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PATTERNS OF PLANT SPECIES COMPOSITION OF A TEMPERATE FLOODPLAIN MEADOW IN RESPONSE TO FINE-SCALE TOPOGRAPHY

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With 4 figures, 1 table and 2 appendices
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Summary: Floodplains are vital and diverse habitats, providing essential ecosystem services. In Germany, the total surface of floodplain meadows has decreased by over 80% since the 1950s due to human activities such as river channelisation and embankment as well as land use intensification, leading to changes in nutrient and pollutant input. However, effects of these changes on floodplain vegetation remain understudied, primarily due to their recent occurrence. Here we investigate the effects of terrain elevation, flow distance to permanent water bodies (rivers and clay ponds), groundwater-surface distance and thickness of the alluvial clay layer on the plant species composition of the floodplain meadows 'Papitzer Lachen' in Northwest Saxony, Germany. We make use of the Ellenberg indicator system to approach statistical results from an ecological point of view. We recorded the vegetation species composition on 20 relevés of 10 m x 10 m (100 m2) each across different floodplain meadow types along an elevation gradient. We classified the plant communities phytosociologically. In addition, we performed an ordination of the plots (detrended correspondence analysis, DCA) and compared the resulting axes to environmental variables using Pearson's correlation coefficient. As abiotic factors, we used the elevation of each plot measured via DGPS in the field, least cost path to the next water body derived from a digital elevation model, groundwater-surface distance as well as thickness of the alluvial clay layer. We calculated the mean weighted Ellenberg indicator moisture value for each plot and compared it to the DCA results. Three of the stands were classified as *Scutellario-Veronicetum longifoliae* Walther 1955, eleven as *Arrhenatheretum elatioris* Braun 1915 and six as a *Silaum-silaus*-community. The relevés could be roughly separated in two groups along the first DCA axis. The first DCA axis showed significant correlations ($p < 0.05$) with ground elevation ($r = -0.54$) and alluvial clay layer thickness ($r = -0.68$) but no significant correlations with groundwater-surface distance and proximity to water bodies. The weighted mean Ellenberg indicator moisture values significantly correlate with distance to groundwater table ($r = -0.59$) and confirm a moisture gradient. The main explanatory variable for variation in the vegetation appears to be hydrology. However, variability in water levels which is typical for floodplains has declined. Main reasons are a smaller amplitude of water levels due to river regulation and long periods of droughts. This underlines the strong anthropogenic influence on floodplains. As floodplains are, especially due to their dynamic hydrology, particularly species-rich ecosystems, this study helps to document and understand this diversity to support a conservation value.

Keywords: Wetness gradient, alluvial grassland vegetation, plant ecology, detrended correspondence analysis (DCA), Weiße Elster, Luppe

1 Introduction

Floodplains and particularly floodplain meadows fulfil crucial ecological, economic and social ecosystem services (Opperman et al. 2017, Petsch et al. 2022, Scholz et al. 2012, Tockner et al. 2000). Among other things, floodplains influence the carbon cycle (Soussana et al. 2007), water balance (Petsch et al. 2022), erosion control (Wawer et al. 2013), material management, human health (Petsch et al. 2022), retain nutrients and pollutants (Brunke & Gonser 1997, Hill 1996) and provide habitat for flora and fauna (Dierschke 2007). Floodplains are further considered to be among the most complex, species-rich and threatened habitats in Europe (Tockner et al. 2000).

Floodplains are characterised by frequent inundation or pronounced interaction with water bodies. The hydrological regime consists of one or more main rivers, sometimes with various small tributaries ('braided river systems'). The soils of floodplains have a high water storage capacity (Vásconez Navas et al. 2023) and contribute to the water retention in case of flooding events. During a flood, the water usually stands still on the flooded areas, causing the fluvially transported materials, such as fine soil, clay or (decomposed) biomass, to be deposited on the ground. The deposits overlie the present soil, fostering nutrient richness, and are thus of importance to animals and plants. However, the distribution of material deposition features a pronounced spatial variation across the flooded area. As a result, a complex microtopography,

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consisting of a system of channels, depressions and higher areas is formed, which deepens as the water runs off while remaining partially filled even after the flood recedes. The outcome is a varied range of habitats for plants and animals with different site conditions, e.g. soil composition, moisture and nutrient contents. This results in a typical floodplain zonation of plants, which is mainly determined by the degree of flooding (Blom & Voesenek 1996, Costa 2004). Due to the recurring alternation between flooding and drying out, as well as the complex geomorphology, plants have developed various adaptations to the site conditions over time (Crawford 1996). The floodplain grasslands therefore exhibit a very high taxonomic and structural diversity. Functioning as a corridor between uplands and lowlands, continental stream valley species, such as *Cnidium dubium* or *Scutellaria hastifolia*, are characteristic.

Furthermore, floodplain grasslands are species-rich in endangered wildflowers, grasses, and forbs (Habel et al. 2013, Joyce & Wade 1998), and productive. In general, these characteristics increase with the distance from the river. Crucial to the development of plant communities in Central Europe are the nutrients phosphorus and nitrogen (Noe 2013). Species-rich and species-poor stands differ in soil phosphorus levels (Gilbert et al. 2009). Additionally, the site characteristics are masked by land use. Under mowing, species-rich stream valley meadows develop, while grazing on the other hand can promote the development of species-poor grassland dominated by *Elymus repens* (Teubert, personal communication, 2022).

Human impact on these complex processes can have severe consequences. The industrial development caused floodplain ecosystems to be more adversely affected than other natural systems (Scholz et al. 2009). Regular flooding events have decreased due to channelisation and river embankments (Bayley 1995, Godreau et al. 1999). Moreover, ever-changing nutrient and pollutant input as well as land use changes (Msofe et al. 2019) affect the natural functions of these systems, including biodiversity and stability (Arts et al. 1990).

Especially the species-richness of floodplain meadows is changing or diminishing because of human impacts (Briemle & Ellenberg 1994, Hejcman et al. 2013, Krause et al. 2011, Norderhaug et al. 2000, Prach 2008). In Germany, the total area of floodplain meadows has declined by over 80% since the 1950s (Krause et al. 2011, Wesche et al. 2012). Therefore, they are protected by the EU Habitats Directive (92/43/ECC; habitat type 6440: alluvial meadows of *Cnidion dubii* and habitat type 6510: lowland hay meadows *(Alopecurus pratensis, Sanguisorba officinalis)*) (Ludewig et al. 2014). Additionally, floodplains and their associated habitats are protected by national law (German Federal Nature Conservation Act: § 30 BNatSchG). The drivers of their decline are predominantly local factors such as land-use change and intensification, fertilisation as well as water regime alteration (Gilhaus et al. 2017, Leuschner et al. 2013, Norderhaug et al. 2000, Prach 2008), whereas large scale trends such as climate change and increased atmospheric nitrogen deposition play a secondary role (Krause et al. 2011, Wesche et al. 2012). To be more specific, Joyce (2001) found that fertilisation significantly reduced species diversity and simplified plant community structures as inter-specific competitive relations shift. Thus, biologically diverse floodplain meadows are vulnerable to agricultural intensification and other activities that promote enhanced nitrogen levels (Hejcman et al. 2013, Joyce 2001, Tischew et al. 2018). Human-induced alterations of the local hydrological regime, such as dams and dykes, also modify the spatial distribution and species composition of floodplain plant species, as pointed out by Leyer (2004, 2005). The main objectives of such artificial modifications are the stabilisation of fluctuating water tables or prevention of flooding. However, responses of plant species to altered hydrological conditions were often not considered adequately in the past. For instance, within the scope of an assessment of habitats decoupled from flood events by dykes and dams at the Middle Elbe River, species of habitats high above the water table were found to have colonised lower located areas, where water level fluctuations were reduced, indicating increasing drought stress at higher elevation habitats and drier conditions in the low areas. Moreover, changes in phytosociological associations as well as individual plants were associated with the changed hydrological regime by dams and dykes (Leyer 2004). The causes are not only altered water levels, but also reduced hydrological connectivity due to fragmentation, which is driving seed dispersal as well as the exchange of energy and matter in the form of nutrients, suspended sediments and biomass in a floodplain ecosystem (Johansson et al. 1996, Tockner et al. 1999).

Due to these dynamics, more detailed research, particularly on these complex ecosystems, is necessary. There is limited knowledge of plant distribution in floodplain systems regarding the mechanisms of anthropogenic overprinting, especially through water management and agricultural interventions. Therefore, this study focuses on vegetation structures in the floodplain meadows surrounding the 'Papitzer Lachen' near Leipzig, Germany. As the hydrological regime plays a crucial role for taxonomic and structural diversity (Brown et al. 1997), this study investigates the variation in plant species composition at different sites in the meadows in terms of topography and hydrology. Specifically, it addresses the following research question:

- Do fine-scale variation in hydrological and topographic variables, i.e., terrain elevation above sea level, groundwater-surface distance and thickness of the alluvial clay layer, still have a primary impact on the plant species composition of floodplain meadows, despite the manifold human overprinting?

2 Methods

2.1 Study area

The study area 'Papitzer Lachen' is part of a floodplain forest and open space mosaic of the Elster-Luppe floodplain in the city of Schkeuditz in Northwest Saxony, Central Germany (51.380° N, 12.243° E, Fig. 1-a). The area is located in a temperate climate and lies in the rain shadow of the Harz Mountains, with a mean annual air temperature and total annual precipitation of 9.7 °C and 543 mm, respectively.

The ecosystem characteristics of the study area are mainly determined by the geology and landform. Gravel and sandy sediments, formed as terraces during the Pleistocene, are the parent substrate. On top, a layer of alluvial clay, mostly 2 to 3 m thick, is accumulated, which mostly forms soils of the Vega or Gley type (Eissmann 2000, Eissmann & Tinap 2005, Klimo & Hager 2001, Kirsten et al. 2022, Wolf & Alexowsky 2008). The study area is situated between the Weiße Elster River in the North and the Neue Luppe River in the South-East, with the former delta-like river courses and channels now identified by differences in elevation. The area was heavily affected by human activities, including loam and sand mining, use as cattle pastures and river regulation. Natural flooding events are reduced due to cut-off tributaries, embankments, and flood-proof runoff systems. The Weiße Elster has a technical defined discharge and is dammed by watermills. The Neue Luppe functions as a funnel, withdrawing groundwater from surrounding areas and causing a lowering of the groundwater level in the region (Nebel et al. 2022, Putkunz 2011, Reichhoff 2011, Scholz et al. 2022, Vlaic et al. 2017). Since 1976, the area has been part of the nature reserve *Luppenaue*, the NATURA 2000 site Leipziger Auensystem and is currently being revitalised as part of the project *Lebendige Luppe* to restore natural floodplain dynamics and preserve its diverse plant and animal species (Scholz et al. 2022).

In 2022, the mean annual temperature at the measuring site Leipzig-Schkeuditz was 11.3 °C and total precipitation 373 mm (meteostat 2024). The year is considered warmer and drier, with substantially less precipitation from May to September. The mean run-off of the hydrological year 2022 (22.3 m^3 s^{-1}) of the next public gauging station Oberthau is a little bit lower than the long-term mean (1972–2018) of 25.9 m^3 s^{-1} (LHW 2024a). However, the months of May–September exhibit a comparatively extreme low run-off (mean 11.6 m^3 s^{-1}; LHW 2024b), which is very close to the mean long-term value of measured low water. The last remarkable overbank flooding of the meadows was in June 2013 and flooded directly over the Weiße Elster and through seepage water from the Neue Luppe (Scholz et al. 2022).

The vegetation is dominated by alluvial meadows and hardwood (*Querco-Ulmetum minoris* Issler 1924) and oak-hornbeam forests (*Stellario holosteae – Carpinetum betuli* Oberd. – *Carpinion*) forests, with several reed and aquatic plant communities present in the rivers and clay ponds (Engelmann et al. 2022, Kubitz & Gutte 1999). In addition, various fringe and tall forb communities can be found in the transition between water-bearing ponds and meadows. The floodplain grassland in the study area primarily consists of temperate lowland hay meadows (EU habitat type 6510) of the alliance *Arrhenatherion elatioris*, and of small areas of wet alluvial meadows (EU habitat type 6440 of the alliance *Cnidion*). In particular, these mesic meadows are vegetation units of the alliance *Arrhenatherion elatioris* Koch 1926, with the main association of planar false oat-grass meadows (*Arrhenatheretum elatioris* Braun-Blanquet 1915) (Dierschke 1999, Jäger et al. 2002). The sites owe their productive power mostly to promoting human interventions, such as mowing and nutrient input (Dierschke 1997).

2.2 Additional GIS data

Land use data containing permanent water bodies were obtained from Saxony's State Office for Environment, Agriculture and Geology (LfULG 2022). Information on the groundwater-surface distance as well as the thickness of the alluvial clay layer was provided by the Helmholtz Centre for Environmental Research (UFZ).

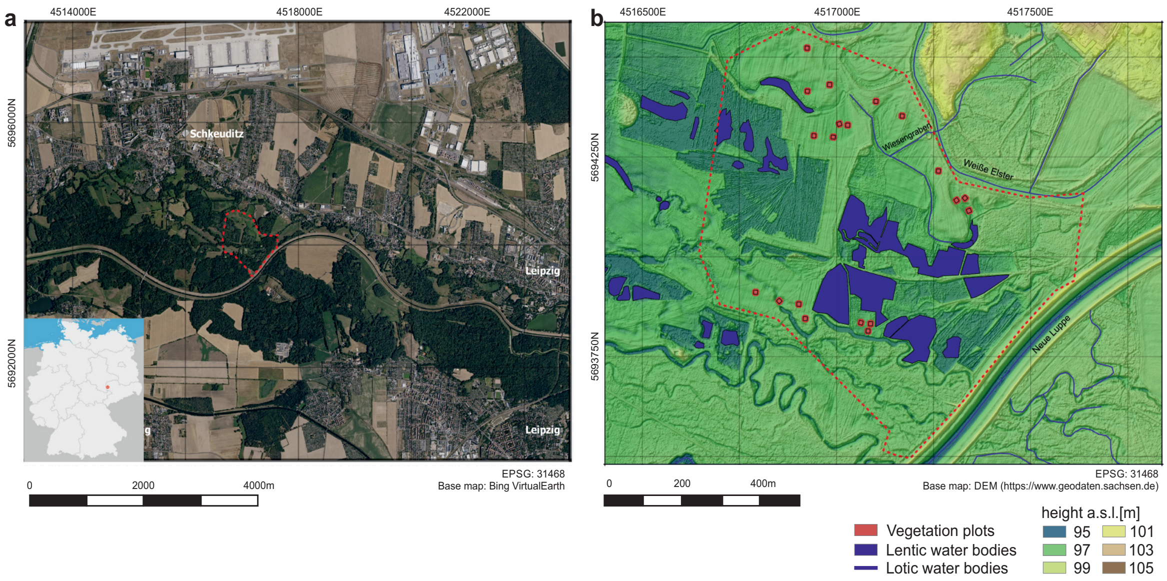

Fig. 1 a: Geographic position of the study area 'Papitzer Lachen' in Northwest Saxony, Germany. b: Overview of the vegetation sampling sites (red squares) and permanent water bodies (rivers and clay ponds, blue) in the 'Papitzer Lachen'. The colouring of the base map (DTM) describes the elevation above sea level (height a.s.l. [m]), the values in the legend are the respective class centers.

The values of the alluvial clay layer and of the groundwater-level were obtained from Lebendige Luppe/IBGW groundwater model. The groundwater data used represent the mean of the vegetation period (March – September) for the year 2021. To obtain the values for groundwater surface water distance for each vegetation plot the modelled ground water level has been intersected/interpolated with the digital terrain model (DTM). The DTM with a resolution of 1 m x 1 m was provided by the state survey department of Saxony (Landesamt für Geobasisinformation Sachsen 2022). The absolute vertical accuracy of the laser scan data is up to ±0.15 m, the horizontal accuracy up to ±0.30 m. The high resolution makes the data set ideal for representing slight changes in elevation in order to detect vegetation patterns on a small scale. For an overview of the study area's morphology, a hillshade raster was derived from the DEM with the tool *Hillshade* using the Open Source Software QGIS 3.16 (QGIS Development Team 2022). The DEM underlay by the hillshade raster is shown in Figure 1-b.

2.3 Vegetation sampling

Vegetation was sampled on 20 plots of 10 m x 10 m each (100 m^2) on different floodplain meadows surrounding the water ponds 'Papitzer Lachen'. The plot distribution was following a stratified random design generated in QGIS 3.16 (QGIS Development Team 2022). The meadows in the area showed an amplitude of 1.83 m in elevation. Thus, the lidar-derived Digital Terrain Model (DTM, Geobasisdaten Sachsen) was classified into three levels of 0.61 cm each and randomly located points were calculated for each height level, respectively. Therefore, the sampling points are stratified along the elevation gradient. In the field, the elevation of the corner points of each plot was measured via Differential Global Positioning System. The relevés are displayed as red squares in Figure 1-b.

Between June and August 2022, plant species presence and their abundance were recorded on all plots using the Braun-Blanquet scale (Braun-Blanquet 1964). Plant species nomenclature follows that of Wisskirchen & Haeupler (1998) and Jansen & Dengler (2008) ("GermanSL"). Since we recorded the vegetation between June and August, certain species could not always be clearly differentiated. It was difficult to identify species of the genus *Poa* towards the end of the vegetation period. These were partly classified as *Poa* spec. The same applies to *Festuca pratensis* and *F. arundinacea*, which in the data set we merged into *Festuca pratensis et arundinacea*. Based on their species composition, the vegetation plots were classified phytosociologically according to Mucina et al. (2016), Schubert (2001) and Schubert et al. (2001). For statistical analyses, the cover-abundance scores were later transformed to a representative percentage score: *r* = 0.01; + = 0.2; 1 = 2.5; 2a = 7.5; 2b = 20.0; 3 = 37.5; 4 = 62.5; 5 = 87.5.

2.4 Statistical analyses

The recorded vegetation data were subject to a detrended correspondence analysis (DCA, Hill & Gauch 1980) using the R software (R Core Team 2022; vegan package 2.6.4). In total, 116 plant species in 20 plots were included in the ordination. As settings of the DCA we used detrending by 26 segments, no downweighting of rare species, no log-transformation of abundances and vector-scaling proportional to r^2.

To be able to statistically compare the result of the ordination with environmental variables, we first derived proximity to water bodies from the DTM. For each relevé, we calculated the least cost path respective to the elevation from the plot centroid to the next permanent water body (loam puddles or rivers) using the DTM and the QGIS 3.16 plugin *Least-cost path* (QGIS Development Team 2022). This algorithm calculates the most direct way, minimising the cost of overcoming the terrain. In addition, we computed the elevation for each plot from the mean of the measured elevation of the four vertices. The groundwater-surface distance as well as the thickness of the alluvial clay layer were provided by the UFZ.

All these variables were tested for correlations with the three main axes of the DCA by calculating Pearson's correlation coefficient with a 5% significance level (α = 0.05) using R software (R Core Team 2022), in an attempt to explain the statistical variances using a geographical approach. We employed a permutation test because the conventional Pearson's r-test was unsuitable due to pseudoreplication. To get a coarse overview of ecological plant characteristics, we used the Ellenberg indicator system (Ellenberg 1979). For each vegetation plot, we calculated the mean indicator values for moisture, reaction, nitrogen, flooding, and alternating moisture, both weighted by species abundances and unweighted. These were then fitted to the axes scores and used as vectors in the DCA plot. We also created a correlation matrix of the mean weighted Ellenberg indicator values and the environmental variables to test the effect of small-scale variations.

3 Results

The recorded plant species are shown in a species x plot matrix in Appendix 1. Overall, we identified 118 plant species. All vegetation plots recorded belong to the class of anthropogenic managed pastures, meadows and tall-herb meadow fringes at low and mid-altitudes (*Molinio-Arrhenatheretea* Tx. 1937).

Three plots are stream valley tall-herb fringe wet meadow communities. They were assigned to the association *Scutellario hastifoliae-Veronicetum longifoliae* Walther 1955 from the alliance *Veronico longifoliae-Lysimachion vulgaris* (Passarge 1977) Bál.-Tul. 1981. Eleven relevés are mesic meadows and pastures and were classified as *Arrhenatheretum elatioris* Braun 1915 from the alliance *Arrhenatherion elatioris* Koch 1926. The remaining six records were sociologically not clearly classifiable. After careful consideration they were assigned to the *Silaum silaus*-communities of the *Arrhenatherion elatioris* Koch 1926.

Figure 2 visualizes the distribution of the recorded plant species across the classified community. *Scutellario hastifoliae-Veronicetum longifoliae*-communites feature 24 species that did not occur in the other communities. *Silaum silaus*-communities and *Arrhenatheretum elatioris* associations comprise 10 and 22 unique species, respectively.

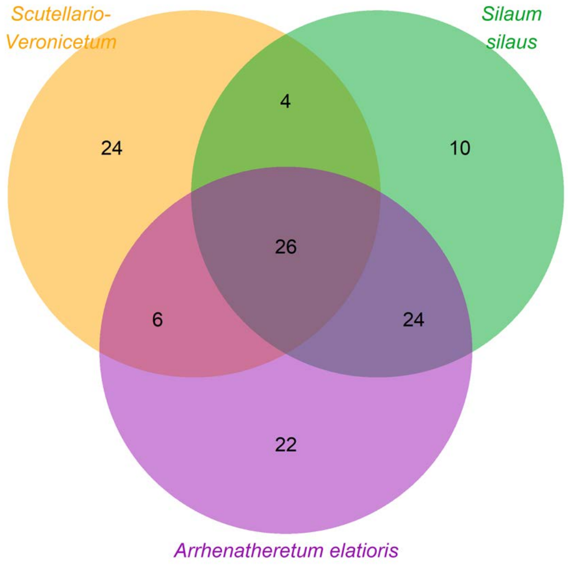

Fig. 2: Venn Diagram showing the distribution of plant species numbers between the classified associations *Scutellario hastifoliae-Veronicetum longifoliae*, *Arrhenatheretum elatioris* and *Silaum silaus*-communities. Super-imposing areas denote species intersections, whereas clear colors mark exclusionary species amounts for each community.

The number of species intersections between *Scutellario hastifoliae-Veronicetum longifoliae* and *Silaum silaus* was four, for *Scutellario hastifoliae-Veronicetum longifoliae* and *Arrhenatheretum elatioris* six species and *Arrhenatheretum elatioris* and *Silaum silaus* share 24 species. All three classified associations and communities have 26 determined species in common.

The first and second axis of DCA (axis 1: eigenvalue 0.71, axis length 4.75 SD; axis 2: eigenvalue 0.43, axis length 2.93 SD) ordinations space as well as the distribution of the phytosociological associations and trends in the environmental variables investigated are shown in Figure 3. Indicated by the eigenvalue of 0.71, most of the variability in the data set is explained along the DCA axis 1. Additionally, the distribution of recorded plant species as well as the mean Ellenberg indicator values in the ordination space are shown in Figure 4. The plant species names are placed according to their ordination score of the first two DCA axes. The mean Ellenberg F-values per plot significantly correlate with the respective depth to the groundwater table ($r = -0.59$).

Table 1 shows the squared correlation coefficient of the first two DCA axes and the investigated environmental variables as well as the mean Ellenberg indicator values. Two of the variables considered are significantly correlated with the first DCA axis: ground elevation and thickness of the alluvial clay layer. Their values decrease with increasing site scores of the first DCA axis. Two of the Ellenberg indicator values are significantly correlated with the first DCA axis: F-value and alternating moisture indicator. Their values increase with increasing site scores of the first DCA axis. All remaining correlations were not significant at the 5% significance level.

4 Discussion

In the meadows surrounding the 'Papitzer Lachen', we found three grassland associations (*Arrhenatheretum elatioris* Braun 1915, *Silaum silaus* and *Scutellario hastifoliae-Veronicetum longifoliae* Walther 1955). Along the first DCA axis, the plots could be roughly divided into two groups. The most explanatory factors for patterning these differences are ground elevation, groundwater-surface distance and thickness of the alluvial clay layer, indicating a moisture gradient. The proximity to the next permanent water body was not as relevant.

4.1 Classification of vegetation records

The three plots classified as *Scutellario hastifoliae-Veronicetum longifoliae* Walther 1955 are a transitional plant assemblage between stream valley meadows and nitrophilous forb stands. According to Teubert (personal communication, 2022), the formation

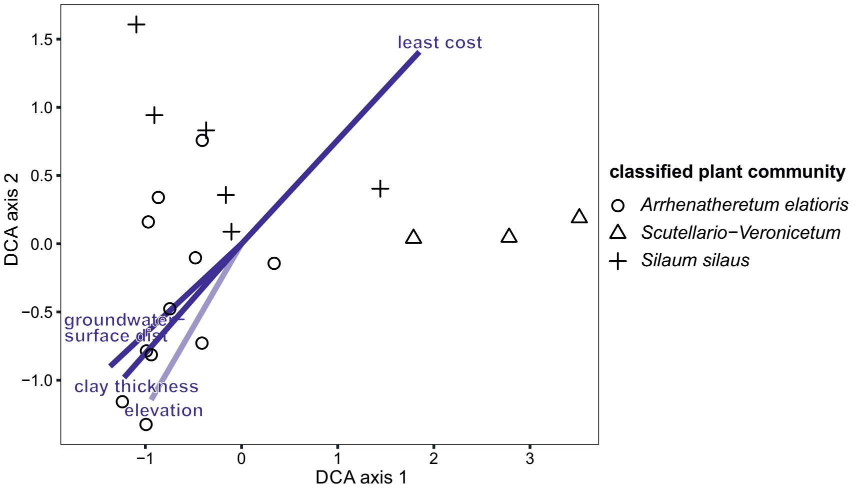

Fig. 3: DCA scatter plot showing the 20 relevés with their phytosociological classification in the ordination space. Axis 1: eigenvalue 0.71, axis length 4.75 SD; axis 2: eigenvalue 0.43, axis length 2.93 SD. Vectors indicate correlations between ordination site scores and investigated environmental variables (ground elevation, ground-surface distance, thickness of alluvial clay, least cost path to next water body). The vectors point in the direction towards which the environmental vectors change most rapidly and to which they have maximal correlations in the ordination space.

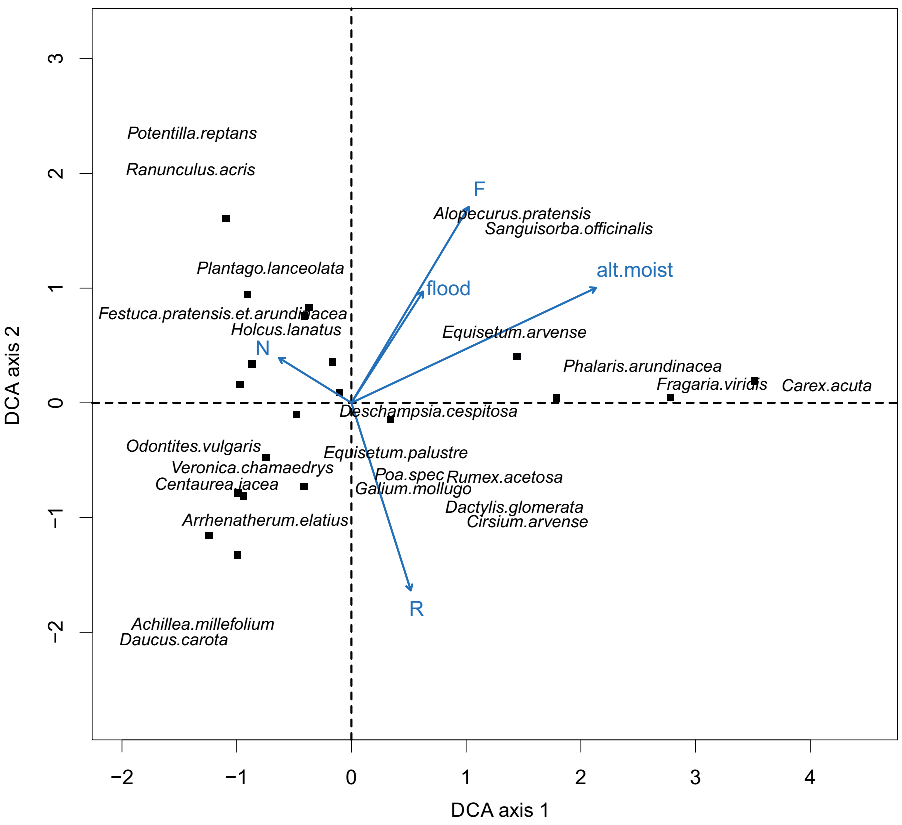

Fig. 4: DCA scatter plot showing the 20 relevés (black squares), the recorded plant species and the Ellenberg indicator values (blue arrows: F = moisture, R = reaction/acidity, N = nitrogen, alt.moist = alternating moisture indicator, flood = flood indicator) in the ordination space of the first two DCA axes. Vectors indicate correlations between ordination site scores and Ellenberg indicator values. The vectors point in the direction towards which the indicators change most rapidly and to which they have maximal correlations in the ordination space.

changed over the past decades. Today, the share of species adapted to flood-related disturbances (*Poa palustris, Potentilla anserina, Stellaria palustris*) decreased or disappeared entirely, while the abundance of meadow species (*Rumex acetosa, Silene flos-cuculi*) and flooding intolerant species (e.g. *Veronica chamaedrys, Fragaria viridis*) increased. Possible reasons are changes in land use and modifications of the hydrological regime and the fact of the absence of flooding or high ground water table. Characteristic species for alluvial meadows and stream valleys with a high conservation value are *Thalictrum lucidum*, *Veronica longifolia*, *Sanguisorba officinalis* or *Selinum carvifolia*.

The plots belonging to the declining *Arrhenatheretum elatioris* Braun 1915 sites (Schubert et al. 2001) are floristically impoverished due to conversion from grazing to mowing. We identified 22 species occurring only in this community (see Fig. 2), which are predominantly tall and with high productivity (Dierschke 1997).

Plots affiliated to the *Silaum silaus*-community contain both wetland indicators and fresh meadow species, indicating the floodplain typical change of wet and dry periods. However, many species characteristic for this community are missing. This is due to the former intensity of grassland management as well as devastation of the water regime, in particular river regulation.

4.2 Interpretation of the DCA

Neighbouring data points in the DCA space (Fig. 3) show a similar plant species composition. The DCA resulted in a rough grouping of the plots, which resembles the phytosociological grouping and hence can be justified from a phytosociological point of view.

Statistically, DCA axis 1 suggests a strong gradient with high beta diversity. The axis length of 4.75 SD indicates that the most distant samples along axis

Tab. 1: Correlation coefficients between sample scores of the first three DCA axes and environmental variables (ground elevation above sea level (a.s.l.), least cost path to next permanent water body, distance to groundwater table, thickness of alluvial clay layer) and mean Ellenberg indicator values (F = moisture, R = reaction/acidity, N = nitrogen, alt.moist = alternating moisture indicator, flood = flood indicator). Least cost path to next permanent water body does not have an interpretable numeric unit. Permutation-based significant p-values ($p < 0.05$) are printed in bold.

	Axis 1	Axis 2
Eigenvalue	0.71	0.41
Ground elevation a.s.l. [m]	**–0.54**	**–0.36**
Least cost to next water body	0.44	0.30
Distance to groundwater table [m]	–0.46	–0.13
Thickness of alluvial clay [m]	**–0.68**	**–0.36**
F	**0.49**	**0.45**
R	0.22	–0.45
N	–0.22	0.05
alt.moist	**0.72**	**0.27**
flood	0.29	0.25

1 (203001 and 153003) represent the maximum difference in species composition in the data set, with a complete species turnover (Hill & Gauch 1980), i.e. having no species in common. Vegetation plots on the positive side of the first axis are characterised by wet indicator species (e.g. *Filipendula ulmaria, Lysimachia vulgaris, Stachys palustris*), whereas those on the left feature rather mesic or dry indicator species (e.g. *Achillea millefolium, Arrhenatherum elatius, Daucus carota, Odontites vulgaris*). The most abundant plant species are distributed in the ordination space accordingly, as shown in Figure 4. The phytosociological classification represented in Figure 3 confirms this pattern. Regarding the data points along the first axis in terms of the quantity of their Ellenberg indicator values (Fig. 4), the plots 153001, 153002 and 153003 show relatively high average values of wet indicators, flood indicators and alternating moisture.

Consequently, DCA axis 1 suggests differences in moisture. As explained by Zelený & Schaffers (2012), small differences in Ellenberg indicator values should be interpreted with caution because of statistical dependencies. Both the comparison of the phytosociological classification and the averages of the Ellenberg indicator values of moisture confirm the assumption of axis 1 representing different moisture conditions. Hence, the next section tackles the question if the four abiotic variables investigated have a significant statistical impact on the varying moisture.

The second ordination axis is more difficult to interpret. Alongside DCA axis 2 of Figure 3, a coarse differentiation of the classified plant communities, i.e., *Silaum silaus*-communities at the lower part and *Arrhenatheretum elatioris* at the upper part, can be observed. Thus, this axis confirms, at least partially, the differences of the phytosociological classification.

4.3 Role of considered environmental variables

The positive correlation of the least cost path to the next water body with the first DCA axis, assuming it describes a moisture gradient, would mean that moisture increases with increasing distance from rivers or clay ponds. Crucially, while Hughes (1997) also found that the distance from an active river channel influences plant species composition in floodplains, his findings showed a decrease in moisture the larger the distance from the river. In this vein, it must be mentioned that the correlation between the distance to the next water body and the first ordination axis is not significant and that periodically water-bearing bodies, such as many of the clay puddles, were not considered in the calculation. To better understand these contrasting differences in findings between previous studies and current results, it is important to consider the anthropogenic modifications of the topography and hydrological balance when investigating vegetation patterns in the meadows. The water management of the 'Papitzer Lachen', consisting of the Weiße Elster, is regulated by an intake structure since 1997 and was modernised in 2016 to flood the water ponds from March to August to provide excellent amphibian spawning habitats (Vlaic et al.

2017). This water management should also lead to a localised increase of the groundwater level in the surroundings of the water bodies. Only in these rare wet years we have the influence by direct overbank flowing from the Weiße Elster or indirect flooding through seepage water during high discharge of the Neue Luppe. But this happened last time in 2013. The groundwater table below the meadows would probably be deeper without the artificial flooding of the water ponds.

It can be assumed, that despite the aforementioned methodological limitations, former intensive grassland management and insufficient flooding and groundwater dynamics in the meadows is the main reason for the non-significant correlation outcome in the present results. Looking further into the water management structure of the area, it must be considered that consequently, scenarios of low water levels or flood stages that can trespass the riverbanks arise only when there are extreme discharges. Thus, on the one hand, the influence of the nearly non-existent lateral water overflow, i.e. physical disturbance, inundation, nutrient transport, erosion and sedimentation processes, no longer occurs. On the other hand, occurrences of mesic species such as *Arrhenatherum elatius, Daucus carota* and *Veronica chamaedrys* suggest a prolongation of dry phases. Due to these factors, the floodplain meadows underlie complex and ongoing processes of change.

Another pivotal factor to take a closer look at is the groundwater-surface distance. Although the elevational gradient on the investigated floodplain meadows ranged only across 1.83 m, the main variation in the species composition shows a significant negative correlation to the terrain elevation. Plots on the right side of Figure 3 are mostly located at a lower elevation than those on the left side. *Arrhenatheretum-elatioris*-meadows, which typically tend to colonise elevated sites, and wet meadows that develop in lower areas (Dierschke 1997), are distributed accordingly. Thus, wetness increases with decreasing ground elevation, assuming DCA axis 1 describes a moisture gradient. Titus (1990), who investigated a floodplain swamp in Florida with a comparable elevational range, comes to a similar conclusion, with ground elevation strongly influencing plant seedling distribution. Titus further states that the elevation determines the duration of inundation and the substrate moisture content. Given that inundation in the surrounding of the 'Papitzer Lachen' is reduced, the influence of the groundwater-surface distance on soil moisture is the most explanatory factor of vegetation patterns. Other studies, albeit analysing different types of vegetation and in different climatic zones, also found that the "elevation of the terrain is for most species the best predictor explaining their absence and presence" (Wassen et al. 2003: 36). Elevation and the derived groundwater surface distance frequently explains the largest proportion of the deviance in vegetation data and thus, essentially influences the spatial distribution of vegetation communities in floodplains (Fernández-Aláez et al. 2005, Hughes 1997, Scholz et al. 2009, Verrelst et al. 2009, Wassen et al. 2003). Species tolerant to flooding and physical disturbance are usually found at lower elevations, whereas less flood resistant species are higher located (Henle et al. 2006, Hughes 1997). Although the results of other studies confirm that ground elevation and groundwater-surface distance are the main environmental drivers patterning floodplain vegetation, clustering plant communities only based on their position in the ordination space is not always sufficiently precise (Verrelst et al. 2009). This is also the case in the present study.

The groundwater is heavily influenced by the artificial water feeding of the clay ponds from the White Elster via an intake structure. It is responsible for differences in wetness, which is reflected in the species composition. Plots closer to the groundwater contain species such as *Phragmites australis* and *Carex acuta*, while for example *Arrhenatherum elatius* or *Daucus carota* colonise terrain with greater depth to the groundwater table. Stromberg et al. (1992, 1996) investigated the relationship between groundwater-dependent vegetation traits and groundwater-surface distance. According to their results, vegetation becomes increasingly stressed with increasing distance to the groundwater and vegetation closer to the groundwater table features taller statures, larger canopy volumes and larger leaflets. The study area (Arizona, USA) indeed showed larger fluctuations of groundwater-surface distances compared to the 'Papitzer Lachen', however, the results can be transferred to smaller scales. Consequently, groundwater depletion is a pivotal variable to be considered when examining vegetation structures. As explained before, groundwater withdrawal takes place by the Neue Luppe River during low water periods, thus constituting an important factor in explaining species distribution. According to Stromberg et al. (1996), a predicted response to groundwater decline is a sequential ceasing of riparian flora, which can also be observed in the floodplain meadows around the 'Papitzer Lachen'. In more pristine floodplain systems, the groundwater level, and with it the vegetation, depend more on the water level of surrounding rivers (Hughes 1997). This means that water levels of the Neue Luppe and Weiße Elster would be another important hydrological variable to consider. Consequently, other factors such as management practice, (historical and present) rainfall, soil moisture, soil structure or nutrient content, which is not investigated in this work, are likely to show a greater impact on the vegetation (Ludewig et al. 2014).

The thickness of the alluvial clay layer shows a highly significant correlation to the first DCA axis and thus also explains a large proportion of variability in the recorded vegetation data. Obviously, besides other substrate types and their particle sizes, it is responsible for plant-available water in the soil. Several of the studies mentioned addressed this topic in addition to elevational aspects. Although the soil moisture content could not be measured directly in our study, the thickness of the alluvial clay, ground elevation and groundwater-surface distance contribute to the soil moisture and can therefore be seen as proxies in explaining variability in the data set alongside the first axis in the ordination space. It is important to mention that these variables are correlated with each other, which can be observed in Figure 3. The vectors describing correlations with ground elevation, groundwater-surface distance and thickness of alluvial clay all point in similar directions and have similar lengths. This means that their values change along the same site scores of the DCA. The correlation matrix in Appendix 2 confirms a statistical correlation between terrain elevation, groundwater-surface distance and thickness of the alluvial clay layer. Hence, these variables must not be evaluated independently. As shown in the results, none of the environmental variables considered could be related significantly to the second DCA axis. The reason for this may be that the first axis describes a gradient in moisture. As all four variables regarded are also related to moisture circumstances, the other axes must be interpreted with different environmental criteria.

4.4 Other relevant geographic factors

Another important factor that has not been considered quantitatively is soil substrate underlying the alluvial clay. Substrate influences the vegetation composition as it constantly interacts with the water and nutrient balance (Hughes 1997). The type of substrate and its grain size have a significant impact on the storage capacity of water in the soil. The nutrient balance improves the more clayey the substrate and has eminent effects on plant species competition (Keddy et al. 2000). Härdtle et al. (2006) studied floodplain meadows of the Elbe valley and found that the phosphate supply in the soil strongly influences vegetation richness and composition. For instance, with increasing phosphate supply, productivity, and with it competition for light, increases. As a result, the abundance of graminoids rises and often floodplain-characteristic low-growing species decrease or vanish (Grevilliot et al. 1998). To better understand the vegetation in the floodplain meadows 'Papitzer Lachen', the soil substrate and nutrient balance must be studied in more detail.

Aspects of land use are also crucial for the vegetation composition (Härdtle et al. 2006). In the study area, the predominant use today is mowing (twice a year). On the classified *Arrhenateretum-elatioris*-meadows, however, the former grazing can still be clearly identified. In the past, these areas were eutrophic pastures (*Lolio-Cynosuretum*) without mesotrophic species such as *Daucus carota* and *Picris hieracioides*. Species recorded in this work, such as *Agrimonia eupatoria* and *Daucus carota*, indicate a more extensive use today. The conversion from grazing to mowing already occurred 20 years ago (Teubert, personal communication, 2022), but these areas are still in a kind of intermediate stage, denoted by occurrences of *Picris hieracioides*. The result of the DCA also indicates different land use. Besides the explained differences in moisture, the plots on the far right side of DCA axis 1 in Figure 3 are mown once a year, whereas the remaining ones twice a year. Therefore, the plots on the far right end of DCA axis 1 are rather a meadow fringe ("*Veronica-longifolia*-saum"), which would develop into a *Cnidion-dubii*-meadow if mown twice a year. In addition, these plots differ from the others due to their isolated location. They are, in a sense, a peninsula surrounded by clay ponds and former stream beds, which can be observed in Figure 1-b (three Southernmost red squares close to each).

4.5 Limitations

In the analysis of the influence of the least cost path to water bodies, we only considered permanently water-bearing puddles that the provided land use data from Saxony's State Office for Environment, Agriculture and Geology contains. However, many of the puddles carry water periodically (especially in spring) and thus have an influence on the vegetation at this time. The factor of the artificial flooding of the ponds and indirectly on the vegetation could not be considered in this work. Similarly, the role of grassland use and management history of the grassland could not be investigated in a sufficiently differentiated way in this article, but their influence overlay the results.

Given the relatively low sample size of 20 plots, any generalisations derived from the data should be approached with caution. The number of plots may not adequately represent the full range of vegetation patterns and environmental conditions.

5 Conclusions

The results highlight the disturbed hydrological regime due to anthropogenic river regulation and with it the absence of direct flooding and a severe drought of the last years. The proximity to water ponds and rivers was not as significant because of a smaller amplitude of water levels due to river regulation and drought. Rivers no longer inundate their floodplains and poor water availability due to long-lasting drought events are present (Schnabel et al. 2022, Wirth et al. 2021). Therefore, other factors such as historical or present grassland management or soil substrate obtain more importance for vegetation patterns. The history of different grassland management overlays the results but could not be reconstructed in a sufficiently differentiated way. However, the conversion from grazing to mowing in the past is clearly visible in the vegetation records. On account of these changes, the floodplain meadows surrounding the 'Papitzer Lachen' are in a state of flux. Since it is impossible to restore the pristine hydrological conditions, practical approaches to regain or preserve the flood meadow biodiversity as well as provided ecosystem services could mean the creation or restoration of distinct mesic meadows (John et al. 2016, Kirmer & Tischew 2014, Sengl et al. 2017) or restoration of confluences, i.e., partial revitalisation of former stream beds.

Future research is essential for a comprehensive understanding of dynamics in ecosystems that evolved under anthropogenic land use. It should assess management implications, especially the impacts of human interference in balanced systems, to guide sustainable management practices. Additionally, dynamics and effects of lower ground water tables resulting from droughts and heatwaves should be investigated, e.g. using for the area coupled models for groundwater and surface water or at larger scale taking the UFZ's drought monitoring as a starting point (Zink et al. 2016). This holds the potential for future accurate long-term predictions in response to climatic change-induced droughts, and facilitating proactive restoration measures for effective water resource management. To meet the challenging of the impact of drought and future restoration initiatives in this area, hydrological and botanical monitoring of these valuable grasslands is a prerequisite.

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Data availability

The data used as well as the R script for reproducing our results can be accessed under github.com/lk-erz/Papitzer-Lachen---Patterns-of-plant-species-composition.

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Appendix

Appendix 1: In floodplain meadows 'Papitzer Lachen' recorded vegetation data (June – August 2022).

Species / Plot	143001	143002	143003	153001	153002	153003	163001	163002	173001	173002	173003	183001	193001	203001	213001	223001	233001	243001	253001	263001
Acer campestre				r	+	1														
Achillea millefolium	1		+				+	1	1		+	+	1	2a		1	2b	1	1	
Agrimonia eupatoria	1				+		+	+					+	+		2a	2a	1	+	r
Agrostis capillaris	1	1	2a					+		+	+	1	+		1	1		r		
Agrostis stolonifera											1									+
Ajuga reptans													+							
Alopecurus pratensis	2a	2a	2a	2a	1	1	2a	1	+	+	2a		1		1			1	+	+
Arctium lappa		r																		
Arrhenatherum elatius	2b	2a	1	2a	+		1	3	2b	+	1	2a	2a	2b	2a	3	2b	1	1	+
Bellis perennis											r									
Bistorta officinalis		+																		
Calamagrostis epigejos				2a	3	1											1			
Calystegia sepium				+	r	1														
Campanula patula	+								+				+	+	+					
Cardamine pratensis											+									
Carex acuta				2a		4														
Carex disticha				+	r															
Carex hirta							2a			+										
Carex otrubae				+																
Centaurea jacea	1		1				+	2a	+			+	+	+	1		2a	1	1	r
Cerastium glomeratum																		+		
Cerastium holosteoides	+		+				+	+	+				+		+				r	r
Cichorium intybus																r				
Cirsium arvense			+	2a	+	+	+	+	+		+	+	+	+	2a	1	2a		+	r
Convolvulus arvensis			+														+			
Cornus sanguinea					r															
Crataegus monogyna				r																
Crataegus x media					+															
Crepis biennis		+	+														+			
Crepis capillaris															+					
Dactylis glomerata	+	+	+	2a	+			+		+	+	+	+	1	1	1	+	2a	1	
Daucus carota	2a		1	+			+	2a	1		r		2a	4	1	1	3	3	1	r
Deschampsia cespitosa		+	+	2b	r		2b	1		1	+	+	2a	+	2a	2b	1		4	3
Elymus repens					+				1		+									
Equisetum arvense									+	2b	2b	+	+		2b	+	+			
Equisetum palustre							1	+	+	2a		1	2b	1	+	1	+		+	2a
Euphorbia cyparissias	+																			
Festuca ovina								+												
Festuca pratensis et arundinacea	2b	2a	1				2a	+	2a		3	3	2a	2a			1	2b	1	2a
Festuca rubra	1		+				1	2a	1		+							+		
Filipendula ulmaria		+		1	r	+														
Fragaria viridis	+			2a	3	+														
Fraxinus excelsior					+															
Galium aparine															+					
Galium boreale		+	+	1			+													
Galium mollugo	1	+	+	1	1		+	+	2a		+	2a	1	1	2a	2a	1	1	+	+
Glechoma hederacea	1			1		+		+	1		+	1	+	+	+		+		+	1
Glyceria maxima										2b										
Heracleum sphondylium								r	+				+	1		+				
Holcus lanatus	+	+	1	+			3	+	1	1	2b	1	2a	2a	1	1	1		3	3
Humulus lupulus				+		+														
Hypericum perforatum		r			r									+	+			r		
Hypochaeris radicata														+						
Iris pseudacorus						+														
Juncus effusus										1	1									+
Lathyrus pratensis	1	+	1		+		+	+	+		+	+	+				+	+	1	+
Linaria vulgaris				1	+															
Lotus corniculatus							2a							+						
Lysimachia nummularia		+		1				r			+									r
Lysimachia vulgaris				2b	2a	2b														
Lythrum salicaria				+	+	+				+										r
Malus sylvestris					+													r		
Odontites vulgaris	1	2a	2a		r		+	+	1		+	1	2a	2b	1	1	2a	2a	1	+
Persicaria amphibia						r	+	+			2b				r	+			+	
Phalaris arundinacea	r		+	1		2b	+			2b	+									
Phleum pratense	+	1	2b				2a	+	+	+		+	+		+	+		+	+	
Phragmites australis						2a														
Picris hieracioides	1						+					+			+			r		
Pilosella spec.																	1			
Pimpinella major							+	+	+					+			+			
Plantago lanceolata	+	2a	1				1	1	1	1	2a	1	2a	1	+	+	+	+	+	2b
Plantago major	r		r																	
Poa palustris						+	1			1										
Poa pratensis	2a		1				1	+	+		+	1								
Poa spec.				1	+													2a	1	2a
Poa trivialis		+	+							+		+	+				+			
Potentilla anserina							+													
Potentilla reptans	1	2a	3		+								1					1	1	
Prunella vulgaris	+						+	+	r		+	+	+	+		+	+	+		
Prunus spinosa				2a	r															
Quercus robur		r	r	r																
Quercus spec.					+															
Ranunculus acris	1	2a	1					r	+	r	+	+	+					+		+
Ranunculus repens	+	+	+				+	r	+	r	+	+	+					r	+	+
Rosa canina																+				
Rosa spec.					+															
Rubus caesius				1	1	+											+			
Rubus sect. Rubus				+																
Rumex acetosa				1	+					r	r	1	+	1	+	+			1	
Rumex crispus			r																	
Sambucus nigra			r																	
Sanguisorba officinalis		+	1	2a	+		+						1							
Selinum carvifolia					r			r												
Silaum silaus	1	+	1				+		+			1				r		+		+
Silene flos-cuculi				r	+		r													
Solidago canadensis																	+			
Stachys officinalis	r																			
Stachys palustris				1	+	1														
Stellaria graminea							+	+	+											
Symphytum officinale				1	r	r	+	+		+			+						+	1
Taraxacum sect. Ruderalia	+	1	1				+	r	+	+		+	+	+	r	+	+	+	r	
Thalictrum lucidum				1	r	r														
Torilis japonica				+																
Trifolium dubium									r											
Trifolium pratense	1	1	+				+	+		+	+	1	+	2a			+	+		r
Trifolium repens	+	+	+				+	r	+											
Typha angustifolia										+										
Urtica dioica				r		r				+										
Valeriana officinalis				+	+															
Veronica chamaedrys	1	1	+	+	+			+	1			1	1	1	1	1	1	1	+	
Veronica longifolia				1	r															
Veronica serpyllifolia	+							+						+	+		+			
Vicia cracca				+	r						+			+						
Vicia sepium	+						1	+			+	+	+	+	+	r			1	1
Viola hirta	+												+							
Viola odorata					+															

Appendix 2: Correlation matrix of the intercorrelations of the environmental variables (elev = terrain elevation, clay_mean = thickness of alluvial clay, gw_mean = groundwater-surface distance, lc = least cost path to next water body).