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Environmental controls of plant species richness and species composition in black alder floodplain forests of central Slovakia

Bestimmende Standortfaktoren für den Artenreichtum und die Artenzusammensetzung von Pflanzen in Schwarzerlen-Auenwäldern der Zentralslowakei

Michal Slezák[1, 2, *], Richard Hrivnák[2] & Ján Machava[3]

[1]*Department of Biology and Ecology, Faculty of Education, Catholic University in Ružomberok, Hrabovská cesta 1, 034 01 Ružomberok, Slovak Republic;*
[2]*Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, 845 23 Bratislava, Slovak Republic;*
[3]*Institute of transdisciplinary study in Environment, Faculty of Education, Catholic University in Ružomberok, Hrabovská cesta 1, 034 01 Ružomberok, Slovak Republic*
**Corresponding author, e-mail: slezak.miso@gmail.com*

Abstract

Vegetation patterns of floodplain forests are highly variable across different habitats in European regions. Their plant communities have been well described from the phytosociological point of view, but plant species richness and composition patterns and their underlying environmental factors are still insufficiently known. Sixty-one vegetation plots of black alder-dominated floodplain forests were sampled in central Slovakia in order to find main environmental predictors affecting floristic diversity of their vegetation. For each vegetation plot with a constant size (400 m^2), vascular plant species and a set of topographic, climatic, soil physical and chemical characteristics were recorded. A generalized linear model was applied to explain relevance of environmental factors on changes of species richness, whereas the relationship between species composition and explanatory variables was tested using ordination methods. Main gradients of species compositional variation were soil moisture, light, elevation and soil chemistry-related variables. Vascular species richness of plots varied between 19 and 59 (mean 38). Herb-layer species richness was positively related to the soil pH, stream power index and negatively to the concentration of soil iron. These linear trends were accompanied by a hump-shaped response to sand content and a U-shaped response to elevation.

Keywords: *Alnus glutinosa*, alpha diversity, elevation, herb-layer vascular plants, moisture, plant community, soil chemistry

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Temperate floodplain forests represent a dynamic ecosystem shaped by both natural conditions and human activities. These broad-leaved deciduous forests colonise a mosaic of many different habitat types along moisture, soil reaction and climatic gradients throughout

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the European landscape (DOUDA et al. 2016). This habitat diversity supports the coexistence of vascular plants with different ecological niches and origins (HÄRDTLE et al. 2003, DOUDA et al. 2012, LIENDO et al. 2016, STEFAŃSKA-KRZACZEK et al. 2016) including wetland species, forest herbs, but also grassland and ruderal species (PIELECH et al. 2015, BIURRUN et al. 2016). They usually form medium- to species-rich plant communities (SLEZÁK et al. 2014, PIELECH 2015), which can host extraordinarily high numbers of vascular plant species locally (CHYTRÝ et al. 2015).

Biodiversity research of floodplain forests focuses on determination of causal factors and potential mechanisms underlying plant species coexistence and community assembly. Recent findings generally support the role of both deterministic responses to environmental gradients (i.e. biological or niche-based; SCHMIDA & WILSON 1987) and stochastic (i.e. neutral; HUBBELL 2001) processes. They may act simultaneously to regulate spatial and temporal variation of floodplain plant diversity and composition (e.g., DOUDA et al. 2012), however, their effect and relative importance appear to be scale-dependent. Our study reports on floodplain diversity patterns primarily in relation to environmental gradients irrespective of spatial assembly events (e.g., dispersal limitation).

Previous studies suggest several environmental drivers of species composition and diversity that explain the high ecological variability of floodplain forests. Hydrological and soil factors are well known as two of the key factors which interact to govern their vegetation structure (DE JAGER et al. 2012). Hydrological regime controls spatial distribution of various ecological processes and site-specific properties, with flooding disturbance and associated fluvial events being the most pronounced ones (PARKER & BENDIX 1996). For example, flood duration is considered to be the main cause of the differences in the length of anaerobic and aerobic conditions which in turn affect the nutrient regime (PONNAMPERUMA 1972), whereas its magnitude plays an important role in sedimentation rate (movement and deposition of eroded materials) and accumulation of organic matter (PARKER & BENDIX 1996). Stream flow is associated with plant succession through the transport of plant propagules (e.g., seeds, clonal segments) or development of exposed sites favourable for potential establishment, germination and growth of various plant species (BENDIX & HUPP 2000). The foregoing patterns indicate that plant species sorting along hydrological gradient reflects their evolved adaptations to anoxic stress conditions and flood-generated disturbances (VARTAPETIAN & JACKSON 1997, VAN ECK et al. 2004). Among the major soil variables, a high importance has been largely addressed to soil chemistry, namely to the soil pH (e.g., HÉRAULT & HONNAY 2005, NAQINEZHAD et al. 2008), presumably as a consequence of its effect on the availability and supply of both mineral nutrients and toxic metals in soil substrates. Its relationship with plant community assembly is traditionally viewed in terms of both ecophysiological adaptations of plant species to acidic or basic soils (MARSCHNER 1991, TYLER 2003) and species-pool hypothesis (ZOBEL 2016). In some phytodiversity studies, the role of landscape configuration (DOUDA 2010), elevation (SLEZÁK et al. 2014) or solar radiation (PIELECH et al. 2015) has also been emphasized in structuring various types of temperate floodplain forests. However, the effect and relevance of these factors considerably varied between regions, most likely due to habitat-related biases (e.g., length of captured ecological gradients) or a set of analysed environmental variables and their interactions.

Although previous research devoted to environmental controls improved the understanding of vegetation diversity patterns in floodplain forests, further scientific effort is needed to assess the potential effect of some other environmental predictors. For example, influence of soil or substrate texture on variation of plant community assembly has been rarely studied

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(e.g., NAQINEZHAD et al. 2008, DE JAGER et al. 2012), even though soil grain size affects water holding capacity, nutrient cycling, content of organic matter (PINAY et al. 1995) and hence, it may be important for vegetation patterns. The other less analysed factor thought to affect species richness and composition of floodplain forests is iron concentration in soil substrate. Poorly aerated waterlogged soils may accumulate higher concentrations of toxic elements (including iron; PONNAMPERUMA 1972) which negatively influence several wetland species (SNOWDEN & WHEELER 1993, LUCASSEN et al. 2000). However, this pattern has been partially overlooked within habitats of floodplain forests, likely due to confound effect of soil pH gradient.

In the Western Carpathians and the adjacent mountain ranges, the variability of temperate floodplain forests has been studied especially from a phytosociological point of view (e.g., DOUDA 2008, SLEZÁK et al. 2014). These studies provided a more detailed insight into the vegetation-environment relationships, but they did not focus on responses of plant species diversity to site-specific conditions. Moreover, they did not measure habitat characteristics directly (mostly with the exception of elevation) but mediated them using expert-based plant indicator values. We are aware of few studies that analysed the relative importance of different soil properties or other site variables for species richness and compositional patterns in the region (e.g., DOUDA et al. 2012, HRIVNÁK et al. 2015, PIELECH et al. 2015).

This study aimed to investigate the relationship between environmental variables and vegetation patterns of temperate floodplain forests. For this purpose, we compiled vegetation data and a broad set of environmental factors related mainly to soil, climate and hydrology from the southern part of the Western Carpathians. We asked how herb-layer species richness and species composition in black alder (*Alnus glutinosa*) floodplain forests respond to environmental factors. The well-established predictors of floodplain forests were accompanied by less analysed variables such as soil texture and soil iron, which have been shown to induce floristic variation in other wetland habitats. Therefore, we generally expected that they would act in concert with other environmental factors to affect vegetation patterns in this type of forests.

2. Study area

The research was conducted in the southern part of the Western Carpathians in central Slovakia (N 48°10′–48°37′, E 19°01′–20°25′; Fig. 1). The black alder stands occupied the riparian zone of streams and small rivers, seepage habitats, banks of ponds (water reservoirs) and waterlogged depressions in the floodplains. Vegetation plots were situated in basins and mountains with a relative warm and dry climate. Their altitudinal range was from 165 m to 641 m (Table 1).

3. Methods

In order to cover ecological variation of black alder floodplain forests in the study area, study sites were selected based on literature sources and expert knowledge of authors. All preserved floodplain forests were surveyed during the period 2010–2012, but only forest stands i) with dominance of *Alnus glutinosa* in tree layer (cover > 50%) and ii) without obvious signs of former plantations or any recent forest management events were recorded. Early successional stages or recently strongly disturbed forests (e.g., uprooted by wild boar) were avoided. In each study site, a vegetation plot with a constant size of 400 m^2 was randomly placed in the central part of a physiognomically and ecologically homog-

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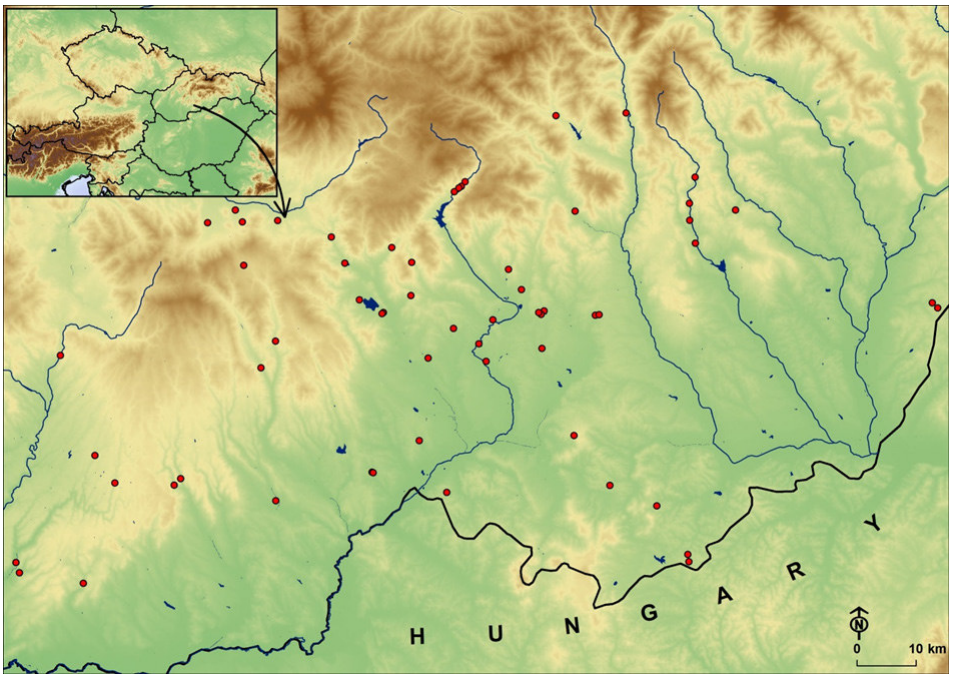

Fig. 1. Distribution map of the vegetation plots in southern part of central Slovakia.

Abb. 1. Verteilung der Vegetationsaufnahmen im südlichen Teil der Zentralslowakei.

enous forest stand. If the study site involved forest stands with contrasting physiognomy or different herb-layer dominants (e.g., riparian vs. seepage habitats), we recorded one plot in each of these stands. A total of 61 vegetation plots were sampled according to the standard European phytosociological approach. For each plot, we recorded vascular plants with their percentage cover in three layers (tree, shrub and herb) using a modified Braun-Blanquet scale (BARKMAN et al. 1964), but only the herb-layer species were used in further analyses. Species richness represents the number of herb-layer species (including phanerophyte juveniles) per sampling plot as a measure of alpha diversity. Nomenclature of vascular plants followed the checklist of MARHOLD & HINDÁK (1998). List of vascular plants merged to aggregate (agg.) level contained only two taxa *Dactylis glomerata* agg. (incl. *D. glomerata* s. lat., *D. polygama*) and *Glechoma hederacea* agg. (*G. hederacea*, *G. hirsuta*).

The following environmental variables were measured and/or calculated for each plot (Table 1). The percentage cover of the tree layer, used as a proxy variable for light conditions, was visually estimated. Geographical coordinates (longitude and latitude with precision up to 10 m) and altitude were measured with a GPSmap 60 CSx device (Garmin Inc., Kansas, US). Mean annual temperature and mean annual precipitation (records from the period 1961–1990), which were derived from raster values computed in the GRASS GIS environment (Grass Development Team, 2010), were provided by the Slovak Hydrometeorological Institute (Bratislava, Slovakia). Stream power index (SPI) and topographic wetness index (TWI) were derived from a digital elevation model (DEM; Geodetic and Cartographic Institute, Bratislava, Slovakia) with a resolution of 10 m using GRASS GIS. SPI is a measure of the erosive power of flowing water and it was calculated as $A_s \times \tan(\beta)$, where A_s is the specific catchment area (i.e. the cumulative upslope area draining through a point divided by the contour width) and β is the local slope angle (MOORE et al. 1991). TWI reflects the tendency of a given site (map cell) to accumulate water and it was defined as $\ln [A_s/\tan(\beta)]$ (QUINN et al. 1991, GRUBER & PECKHAM 2008). Three soil samples were taken from the topsoil mineral horizon (litter layer removed) at a depth of

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Table 1. Descriptive statistics of measured environmental variables and herb-layer species richness (number of vascular plant species per 400 m^2). Explanatory variables used in the analyses are in bold.

Tabelle 1. Deskriptive Statistik der gemessenen Umweltvariablen und Krautschichtvielfalt (Anzahl Gefäßpflanzenarten pro 400 m²). In den Analysen verwendete erklärende Variablen sind fett gedruckt.

Variable name	Mean ± SD	Minimum	Maximum
Altitude [m]	301 ± 88	165	641
Mean annual temperature [°C]	7.83 ± 0.54	6.48	8.87
Mean annual precipitation [mm]	644 ± 47	566	741
Soil C_{tot} [%]	6.58 ± 5.31	1.26	25.8
Soil N_{tot} [%]	0.56 ± 0.40	0.10	1.90
Soil C/N ratio	11.56 ± 2.16	4.93	16.19
Soil pH (in H_2O)	5.64 ± 0.79	3.93	7.36
Soil conductivity [µS/cm]	269 ± 223	105	1614
Soil Ca [mg/kg]	3198 ± 4529	196	34545
Soil Mg [mg/kg]	433 ± 330	79	1818
Soil K [mg/kg]	115 ± 61	31	306
Soil Na [mg/kg]	39.9 ± 47.9	4.8	304.5
Soil Fe [mg/kg]	62.2 ± 51.0	6.0	210.5
Soil P [mg/kg]	20.6 ± 11.6	4.6	64.3
Soil sand [%]	26.2 ± 17.1	1.5	72.3
Soil silt [%]	66.7 ± 15.8	25.0	89.0
Soil clay [%]	7.0 ± 7.2	1.9	57.9
Stream power index	1949 ± 9506	0	71578
Topographic wetness index	9.3 ± 2.1	5.3	14.5
Tree-layer cover [%]	83 ± 6	70	95
Herb-layer species richness	38 ± 9	19	59

0–10 cm and pooled to form a single sample per plot in order to reduce soil heterogeneity. They were air-dried at laboratory temperature, crushed and passed through a 2 mm sieve. Total carbon (C_{tot}) and nitrogen (N_{tot}) contents were determined using an NCS-FLASH 1112 analyzer (CE Instruments, UK) and subsequently, they were used to calculate the C/N ratio. Soil pH and conductivity were measured in distilled water (soil/water ratio of 1/5) using the pH (WTW Inolab pH 720) and conductivity (WTW Inolab Cond 720) meter. Cations of calcium (Ca), magnesium (Mg), potassium (K), sodium (Na) and iron (Fe) were extracted in the Mehlich III solution and determined using an atomic absorption spectrophotometer (SensAA, GBC; UK). Plant-available phosphorus (P) was extracted in the Mehlich II solution and measured by spectrophotometry (AES-ICP). The particle-size distribution (i.e. percentage content of sand, silt, clay) was assessed with Laser analyser (Analysette 22, Fritsch GmbH; DE). Each air-dried soil sample was dispersed in a solution of sodium hexametaphosphate [$(NaPO_3)_6$] using an ultrasonic device.

Multicollinearity of the environmental variables was checked by pairwise Spearman correlations (Supplement E1). From two collinear predictors ($r_s \geq 0.7$), only one predictor was retained for analyses (Table 1). Species composition-environmental relationships were analysed in two steps using unconstrained (detrended correspondence analysis; DCA) and constrained (canonical correspondence analysis; CCA) ordination analyses (ØKLAND 1996) in CANOCO (ver. 4.5, Microcomputer Power, Ithaca, NY, US). Major environmental gradients responsible for species compositional variation were analysed by DCA and interpreted by directly measured variables (Table 1) and unweighted means of Ellenberg indicator values (EIVs) for light and moisture (ELLENBERG et al. 1992). DCA was performed with

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detrending by segments, logarithmic transformation of species cover values and without down-weighting of rare species. Statistical significance of correlations between environmental factors and first two DCA axes was corrected with modified permutation test ($p < 0.05$, 999 permutations; ZELENÝ & SCHAFFERS 2012). Effect of directly measured variables (Table 1) on floristic variation was subsequently tested by CCA. It was performed to assess (i) the marginal effect (independent effect of each explanatory variable), (ii) the conditional effect (partial effect of each predictor) and (iii) the pure effect (variation explained by the target variable using the other as covariables). Interactive stepwise (forward) selection was used to create the most parsimonious set of variables that significantly contribute to the explained variation. Significance of environmental variables was tested using Monte Carlo permutation test (999 unrestricted permutations).

Generalized Linear Model (GLM) with Poisson distribution of errors and logarithmic link function was used to fit variation in species richness. The minimal adequate model was calculated using backward stepwise selection based on the Akaike information criterion, following the recommendation of JOHNSON & OMLAND (2004). Statistical significance of each variable in the final GLM was tested by χ^2 statistic. A non-significant linear term (main term effect) was retained in the model if its higher-order (quadratic) term was significant. Multicollinearity among explanatory variables was checked by calculation of variation inflation factor. The *goodness-of-fit* of the model was expressed by adjusted-D^2 (D^2adj), which was calculated as the percentage of explained deviance adjusted by the number of observations and model parameters (GUISAN & ZIMMERMANN 2000). The GLM residuals were subsequently related to means of EIVs for moisture and light. Significance level of regression was tested by modified permutation test (ZELENÝ & SCHAFFERS 2012) based on 999 permutations. These analyses were conducted in R (ver. 3.0.2, R Core Team 2013).

4. Results

Altogether 255 herb-layer vascular plant species were found in 61 vegetation plots of black alder forest stands. Most frequent species of forest understorey documented in more than 50% plots were mainly eutrophic (e.g., *Aegopodium podagraria*, *Festuca gigantea*, *Galium aparine*, *Impatiens noli-tangere*, *Ranunculus repens*, *Urtica dioica*) and hygrophilous species (e.g., *Caltha palustris*, *Filipendula ulmaria*, *Lycopus europaeus*, *Lysimachia vulgaris*, *Poa trivialis*). The species richness of the herb-layer ranged from 19 to 59 vascular plants with a mean of 38 species per sampling plot (Table 1).

The main floristic differences and ecological gradients are displayed in DCA ordination scatter plots (Fig. 2a, b). Species compositional turnover follows mainly the gradients of moisture (EIV), light (EIV) and soil nutrients (first DCA axis) and combined effect of altitude and soil reaction (second DCA axis). The first two DCA axes accounted for 11.2% of the variance in species data and 25.1% in species-environment relation, whereas first two CCA axes showed lower explained variance in species data (8.4%) and slightly higher values in species-environment relation (30.1%). The CCA with forward selection procedure detected seven variables (altitude, total soil N, soil K, Fe, pH, soil sand and soil C/N ratio) responsible for the species compositional variability in black alder forest stands. While the conditional effect of significant variables was 18.2%, the pure effect reached only 11.8%. The highest amount of variation was explained by altitude (2.8%), followed by soil K (2.6%) and soil pH (2.2%; Table 2).

GLM of the herb-layer vascular plants identified five significant predictors (altitude, soil pH, soil Fe, soil sand, stream power index) jointly explaining 34.4% of the variation in species richness, but their importance was different (Table 3). Soil pH and stream power index showed positive effect on herb-layer species richness, whereas soil Fe had a strong negative influence. The quadratic terms of altitude and soil sand, which were found to be significant,

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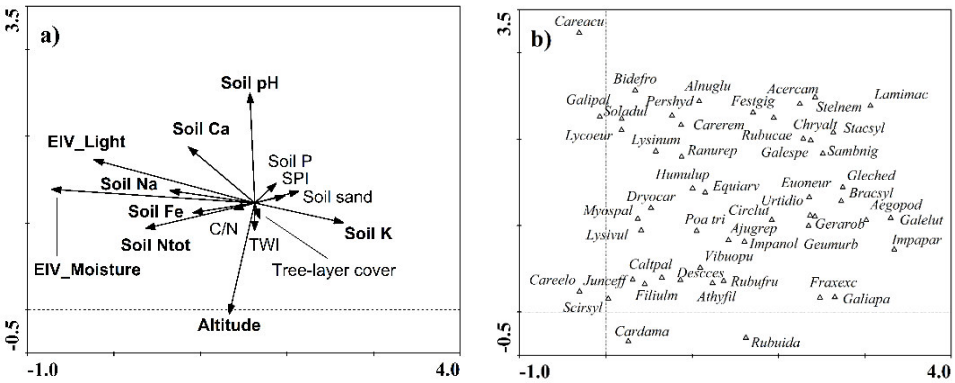

Fig. 2. DCA scatter plots with **a)** all analysed environmental factors projected as supplementary variables (variables significantly correlated with DCA axes are displayed in bold), and **b)** vascular plant species showing the highest weight (≥ 17%) in the analysis. First two DCA ordination axes are shown.

Abbreviations of species names: Acercam: *Acer campestre*, Aegopod: *Aegopodium podagraria*, Ajugrep: *Ajuga reptans*, Alnuglu: *Alnus glutinosa*, Athyfil: *Athyrium filix-femina*, Bidefro: *Bidens frondosa*, Bracsyl: *Brachypodium sylvaticum*, Caltpal: *Caltha palustris*, Cardama: *Cardamine amara*, Careacu: *Carex acutiformis*, Careelo: *Carex elongata*, Carerem: *Carex remota*, Chryalt: *Chrysosplenium alternifolium*, Circlut: *Circaea lutetiana*, Descces: *Deschampsia cespitosa*, Dryocar: *Dryopteris carthusiana*, Equiarv: *Equisetum arvense*, Euoneur: *Euonymus europaeus*, Festgig: *Festuca gigantea*, Filiulm: *Filipendula ulmaria*, Fraxexc: *Fraxinus excelsior*, Galelut: *Galeobdolon luteum*, Galiapa: *Galium aparine*, Galipal: *Galium palustre*, Galespe: *Galeopsis speciosa*, Gerarob: *Geranium robertianum*, Geumurb: *Geum urbanum*, Gleched: *Glechoma hederacea* agg., Humulup: *Humulus lupulus*, Impanol: *Impatiens noli-tangere*, Impapar: *Impatiens parviflora*, Junceff: *Juncus effusus*, Lamimac: *Lamium maculatum,* Lycoeur: *Lycopus europaeus*, Lysinum: *Lysimachia nummularia*, Lysivul: *Lysimachia vulgaris*, Myospal: *Myosotis scorpioides* agg., Pershyd: *Persicaria hydropiper*, Poatri: *Poa trivialis*, Ranurep: *Ranunculus repens*, Rubucae: *Rubus caesius*, Rubufru: *Rubus fruticosus* agg., Rubuida: *Rubus idaeus*, Sambnig: *Sambucus nigra*, Scirsyl: *Scirpus sylvaticus*, Soladul: *Solanum dulcamara*, Stacsyl: *Stachys sylvatica*, Stelnem: *Stellaria nemorum*, Urtidio: *Urtica dioica*, Vibuopu: *Viburnum opulus*.

Abb. 2. DCA-Streudiagramm mit **a)** passive Projektion aller Umweltvariablen (significant korrelierte Variablen sind fett gedruckt), und **b)** Gefäßpflanzenarten mit höchstem Gewicht (≥ 17 %) in der Ordination. Gezeigt werden die beiden ersten DCA-Achsen. Abkürzungen der Artnamen s.o.

indicated a weakly U-shaped and unimodal response, respectively. The values of variance inflation factor suggested lack of multicollinearity among predictors used in the final GLM (Table 3). The regression analysis between unexplained variation (GLM residuals) and means of EIVs did not reveal significant relationship (Fig. 3).

5. Discussion

The compositional variation in herb-layer vascular plants was associated with altitude (climate) and soil chemistry. These results coincide with studies that analysed vegetation-environmental relationships across floodplain forests from local and regional (e.g., NAQINEZHAD et al. 2008, SLEZÁK et al. 2014, PIELECH 2015) to continental scales (DOUDA et al. 2016). Higher importance of elevation than soil nutrients and soil pH likely results from

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Table 2. Species composition variance of herb-layer vascular plants in black alder floodplain forests explained by each variable identified in CCA. Explained variance corresponds to percentage of total inertia. Significant values are in bold. Note: ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$, ns – not significant.

Tabelle 2. Varianzanteile in der Artenzusammensetzung krautiger Gefäßpflanzen in Schwarzerlen-Auenwäldern, welche durch kanonische Prädiktoren in der CCA erklärt werden. Erklärte Varianz entspricht dem Anteil an der Gesamtvarianz. Signifikante Werte sind fett gedruckt. Anmerkung: ***$p \leq 0{,}001$; **$p \leq 0{,}01$; *$p \leq 0{,}05$; ns – nicht signifikant.

	Marginal effect		Conditional effect		Pure effect	
Variables	Eigenvalues	%	Eigenvalues	%	Eigenvalues	%
Altitude	**0.183*****	**3.4**	**0.183*****	**3.4**	**0.147*****	**2.8**
Soil N_{tot}	**0.178*****	**3.4**	**0.165*****	**3.1**	0.090^{ns}	1.7
Soil K	**0.150*****	**2.8**	**0.146*****	**2.8**	**0.139****	**2.6**
Soil Na	**0.144***	**2.7**	0.094^{ns}	1.8	0.091^{ns}	1.7
Soil Fe	**0.139****	**2.6**	**0.127****	**2.4**	**0.113***	**2.1**
Soil pH	**0.133****	**2.5**	**0.123****	**2.3**	**0.117***	**2.2**
Soil C/N ratio	**0.128****	**2.4**	**0.104***	**2.0**	**0.109***	**2.1**
Soil Ca	0.124^{ns}	2.3	0.090^{ns}	1.7	0.090^{ns}	1.7
TWI	**0.109***	**2.1**	0.095^{ns}	1.8	0.090^{ns}	1.7
Soil sand	0.106^{ns}	2.0	**0.115****	**2.2**	0.100^{ns}	1.9
Tree-layer cover	0.097^{ns}	1.8	0.086^{ns}	1.6	0.084^{ns}	1.6
SPI	0.094^{ns}	1.8	0.077^{ns}	1.5	0.077^{ns}	1.5
Soil P	0.093^{ns}	1.7	0.084^{ns}	1.6	0.084^{ns}	1.6
Sum of significant variances [%]	–	21.9	–	18.2	–	11.8

Table 3. Summary statistics of the GLM for species richness of herb-layer vascular plants (Std.coef.: standardized coefficients, S.E.: standard errors, V.I.F.: variation inflation factor, *p*: significance level). D^2adj = 0.344; significant *p*-values are in bold.

Tabelle 3: Zusammenfassende Statsitik des Generalisierten Linearen Modells (GLM) für die Artenzahl krautoger Gefäßpflanzen (Std.coef.: standardisierte Koefficienten, S.E.: Standardabweichungen, V.I.F.: Varianzinflationsfaktor, *p*: Irrtumswahrscheinlichkeit). D^2adj = 0,344; signifikante *P*-Werte sind fett gedruckt.

Predictors	Std. coef.	S.E.	V.I.F.	*p*
(Intercept)	3.646	0.031	–	**<0.001**
Stream power index	0.037	0.018	1.096	**0.044**
Altitude	0.025	0.029	2.191	0.385
Soil pH	0.058	0.024	1.232	**0.013**
Soil Fe	-0.115	0.025	1.275	**<0.001**
Soil sand	-0.005	0.024	1.298	0.827
Altitude^2	0.035	0.013	2.142	**0.009**
Soil sand^2	-0.045	0.020	1.234	**0.022**

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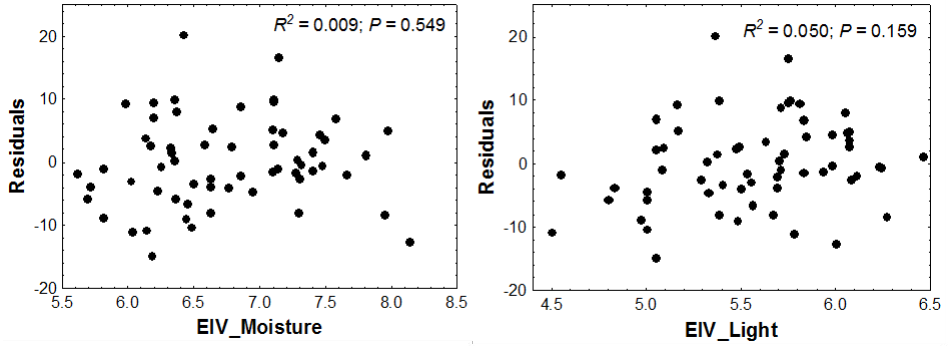

Fig. 3. Relationship between GLM residuals (Table 3) and EIVs for moisture and light. Significance of regression was corrected by modified permutation test using 999 permutations.

Abb. 3. Verhältnis zwischen Residuen des Generalisierten Linearen Modells (Tab. 3) und mittleren Ellenberg-Zeigerwerten für Feuchte und Licht. Signifikanz der Regression korrigiert durch Permutationstest mit 999 Läufen.

the predominance of acidic substrates and a truncated soil pH gradient in the study area. Previous research indicated that environmental conditions of riparian areas highly vary along an altitudinal gradient following important upstream-downstream interactions (PIELECH et al. 2015). In addition to well-established changes of climate, productivity and energy-related variables (RAHBEK 2005, KÖRNER 2007), elevation tends to be also coupled with variations in stream size, hydrological regime (frequency and magnitude of flooding, soil water level), accumulation rates and inputs of dissolved chemical elements (PARKER & BENDIX 1996, HUANG et al. 2013, KUGLEROVÁ et al. 2014, PIELECH et al. 2015). Floodplain forests may share a group of plant species generalists able to thrive across a wide range of site conditions, but they react on these drivers with a continuous species turnover. Significant effect of soil C/N ratio on species composition is consistent with previous observations (e.g., PAAL et al. 2007, NAQINEZHAD et al. 2008) and driven by ecological variation of black alder forest stands across soil moisture gradient with a different mineralization rate of organic matter.

However, the present species composition-environment relationship should be interpreted carefully because there was still much of the unexplained variation by measured variables in constrained ordination. These results may indicate that some important environmental factor was not included. If mean values of EIVs (i.e. factors that we did not measure) were added to explanatory variables and projected onto DCA analysis, an overriding effect of moisture gradient on plant compositional variation was found. This finding is attributable to high level of spatial-temporal heterogeneity in moisture conditions that reflects both local hydrological regime and seasonal fluctuating of groundwater level. Soil moisture induces obvious fine-scale compositional turnover from wet to drier sites as a consequence of competitive hierarchy among vascular plants with different moisture requirements (DOUDA et al. 2012). This pattern is also pronounced outside flooding periods. Although its role itself seems to be trivial, soil moisture may involve a confounding effect of other predictors (HÄRDTLE et al. 2003). However, weak interplay between moisture and other measured factors (r_s < 0.5; Supplement E1) suggested that this process was not relevant in our case. Moisture correlated strongly only with light (r_s = 0.67) whose effect is well-known in shaping of species composition within forest ecosystems due to asymmetric light competition between forest overstorey (canopy trees) and herb-layer vegetation. Dynamic and less stable

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waterlogged soil substrates promote existence of treefall gaps, which increase light transmission through the forest overstorey and in turn modify plant community assembly in floodplain forests (e.g., PIELECH et al. 2015).

In the present study, soil pH and iron content were found to be the most important drivers of variation in species richness data. Herb-layer species richness of floodplain forests was positively related to soil pH, with the highest values at neutral to slightly alkaline sites. A monotonically increasing trend for herb species has already been identified in black alder swamp forests (DOUDA et al. 2012). Several mutually non-exclusive mechanisms to explain observed pattern have been proposed. Firstly, low species richness of vascular plants at very acidic soils is constrained by high phytotoxic effect of the released metal ions (e.g., aluminium) and nutrient limitation (MARSCHNER 1991). If soil pH shifts to slightly acidic or neutral, toxicity is neutralised and nutrient availability becomes more favourable (TYLER 2003), which in turn leads to an increase of species richness. Secondly, the positive linear trend reflects evolutionary origin of the central European floras. In accordance with the species-pool hypothesis (ZOBEL 2016), historical prevalence of high-pH soils in Central Europe (PÄRTEL 2002) restricted modern regional species pool of calcifuge (confined to low-pH soils) vascular plants due to higher extinction rate in the Pleistocene (EWALD 2003). However, many authors consider linear trend between plant species richness and soil pH as a consequence of the truncated pH gradient at its acidic and/or alkaline end (e.g., DUPRÉ et al. 2002). Our findings provided reliable support for this pattern, because we captured the pH gradient without strongly alkaline soils (pH $\geq$ 7.5). Soil iron was found to be responsible for the decline of herb-layer species richness. Significant effect of iron on species richness and composition has been often reported in wetland habitats such as fens or bogs (e.g., SNOWDEN & WHEELER 1993, GĄBKA & LAMENTOWICZ 2008). However, this finding could be an artefact due to both disproportionally higher number of biodiversity studies conducted in treeless wetlands than in floodplain forests and structure of explanatory variables without this soil factor. A high observed variability in iron pools among vegetation plots reflects different availability of soluble iron along a soil pH and moisture gradients (ROZBROJOVÁ & HÁJEK 2008). It is difficult to determine a single causal factor behind the iron content because it may directly and indirectly modify the presence of vascular plants through the toxicity and immobilization of phosphates (PONNAMPERUMA 1972, KOOIJMAN & HEDENÄS 2009). In our case, increasing iron concentrations were associated either with acidic soils, which partially multiplied the effect of pH gradient, or waterlogged soil substrates. MARTIN (1968) also found that the importance of iron toxicity increases towards waterlogged sites creating reducing conditions.

Stream power index, altitude and content of soil sand were determined as additional driving forces for species richness of the herb-layer vascular plants. A significant role of stream power index reflects close interactions between hydrology and topographic conditions across floodplain landscape (PARKER & BENDIX 1996). It was found to be the important driver enhancing species richness in our study. We corroborated the outcomes of previous research that stream power controls vegetation structure of riparian zones (e.g., BENDIX 1999, BENDIX & HUPP 2000, PIELECH et al. 2015). A positive species richness-stream power relationship most likely results from the formation of new exposed sites and variation in sediment deposition which supports fine-scale resource partitioning and higher niche diversity. Plant species richness is widely thought to decline along increasing altitudinal gradient (ADAMS 2009) or to be unimodal with a mid-altitude peak (RAHBEK 2005). In our study, the positive quadratic term indicated a U-shaped trend, however this relationship actually showed minimum

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richness values at the altitudes of 200–300 m and only increasing trend towards higher altitudes, without another obvious peak in richness at lower altitudes. Given a short altitudinal range (165–641 m) and the dominance of lower altitudes across the dataset, higher species richness at higher altitudes presumably did not contradict the existence of unimodal response reported by RAHBEK (2005). One possible explanation for higher species richness at higher altitudes might be the prevailing sites with groundwater discharge in submonane areas. These habitats generally tend to host species-richer vegetation compared with other (non-discharge) riparian forests which have been ascribed to higher nutrient availability (KUGLEROVÁ et al. 2014) and less drought stress during low-river stages (JANSSON et al. 2007). The weakly unimodal relationship between species richness and soil sand peaked at soil sand content about 30%. Similar non-linear response of plant species richness to substrate fineness was reported by NILSSON et al. (1989) in riparian vegetation along two Swedish rivers. The maximum species richness was found on sites with higher soil particle heterogeneity, with declines both towards coarser- and finer-grained sediments. Soil texture heterogeneity creates more available niches that positively support plant species coexistence. If flood disturbance-induced variability of soil grain sizes is taken into account (PARKER & BENDIX 1996), plant community assembly reflects interspecies differences in life-history strategies to disturbance level along successional gradient. The present hump-shaped curve thus could be explained in agreement with the intermediate-disturbance hypothesis (CONNELL 1978, WARD & STANFORD 1983) since the content of finer-grained material (silt and clay) increases at high flood-disturbed sites (DE JAGER et al. 2012). These results are consistent with the findings of POLLOCK et al. (1998) which found the highest plant species diversity on sites subjected to intermediate flood disturbance frequencies within various types of wetland vegetation.

The present study provides better insight into the role of site-specific factors and associated mechanisms that contribute to local plant species richness and affect species turnover along environmental gradients in black alder floodplain forests. Although floodplain diversity patterns may strongly differ among temperate European regions, our results suggest that the effects of moisture, hydrology and soil-related variables (chemistry, but also texture) appear to be generally valid to govern vegetation structure of these forests. In spite of a short altitudinal gradient subjected to analysis, it showed significant effect for species compositional variation and species richness. This pattern suggests that variables related to local catchment areas, which may induce considerable variability in the distribution of abiotic resources and conditions, should also be taken into account by phytodiversity studies in floodplain forests.

Erweiterte deutsche Zusammenfassung

Einleitung – Auenwälder besetzen in Europa Lebensräume mit vielfältigen Standortbedingungen. Sie zeigen nicht nur eine bemerkenswerte regionale Differenzierung (DOUDA et al. 2016), sondern unterscheiden sich auch stark hinsichtlich ihrer Pflanzenartenvielfalt (SLEZÁK et al. 2014, PIELECH 2015), wobei manche Typen eine ungewöhnlich hohe Zahl von Gefäßpflanzenarten aufweisen (CHYTRÝ et al. 2015). Ihre hohe standörtliche Variabilität ergibt sich aus räumlichen und zeitlichen Änderungen im Angebot abiotischer Ressourcen und Wuchsbedingungen, welche ihrerseits die Vegetationsstruktur maßgeblich steuern.

Biodiversitätsforschung in Auenwäldern versucht Ursachen und potenzielle Mechanismen, welche der Koexistenz von Pflanzenarten und ihrem Zusammentreten zu Gemeinschaften zu Grunde liegen, zu bestimmen. Hydrologie und Bodeneigenschaften sind zwei bekannte Umweltfaktoren, die gemeinsam

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die Vegetationsstruktur bestimmen (PARKER & BENDIX 1996, HÉRAULT & HONNAY 2005, DE JAGER et al. 2012). Obwohl frühere Forschungen zu bestimmenden Standortfaktoren das Verständnis der Muster von Vegetationsvielfalt in Auenwäldern verbessert haben, werden weiter gehende wissenschaftliche Untersuchungen benötigt um potenzielle Effekte einiger anderer Einflussgrößen zu bewerten. Deshalb wurden die in Auenwäldern bewährten Faktoren in dieser Studie ergänzt um seltener untersuchte Variablen wie Bodenart und Eisengehalt, welche sich in anderen Feuchtgebietstypen als wichtig erwiesen haben.

In den Westkarpaten und angrenzenden Gebirgszügen ist die Variabilität von Auenwäldern insbesondere durch pflanzensoziologische Studien gut untersucht (z. B. DOUDA 2008, SLEZÁK et al. 2014), wohingegen Studien zur Abhängigkeit der Artenzusammensetzung und –Vielfalt von direkt gemessenen Umweltfaktoren (und nicht nur Experten-basierten ökologischen Zeigerwerten) sehr selten sind (z. B. DOUDA et al. 2012, HRIVNÁK et al. 2015, PIELECH et al. 2015). Die vorliegende Untersuchung hatte das Ziel das Verhältnis zwischen Umweltvariablen (v. a. Bodeneigenschaften, Klima und Hydrologie) und Vegetationsmustern temperierter Auenwälder zu untersuchen. Wir fragten, wie die Artenzusammensetzung und –Zahl des krautigen Unterwuchses in Schwarzerlen-(*Alnus glutinosa*)-Auenwäldern im südlichen Teil der Westkarpaten auf Umweltfaktoren reagiert.

Methoden – Vegetationsaufnahmen der Schwarzerlen-Auenwälder wurden im südlichen Teil der Zentralslowakei nach pflanzensoziologischer Standardmethodik durchgeführt (Abb. 1). Für jede Aufnahmefläche wurden Gefäßpflanzenbestand, Topographie (Meereshöhe), Klima (Jahresdurchschnittstemperatur und -Niederschlag), Hydrologie (topographischer Wetness Index, Strömungsindex), Bodenphysik (Korngrößenanteile von Sand, Schluff und Ton) und Bodenchemie (Gesamt-C und N, C/N-Verhältnis, pH, Leitfähigkeit, pflanzenverfügbarer Phosphor und Verfügbarkeit der Ionen von Ca, Mg, K, Na und Fe) erfasst (Tab. 1). Die Deckung der Baumschicht wurde als Proxy für die Belichtung verwendet. Die Artenzahl der Krautschicht (einschließlich juveniler Gehölze) pro Aufnahmefläche wurde als Maß für die Alpha-Diversität verwendet. Die für die Artenzusammensetzung bestimmenden latenten Hauptgradienten wurden mittels Entzerrter Korrespondenzanalyse (DCA) extrahiert und mit gemessenen Faktoren (Tab. 1) sowie mittleren Ellenberg-Zeigerwerten für Licht und Feuchte (ELLENBERG et al. 1992) korreliert. Der Effekt der direkt gemessenen Variablen (Tab. 1) auf die floristische Varianz wurde anschließend mittels Kanonischer Korrespondenzanalyse (CCA) untersucht, wobei marginale, bedingte und reine Effekte aller Variablen ermittelt wurden. Interaktive schrittweise Vorwärtsselektion wurde benutzt um die Kombination von Prädiktorvariablen mit höchster Parsimonie und Signifikanz zu ermitteln. Die Artenzahl wurde mit einem Generalisierten Linearen Modell (GLM) mit Poisson-Verteilung der Schätzfehler und logarithmischer Link-Funktion untersucht.

Ergebnisse – Insgesamt wurden in der Krautschicht der Schwarzerlen-Auenwälder 255 Gefäßpflanzenarten nachgewiesen. Die stetesten darunter waren eutraphente (*Aegopodium podagraria*, *Festuca gigantea*, *Galium aparine*, *Impatiens noli-tangere*, *Ranunculus repens*, *Urtica dioica*) und hygrophile Arten (*Caltha palustris*, *Filipendula ulmaria*, *Lycopus europaeus*, *Lysimachia vulgaris*, *Poa trivialis*). Die Anzahl der Gefäßpflanzen in der Krautschicht variierte zwischen 19 und 59 (Mittelwert 38) Arten pro Aufnahme. Die Artenzusammensetzung folgte in erster Linie einem Komplexgradienten von Feuchte und Licht (Ellenberg-Zahlen) sowie der Bodennährstoffe (erste DCA-Achse) und einer Kombination aus Meereshöhe und Säurestatus (zweite DCA-Achse; Abb. 2a, b). Die CCA mit Vorwärtsselektion ermittelte als wichtigste Prädiktoren mit höchstem reinem Effekt (d. h. mit höchster erklärter Varianz bei Berücksichtigung anderer Kovariablen) Meereshöhe (2,8 %), K-Gehalt (2,6 %) und pH des Bodens (2,2 %; Tab. 2). Das GLM ergab eine negative lineare Abhängigkeit der Artenzahl vom Eisengehalt der Böden sowie eine positive von pH und Strömungsindex. Signifikante quadratische Terme für Meereshöhe und Sandgehalt wiesen auf schwache U-förmige, unimodale Abhängigkeiten hin (Tab. 3).

Diskussion – In der kanonischen Ordination wurde die Artenzusammensetzung durch Meereshöhe (bzw. Kima) und Bodenchemie erklärt. Diese Faktoren sind bekannt als wesentliche Prädiktoren der Vegetation von Auenwäldern auf verschiedenen Maßstabsebenen (NAQINEZHAD et al. 2008, SLEZÁK et al. 2014, PIELECH 2015, DOUDA et al. 2016). Der relative geringe Erklärungsanteil von pH und Boden-

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nährstoffen ist wahrscheinlich eine Folge des eher kurzen pH-Gradienten und des Vorherrschens sauer verwitternder Gesteine im Untersuchungsgebiet. Die Variation entlang von Höhengradienten wird als Folge von Interaktionen zwischen Ober- und Unterlauf der Gewässer interpretiert (KUGLEROVÁ et al. 2014, PIELECH et al. 2015). Die Hinzunahme von Ellenberg-Zeigerwerten der nicht direkt gemessenen Umweltfaktoren in der DCA verdeutlichte den überragende Einfluss des Wasserhaushalts auf die Artenzusammensetzung. Dieses Muster spiegelt die für Auen typische hohe raum-zeitliche Heterogenität des Wasserhaushalts wider, welcher in komplexer Weise vom Überflutungsregime, Grundwasserstand und Wasserspeicherung in den Böden abhängt.

pH und Eisengehalt der Böden erweisen sich als wichtigste Steuergrößen für die Variation der Artenzahlen der Krautschichtpflanzen. Die positive Beziehung zum pH-Wert ist im Hinblick auf ökophysiologische Anpassungen (MARSCHNER 1991, TYLER 2003) und die Evolutionsgeschichte, welche die Entstehung und Erhaltung deutlich größeren Artenpools kalkliebender Pflanzen gefördert hat (PÄRTEL 2002, EWALD 2003), zu deuten. Der Eisengehalt des Bodens kann die Artenvielfalt der Krautschicht direkt über Toxizität und indirekt über Immobilisierung von Phosphaten beeinflussen (PONNAMPERUMA 1972, KOOIJMAN & HEDENÄS 2009). Erhöhte Eisengehalte wurden einerseits in sauren Böden, wo sie die pH-Effekte verstärken, und andererseits in staunassen Substraten mit reduzierenden Bedingungen festgestellt (siehe auch MARTIN 1968). Der signifikante Einfluss des Strömungsindex spiegelt enge Interaktionen zwischen lokaler Hydrologie und Topographie in Auenlandschaften wider (PARKER & BENDIX 1996). Seine positive Wirkung auf die Artenvielfalt ist ein Resultat der Schaffung von Störstellen und der feinmaßstäblichen Ressourcenaufteilung mit höherer Nischendiversität. In unserer Studie deutet der quadratische Modellterm auf eine U-förmige Abhängigkeit von der Meereshöhe mit einem Minimum bei 200-300 m und ansteigender Vielfalt in größeren Höhen, allerdings ohne offensichtlichen Anstieg im Tiefland. Höhere Artenvielfalt in größerer Meereshöhe kann durch ein Vorherrschen von Grundwasseraustritten in der submontanen Höhenstufe erklärt werden, welche auf Grund besserer Nährstoffversorgung (KUGLEROVÁ et al. 2014) und konstanterem Wasserstand während Niedrigwasser (JANSSON et al. 2007) artenreichere Auenwälder bedingen als Standorte ohne Wasseraustritt. Die schwach unimodale Abhängigkeit zeigte ein Maximum der Artenvielfalt bei rund 30% Sandgehalt, d. h. in einem Bereich hoher Korngrößendiversität. Dieser Zusammenhang kann mit der Intermediate Disturbance Hypothese (CONNELL 1978, WARD & STANFORD 1983) erklärt werden, da der Anteil feiner Sedimente (Schluff und Ton) in häufig gestörten Auen zunimmt (DE JAGER et al. 2012). Die Zusammensetzung der Pflanzengemeinschaften spiegelt also störungsbedingte Unterschiede in den Life-History-Strategien entlang des Sukzessionsgradienten wider (PARKER & BENDIX 1996).

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Spearman rank correlation matrix among measured explanatory variables.

Anhang E1. Matrix der Spearman Rangkorrelationen zwischen gemessenen Umwelt-variablen.

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Supplement E1. Spearman rank correlation matrix among measured explanatory variables. Significant values (P <0.05) are in bold (Altit. – altitude, Cond. – conductivity, CovE3 – tree-layer cover, EIV_L – Ellenberg indicator value for light, EIV_M – Ellenberg indicator value for moisture, Precip. – mean annual precipitation, SPI – Stream power index, Temp. – mean annual temperature, TWI – topographic wetness index).

Anhang E1. Matrix der Spearman Rangkorrelationen zwischen gemessenen Umweltvariablen. Signifikante Werte (P <0.05) fett gedruckt (Altit. – Meereshöhe, Cond. – Leitfähigkeit, CovE3 – Baumschichtdeckung, EIV_L – Ellenberg-Zeigerwert für Licht, EIV_M – Ellenberg-Zeigerwert für Feuchte, Precip. – mittlere jährliche Niederschlagssumme, SPI – Strömungsindex, Temp. – Temperatur-Jahresmittel, TWI – topographischer Wetness Index).

	Temp.	Precip.	C	N	C/N	pH	Cond.	Ca	Mg	K	Na	Fe	P	Sand	Silt	Clay	CovE3	SPI	TWI	EIV_M	EIV_L
Altit.	**-0.78**	**0.76**	0.10	0.07	0.08	**-0.26**	-0.11	-0.13	-0.18	0.02	0.05	-0.17	0.05	0.21	-0.18	-0.23	-0.08	**0.34**	0.23	0.07	-0.08
Temp.		**-0.84**	-0.18	-0.22	0.00	**0.26**	-0.07	0.14	0.21	0.24	-0.02	-0.11	-0.18	-0.17	0.13	**0.42**	0.18	-0.20	-0.04	**-0.35**	-0.09
Precip.			0.07	0.10	-0.01	**-0.38**	-0.06	-0.24	**-0.36**	-0.20	-0.02	0.03	0.02	0.12	-0.11	**-0.32**	-0.02	0.15	0.18	0.18	0.00
C				**0.94**	0.24	-0.24	**0.71**	**0.43**	**0.41**	0.11	**0.58**	0.23	0.12	**-0.39**	**0.37**	0.20	0.00	-0.20	0.05	**0.43**	**0.37**
N					0.00	-0.19	**0.74**	**0.42**	**0.39**	0.08	**0.49**	**0.40**	0.17	**-0.45**	**0.45**	0.16	-0.09	**-0.25**	-0.03	**0.46**	0.02
C/N						-0.04	0.01	0.06	-0.03	-0.14	**0.27**	**-0.28**	0.01	**0.43**	**-0.46**	-0.24	**0.28**	0.19	0.25	0.16	0.02
pH							0.08	**0.53**	**0.37**	-0.08	-0.04	**-0.30**	0.11	0.08	0.00	-0.11	**-0.29**	0.03	-0.15	0.06	0.13
Cond.								**0.61**	**0.60**	-0.01	**0.60**	**0.28**	0.15	**-0.34**	**0.33**	0.10	-0.07	-0.23	0.01	**0.49**	**0.47**
Ca									**0.81**	0.13	**0.47**	-0.25	0.07	**-0.27**	**0.27**	0.15	**-0.27**	-0.07	0.11	**0.33**	**0.35**
Mg										0.16	**0.46**	-0.16	0.06	**-0.30**	**0.30**	0.23	-0.21	-0.17	0.10	**0.25**	**0.27**
K											0.00	-0.09	-0.09	**-0.30**	0.23	**0.56**	0.03	0.15	**0.31**	**-0.41**	-0.14
Na												-0.06	0.01	-0.16	0.14	0.10	-0.06	-0.04	0.24	**0.49**	**0.44**
Fe													0.07	-0.24	**0.27**	-0.03	-0.03	-0.23	**-0.30**	0.25	0.19
P														0.22	-0.13	**-0.37**	-0.14	0.05	-0.20	0.05	-0.06
Sand															**-0.94**	**-0.78**	0.14	**0.34**	0.08	-0.06	**-0.31**
Silt																**0.62**	-0.14	**-0.30**	-0.11	0.10	**0.33**
Clay																	0.00	-0.20	0.09	-0.24	0.11
CovE3																		0.12	0.12	-0.02	0.07
SPI																			**0.58**	-0.04	-0.09
TWI																				0.03	0.06
EIV_M																					**0.67**

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Autor(en)/Author(s): Slezak [Slezák] Michael [Michal], Hrivnak Richard, Machava Jan

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