegetation and seed bank, in terms of Bray-Curtis dissimilarity index, was not affected by the position of a plot on the transverse transect (LMM, P = 0.908; Table 6) or the duration for which a gravel bar is exposed (P = 0.227) or the species richness of the vegetation (P = 0.186). However, the difference between the species composition of the vegetation and seed bank decreased with seed-bank species richness (P = 0.032, Fig. 8).

Table 6. The effect of the position on the transect (transverse), duration of gravel bar exposure in the previous year (unflooded–1), vegetation and seed-bank species richness on the difference in the species composition of the vegetation and seed bank revealed by a linear mixed model. Full model with random effects (locality, transect and year) explained 18.8% of the variance, fixed effects explained 7.8% of the variance. The explained variance (EV) is shown for significant predictors.

Model	χ^2	Df	EV (%)	Effect	P
Full model			18.8		
Transverse	0.01	1	–		0.908
Unflooded–1	1.46	1	–		0.227
Vegetation species richness	1.75	1	–		0.186
Seedbank species richness	4.58	1	3.5	–	0.032

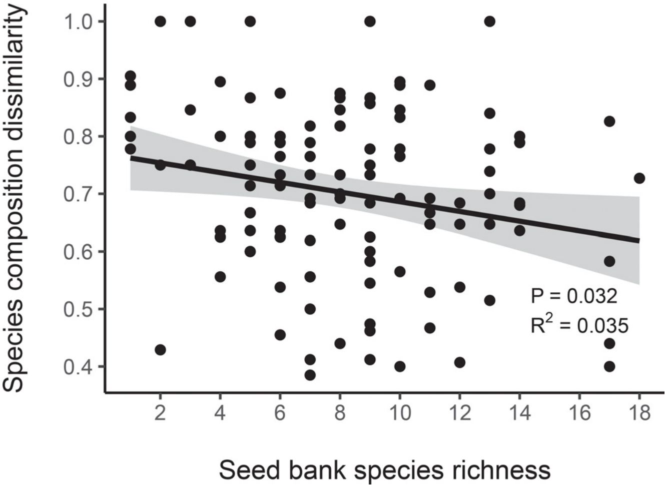

Fig. 8. Relationship between the seed-bank species richness and species composition, and difference between seed bank and vegetation, expressed as Bray-Curtis dissimilarity index. Regression line shows fit of linear model, grey area indicates 95% confidence interval. The regression line was created based on the linear model (LM) with only the response (Bray-Curtis dissimilarity index) and the predictor (seed-bank richness) values included.

Discussion

Flooding affects species composition of vegetation

The duration of submergence affected the species composition of vegetation and is known to be a key factor in riparian ecosystems (Tabacchi et al. 1998, Surian et al. 2015). More moisture-demanding species, mostly with a ruderal life-strategy, such as *Lythrum salicaria* were more abundant in areas that were submerged the longest. In contrast, perennial species with stress tolerant life-strategies able to tolerate drought, such as *Inula britannica*, *Herniaria glabra* and vegetatively spreading species such as *Agrostis stolonifera* and *Rorippa sylvestris*, were more abundant in plots that were submerged for a short period, both in the seed bank and vegetation (Figs 4A and 5A). This corresponds with the findings of Fraaije et al. (2015), who report that along a hydrological gradient there is a clear pattern in the seed distribution of riparian species of plants. Unlike in this study, however, no significant differences in the species composition of the seed bank were recorded far away from the river, as is reported by Fraaije et al. (2015) and Goodson et al. (2003). This is probably due to fewer differences in the species composition of the seed bank, which indicates that environmental filtering plays an important role. The gravel bars have a very marked transverse gradient in moisture, submergence and temperature (Šumberová & Lososová 2011); these strong environmental filters acting on a scale of a few meters limit species survival.

Analysis of the effect of mean seed mass revealed that heavy seeds occur further from the river and that mean seed mass also increases with the percentage of sand in the sediment. Seed distribution on gravel bars is the result of local seed rain and sedimentation that are working in a complementary way. In the current study, the most common species growing close to the water, such as *Eragrostis albensis*, *Cyperus fuscus* and *Lythrum salicaria*, have lighter seeds than species that grow far from the river, such as, species of *Chenopodium* and *Galinsoga* (Supplementary Table S4). In contrast, during sedimentation lighter seeds are deposited farther from the river due to weaker water flow. Sedimentation and local seed rain work against each other, but in the current case, the local seed rain seems to be a stronger driver of seed mass. The seeds of most of the species that were recorded had a local, nonspecific dispersal mode, and other dispersal strategies such as anemochory or zoochory were much less represented. However, seed deposition is only one of the factors that affect the spread of plants. Seed shape and structures, such as a pappus or awns, also play an important role in seed sedimentation and remobilization.

Similarity of the species composition of the vegetation and seed bank

There was a greater between-year variation in the species composition of vegetation than in the seed bank. This was due to the greater number of species in the vegetation than in the seed bank, which was influenced by the smaller size of the area sampled for determining the seed-bank sampling (2.4 vs 60.0 m^2) and the fewer seasons (two vs three) studied compared to the vegetation survey. Moreover, not all species present in the seed bank germinated. The alternative method to using seedling emergence would be the extraction of seed from the substrate by flotation, followed by germination. Seed extraction, however, underestimates the occurrence of small-seeded species of the families *Cyperaceae*, *Lythraceae*, *Juncaceae* and *Chenopodiaceae* (Price et al. 2010), which were common in the samples collected. Attempts were made to reduce the number of seeds that did not germinate by providing optimum conditions for germination and by stratifying the seeds in the experimental garden in the second year of planting, by continuing the cultivation of sediment in the second year. This provided a further 9.6% and 4.7% germination in 2021 and 2022, respectively. Another potential limitation of this study could be that the seed bank was based on samples from relatively shallow sediments and only one soil sample. This method does not fully account for the high spatial variability in the seed bank.

Differences between the species composition of the seed bank and vegetation were largely due to the absence of species that spread vegetatively, mainly perennial grasses such as *Phalaris arundinacea* and *Agrostis stolonifera*, which were dominant in some plots, but not a single *P. arundinacea* seedling emerged from the seed-bank sample (Supplementary Table S3). *Urtica dioica*, another perennial, that can spread vegetatively, was also under-represented in the seed bank. Apart from these, there were also some annuals with high seed productions, such as *Ranunculus sceleratus*, *Persicaria mitis*, *Erigeron annuus* and *Solanum lycopersicum*, whose low representation in the seed bank in relation to their abundance in the vegetation remains unclear. An alternative explanation for the under-representation of grasses in the seed bank could be that their very light seeds, which often have awns, are deposited at sites with very fine sediments (mud or clay), which were not included in this study. However, this seems less likely than by clonal spread, as grasses were common on gravel bars.

In contrast, some species were more abundant in the seed bank than in the vegetation. This was the case for most of the species with a ruderal life-strategy, such as *Cyperus fuscus*, *Eragrostis albensis*, *Lythrum salicaria* and all the species of *Chenopodium* (*C. polyspermum*, *C. album* agg., *C. glaucum*). The difference recorded here is probably related to their massive production of seed, some of which can remain viable for decades (Richert et al. 2016), which is typical for species of disturbed and emergent habitats (Šumberová & Lososová 2011). In addition, the number of seeds was greater at frequently flooded sites close to the river, than for sites far from the river (Fig. 9). Some of the species that were considerably over-represented in the seed bank, such as *Lythrum salicaria* and *Cyperus fuscus* (see Supplementary Table S3) usually grow near water. Both these species are known for their massive seed production, seed-bank formation and good ability for dispersal by water (Welling & Becker 1990, Poschlod 1996). *Cyperus fuscus* is also known for its large seed bank that can persist for decades (Poschlod 1996).

Vegetation and seed bank had 42% of the species in common, which is within the range of 18–76% given by Hopfensperger (2007) who reports the similarity in species composition of the vegetation and seed banks in different ecosystems. The relatively high overlap between the species composition of seed banks and vegetation is due to regular annual disturbances; seed-bank formation is often the only way to survive in unpredictable conditions. High similarity between vegetation and seed banks is reported in other heavily disturbed ecosystems, e.g. weeds of arable land (Shaukat & Siddiqui 2004). In addition, decrease in similarity of species composition with time since disturbance and ongoing succession is reported in both forest and wetland ecosystems (Hopfensperger 2007).

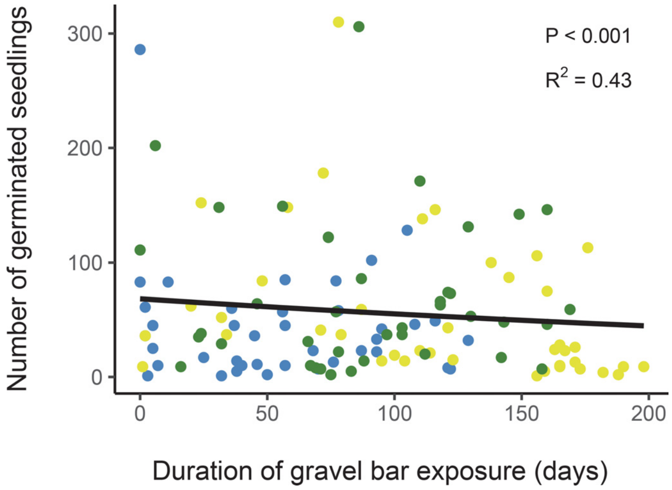

Fig. 9. Relationship between duration of gravel bar exposure and number of seedlings per plot (sediment sample). Regression line shows the fit of a generalized linear model. Colours give information on plot position on the transverse transect: 🔵 plots nearest the river, 🟢 plots in the middle, 🟡 plots on the top of gravel bars.

Potential impact of alien plants

Alien species (as classified by Pyšek et al. 2022) accounted for 37% of all species recorded, which is typical for riparian habitats that are among the most invaded (Chytrý et al. 2005, Pyšek et al. 2022). As both endangered and alien species co-occur in the same habitat raises an important question, i.e. what is the potential impact of aliens on native species, but we are not aware of any study assessing the impact of alien species on the flora of gravel bars. From our field experience the vegetation was very sparse, so there is probably little competition between species for light and nutrients and water is usually abundant for the plants with deep roots. The possible influence of allelopathy is limited due to regular long periods of submergence, which does not favour the accumulation of allelochemicals. Furthermore, the list of alien species, both in the seed bank and the vegetation (Table 5), clearly shows the predominance of annuals (40 annuals to 9 perennials), which are not very competitive, but can further spread into the surrounding landscape.

The most problematic species, because of their abundance and ability to form dense stands, are probably *Eragrostis albensis*, which quickly colonizes newly emerged wet sites, and *Digitaria sanguinalis* and *Echinochloa crus-galli* in drier sites. The latter two are drought-tolerant C4 grasses and can take advantage of their better performance in the hot conditions on the upper parts of gravel beds. *Ambrosia artemisiifolia*, which also grows in dry sites and was locally abundant at two human-influenced localities, needs to be monitored because of its highly allergenic pollen. In addition, alien species are constrained by regular flooding, which limits the survival of strong competitors. Based on hydrological modelling, their impact may be greater due to the larger area of gravel bars resulting from reduced runoff in the vegetative season and the same runoff in the winter due to climate change (Havlíček et al., unpublished).

Conclusions and implications for nature conservation

This study revealed that the species composition of the vegetation on gravel bars is determined by regular flooding, with the highest diversity recorded at the sites where annual species with a ruderal life-strategy and stress-tolerant perennial species co-occur. In the germination experiment, most seedlings started to grow as soon as conditions were suitable for germination and less than 10% of the seeds germinated in the second year. This indicates that renewal of the seed bank by seasonal floods, which uncover buried seed (O'Donnell et al. 2014), wash out seed deposited on the river bed (Gurnell et al. 2007) and transport seed from upstream, is important for the survival of rare species. This mechanism becomes more important after years when the gravel bars were exposed for a too short a period for the plants to produce seed. Seed burial and redistribution also contribute to the spread of germination over a number of years when not all seeds germinate (Pausas et al. 2022). These factors are provided by the fluvial regime of the river and the connectivity of the Elbe, which still exist in the area studied. Habitat conservation, therefore, depends on maintaining the natural fluvial processes, including fluctuations in water level, transport of sediment and associated disturbances, which are critical for habitat development and maintenance.

Supplementary materials

Data S1. R code for univariate and multivariate analyses.
Fig. S1. Pearson correlation heatmap for seed bank and vegetation species richness and environmental variables.
Table S1. Overview of the characteristics of localities studied.
Table S2. Summary of mean, minimum and maximum values of the environmental variables, seed bank and vegetation characteristics of the plots studied.
Table S3. Comparison of the frequency of species in vegetation and seed bank in 2021 and 2022.
Table S4. Seed mass of the ten most common species (based on the number that germinated) in the seed bank.

Supplementary materials are available at https://www.preslia.cz

Acknowledgements

We would like to thank Lenka Moravcová, František Krahulec and Jan Prančl for their help with seedling determination, Anna Lučanová for her help in the field and gardeners David Cmíral and Miroslav Chmelař for taking care of the germination experiment. We are grateful to Jiří Prošek for an aerial drone image. We thank the authorities of the České Švýcarsko National Park, the Labské pískovce Protected Landscape Area and the České středohoří Protected Landscape Area for their kind permission and assistance in carrying out research in these areas. This study was funded by the Technology Agency of the Czech Republic, grant number SS03010279 (Management optimization of the Elbe lower reach with respect to the presence of 3270 biotope and improvement of the hydromorphological state as based on an interdisciplinary study) and also supported by the long-term research development project No. RVO 67985939 of the Czech Academy of Sciences. We thank Tony Dixon for improving our English and two reviewers for their valuable comments.

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Faktory prostředí utvářejí vztah mezi semennou bankou a vegetací na periodicky obnažovaných štěrkopískových náplavech Labe

Říční břehové ekosystémy patří k nejcennějším přírodním biotopům pro svou rozmanitost a ekosystémové funkce, ale intenzivní využívání člověkem vedlo k jejich úbytku a degradaci. Jednou z posledních relativně přirozených řek ve střední Evropě je Labe s více než 600 km vodního toku bez jezů. Díky relativně přirozenému říčnímu režimu se zde zachovaly pravidelně obnažované štěrkopískové a bahnité náplavy se specifickou vegetací včetně několika ohrožených druhů. V této studii jsme se zaměřili na faktory související s fluviální dynamikou, které určují druhové složení rostlin na periodicky obnažovaných štěrkopískových náplavech Labe v České republice. Studovali jsme 40 km dlouhý úsek řeky mezi Ústím nad Labem a česko-německou hranicí. Zde jsme vybrali 10 lokalit, na kterých jsme založili 60 trvalých ploch o velikosti 1 × 1 m, které byly uspořádány do transektů kolmých na tok řeky. Plochy v transektech byly uspořádány po třech, na větších lokalitách bylo celkem devět ploch a na menších tři plochy. Na plochách jsme určili všechny druhy cévnatých rostlin v optimální fázi vývoje vegetace a ze sedimentu odebraného poblíž trvalých ploch jsme kultivovali semennou banku. Z faktorů prostředí jsme analyzovali zrnitost a chemické vlastnosti sedimentu a zjistili délku zaplavení ploch pomocí hydrologického modelování. Naše výsledky ukazují, že druhové složení vegetace bylo nejvíce ovlivněno dobou obnažení plochy, které oddělilo druhy déle a krátce zaplavených stanovišť. Druhové složení semenné banky nebylo významně ovlivněno zkoumanými faktory prostředí, druhy se ale lišily svými funkčními vlastnostmi, kde na jedné straně spektra byly stres tolerující druhy schopné klonálního šíření a na druhé druhy s ruderální životní strategií náročné na světlo a vlhkost. Silný gradient podmínek prostředí směrem od řeky umožňuje koexistenci druhů s velmi odlišnými nároky na malém prostoru, a má tak zásadní význam pro druhovou bohatost štěrkopískových říčních náplavů.

How to cite: Čuda J., Hadincová V., Petřík P., Hummel J., Sejfová Z., Borovec J., Bureš L., Wild J. & Hradecký J. (2024) Environmental factors shape the relationship between seed bank and vegetation on periodically emerged alluvial gravel bars of the Elbe river. – Preslia 96: 223–246.

Preslia, a journal of the Czech Botanical Society

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