



Biodiversity changes in the Lower Havel floodplain near Gülpe, Germany. How adapted land and water management influence grassland vegetation over 40 years

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Abstract Floodplains are known to be hotspots of biodiversity, but are threatened due to water regulation and land-use practices by humans. The Gülpe case study on the Havel River in Germany offers a valuable opportunity to analyze the change in plant diversity and habitat function due to a transition from intensive agricultural management to an extensive management aligned with Natura2000 goals over the past 40 years. This study compiled a vegetation survey of 407 plots based on a vegetation survey conducted in 2020, combined with three previous surveys spanning several decades in the same floodplain. For each plot, plant diversity (number of species, Shannon Diversity Index) and further indicators of rareness (Red List species), of representativeness (river corridor plants), and of hemeroby (neophytes) were calculated for the total dataset and a stratified grassland dataset. Non-metric multidimensional scaling was performed to obtain deeper insights into temporal changes of species composition and selected species. Hydrological data and information on agricultural practices as well as Ellenberg Indicator Values were compiled to gain information on habitat function. The results show that the Gülpe floodplain exhibits high plant diversity, though species composition has changed significantly in recent decades. The number

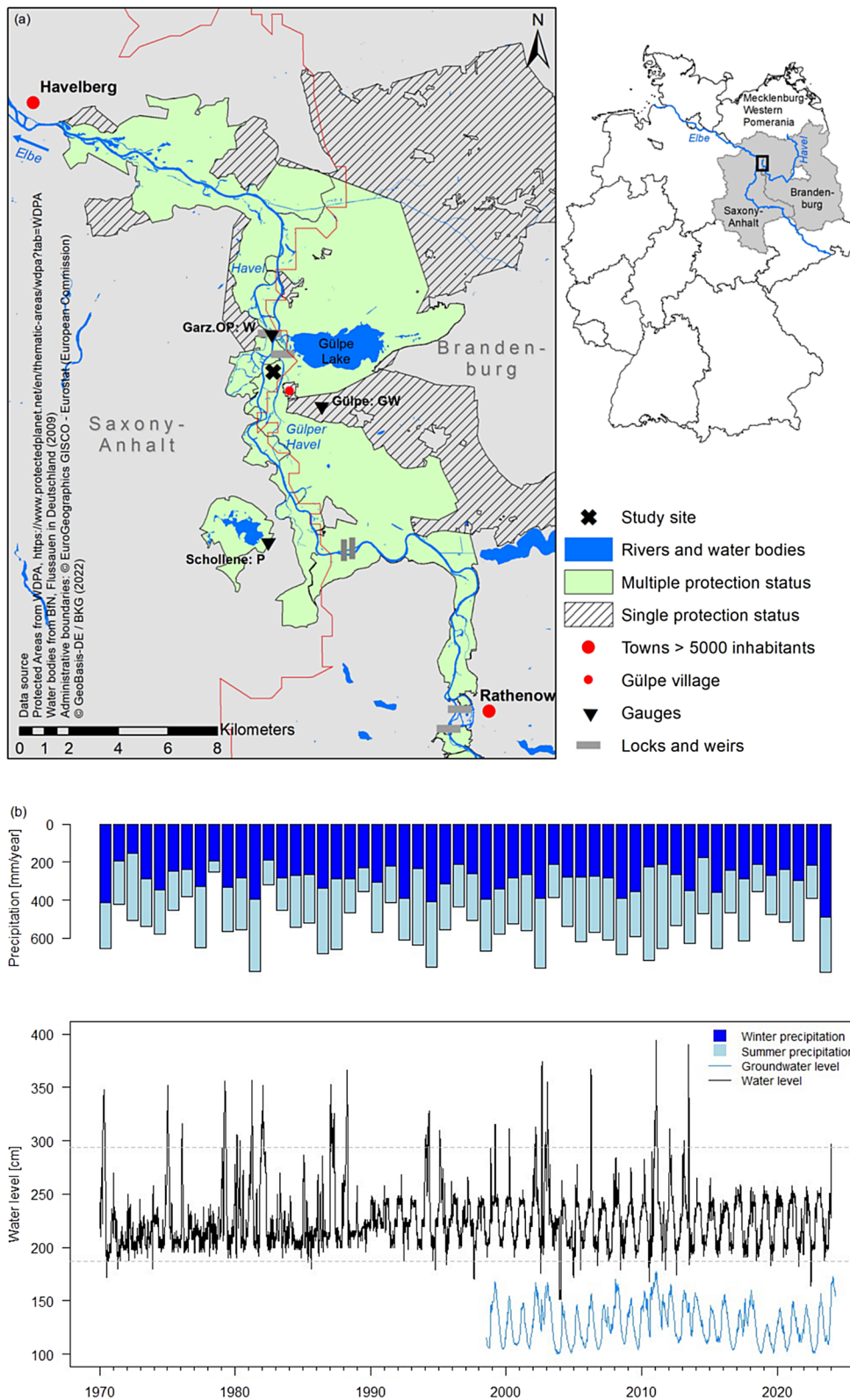
of river corridor plants and Red List species remain at a high level. The indicator species *Selinum dubium* (former *Cnidium dubium*) of the Natura2000 Habitat Type *Cnidion dubii* appeared at the study site in 1995 and has since established widespread populations, indicating that the land-use extensification has supported the reestablishment of important habitat functions in Gülpe.

Keywords Environmental history · Plant diversity · Meadows · Natura2000 · Grassland management · Inundation

Introduction

Floodplains provide humans with a remarkable number of ecosystem services (ES) (Scholz et al. 2013; Stammel et al. 2022). While biodiversity itself is not universally classified as ES (Costanza et al. 1997; Haines-Young and Potschin 2010), it is recognized as the foundation of several ES (MEA 2005) and plays a role as a regulator of underlying ecosystem processes (Mace et al. 2012). Therefore, habitat provision is identified as ES in other literature (Scholz et al. 2013; Fischer-Bedtke et al. 2020), as it forms the foundation for biodiversity and facilitates other ES. The conservation of biodiversity in general and the protection of floodplain-specific habitats in particular is of paramount importance for the long-term functioning and resilience.

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◀**Fig. 1** **a** Location of study site in Germany and in relation to the borders of federal states Saxony-Anhalt and Brandenburg (red line). **b** Annual precipitation sums (P) at gauge Schollene: P are separated in time, when the Havel is under summer regulation (May – September; light blue) and winter regulation (October – April; blue). Daily water levels (W) of the Garz. OP: W gauge (black line) recorded in cm relative to the gauge zero point in m above Normalhöhennull (NHN—according to the Deutsches Höhenreferenzsystem 2016—DHHN 2016, comparable to meter above sea level a.s.l.), with groundwater levels (blue line, Gülpe: GW) in m above NHN and markings of high and low water levels (dashed line), according to the Wasserstraßen- und Schifffahrtsverwaltung des Bundes (WSV)

Floodplains, the area of land adjacent to a river which experiences flooding during periods of high streamflow, in general represent centers of biodiversity (BMUB and BfN 2015), as the alternation of flooding and dry phases creates a variety of microhabitats (Tockner and Stanford 2002), each hosting specialized communities of flora and fauna (Naiman and Décamps 1997; Ward et al. 1999). Hence, floodplain ecosystems fulfill important habitat functions for plant species including plant species restricted exclusively to floodplain ecosystems (Burkart 2001).

However, despite their importance floodplains have been degraded in Europe for centuries (EEA 2016), with up to 90% lost along the large rivers in Germany (BMU and BfN 2021) due to river regulation. The remaining floodplains, including the Havel floodplain where this study is set, are predominantly used for agriculture, while floodplain forests, which should cover more than 90% of recent floodplains in Germany, occupy only 8% of frequently inundated floodplains (Natho 2021).

Historically, intensive agricultural practices, including draining and fertilization, transformed much of the area into arable land. After the German Democratic Republic (GDR) era, land use in the study site shifted to more extensive management aligned with Natura2000 goals, focusing on species and habitat conservation. The floodplain, part of a designated nature reserve, Natura2000 site, and Ramsar site, is classified as the endangered Habitat Type (HT) *Cnidion dubii*. Regular mowing has maintained species-rich meadows, which serve as valuable habitats and prevent succession to scrub or forest (Ellenberg and Leuschner 2010)—a process that would otherwise lead to reduced biodiversity (Haase 1995). However, its characterization as endangered Habitat Type *Cnidion dubii* must not be discarded.

Therefore, its protection, monitoring, and development according to Natura2000 requirements (European Commission 2019) need to be implemented, harmonizing demands of navigation, food production, nature conservation, and recreation. The floodplain considered here offers a unique possibility to compare four vegetation surveys at the same site over the past 40 years and the effects of different environmental conditions on the habitat function of a near-natural grassland floodplain.

The objective of this study is to quantify the habitat function of the floodplain near Gülpe by means of indicators for rareness, hemeroby, and representativity as well as by Ellenberg Indicator Values (EIV). Consequently, the research will address the following questions:

- (1) How species-rich is the Havel River floodplain and especially the potentially area of *Cnidion dubii* meadows?
- (2) How has the plant diversity and plant composition changed over the past 40 years?
- (3) In addition to changes in agricultural management, are there also changes observable in water management and climate that might affect biodiversity and habitat function?

Material and methods

Study site

The study site "Gülpe floodplain" is located in north-eastern Germany, on the border of the federal states of Brandenburg and Saxony-Anhalt (Fig. 1a) in the vicinity of the village Gülpe at river km 128 of the Havel, a lowland river. This region is characterized by a continental temperate climate. Several weirs are located along the entire length (334 km) of the Havel River from its origins in the federal state of Mecklenburg-Western Pomerania, through the states of Brandenburg, Berlin, and Saxony-Anhalt, ultimately discharging into the Elbe River (Fig. 1a). The long-term average streamflow at the Havelberg gauge, located approximately 25 km downstream of Gülpe, is 105 m³/s (BfG 2024). The low gradient of only 40 m from the source to the mouth of the Havel River results in very slow flow velocities and

high groundwater levels (Promny et al. 2021). Especially between Rathenow and Havelberg, six locks and weirs further reduce the flow velocity along the Lower Havel River (WSA Spree-Havel 2024; see Fig. 1a).

The Havel River used to be a federal waterway, but commercial ship traffic was prohibited in 2008. The largest restoration project in Europe, encompassing an area of approx. 9,135 ha, is currently carried out in the Lower Havel. In 2015/16, four measures were implemented in the Gülpe floodplain to enhance lateral connectivity (NABU 2023). These measures included the removal of embankments (construction of flood troughs) and the dismantling of revetments (NABU n.d).

Current flooding situation

The size of the study site is 110 ha, situated between the Gülpener Havel and the Havel River (see Fig. 1a), not too far from where the Havel empties into the Elbe River. As a result, in case of a large Elbe flood, floodwater from the Elbe River is diverted into the Havel River, leading to widespread inundation of floodplains as experienced in 2002, 2006, and 2013, even though the Havel itself rarely experiences its own floods. However, flooding of the Gülpe floodplain occurs regularly between November and April due to a weir management regime allowing higher water levels during this period (WSA Spree-Havel 2021). The goal of these winter water levels is to allow inundation of floodplains – as a result of intensive yearly discussions between representatives of water authorities, farmers, and the nature conservation organization NABU's advisory board (WSA Spree-Havel 2024). Depending on water availability, some very low-lying areas might still remain connected until May.

Historical and present agricultural use

The Lower Havel floodplains have been a cultural landscape for centuries (Haase 1995). Intensive agriculture was practiced until the late twentieth century. Thus, several hydro-engineering measures in the Lower Havel region, along with land melioration activities from the 1960s to the 1980s, have led to lowered groundwater levels and a decline in surface water areas (Zielhofer et al. 2022). At least until 1988,

land use and fertilization in the floodplain near Gülpe was still being intensified, accompanied by drainage measures. This led to faster removal of floodwaters, eutrophication of water bodies, high grazing pressure, and mowing multiple times per year (Fischer 1989). Until 1999, larger parts of the lower-lying Gülpe floodplain were still used for grazing, while potatoes were cultivated in higher-altitude regions (Ecological research station Gülpe, personal communication in January 2024). Since 2000, however, the floodplain is part of the Natura2000 network (site 3239–301) with the protected HT 6440 (*Cnidion dubii* meadows). The current management practice involves mowing the study site twice a year, with restrictions in place to protect ground-nesting birds by prohibiting mowing before June 15th (MUGV and LUGV 2016).

Comparative vegetation data

Four vegetation surveys were conducted at the study site over the past 40 years (Table 1). The first survey took place in 1981/82 (Fischer_82), followed by a survey conducted by Burkart from 1993 to 1995 (Burkart_95). Wesche conducted a survey in 2008 (Wesche_08), and the most recent survey was conducted in 2020 (Kra_20). Analogue vegetation data were provided for the Fischer_82 (personal communication) and Burkart_95 survey (Burkart 1998), while digital vegetation data were available for the Wesche_08 survey (provided by Wesche, personal communication in October 2019).

The surveys Fischer_82, Burkart_95 and Kra_20 were conducted using the Braun-Blanquet method (Dierschke 1994); Wesche_08 used the Londo scale (Londo 1976). However, no additional information is available regarding Fischer_82's surveying methods. The vegetation surveys differ in the length of survey periods (between one and three years and two to five months each year), number of plots (between 22 and 239), and plot sizes (see Table 1). Additionally, the vegetation surveys of Burkart_95 and Wesche_08 covered a larger area than the study site depicted in Fig. 1a. Considering the plots in the Gülpe floodplain only reduced the number of plots from 377 to 61 in Burkart_95 and from 46 to 22 in Wesche_08 as reported in Table 2. Coordinates of plots were available for the vegetation surveys from Wesche_08 and the survey conducted for this study (Table 1). Since

Table 1 Summarized characteristics of vegetation surveys conducted at the study site in the past 40 years

Name of survey	Fischer_82	Burkart_95	Wesche_08	Kra_20
Year	1981, 1982	1993, 1994, 1995	2008	2020
Surveyor (reference)	Fischer (unpublished)	Burkart (1998)	Wesche et al. (2012)	Kra (this study)
Survey period	1981/82, month unknown	May – September 1993, 1994, 1995	June, August 2008	May, June, August 2020
Number of plots	239	61	22	85
Plot size [m ²]	3–400	5–50	15–25	10
Coordinates available	No	No	Yes	Yes
Considered flora	Vascular plants	Vascular plants, bryophytes	Vascular plants	Vascular plants, bryophytes
Processing steps of data preparation for this analysis	Digitalization of data and map; Homogenization of head data and monitoring data	Digitalization of data and map; Homogenization of head data and monitoring data	Homogenization of head data and monitoring data	Homogenization of head data and vegetation survey

bryophytes were not recorded in all studies, they were excluded from the Burkart_95 and Kra_20 datasets.

Burkart (1998) explicitly stated that the plots were selected non-randomly in the field and assessed only once during the total survey period. This approach resulted in an over-emphasis on sites with occurrences of *Selinum dubium* (formerly *Cnidium dubium*) (Burkart 1998). In contrast, the Wesche_08 survey attempted to resample the plots established by Burkart_95 in grassland stands and supplemented them with a set of stratified randomly selected sampling points in areas that were formerly grassland, based on earlier vegetation maps (Wesche et al. 2012). The selection of the 85 plots surveyed by Kra_20 is described in detail in the following section.

Fieldwork

The fieldwork for the survey Kra_20 was conducted between May and August 2020, with the objective of recording the change in plant diversity of the study site in comparison to past vegetation surveys.

The initial task was to relocate and resurvey the plots originally established by Burkart (1998), which had been permanently marked with buried magnets. Despite having georeferenced aerial imagery from Burkart and extracted corresponding GPS coordinates, only three plots could be successfully identified. To overcome this limitation, the study design was adapted and followed the methodology of Burkart's (1998) vegetation survey by

choosing representative plots along elevation gradients. Using vegetation unit maps from Fischer (1989) and Burkart (1998) as well as a high-resolution Digital Elevation Model (1 × 1 m; Landesvermessung und Geobasisinformation Brandenburg (LGB 2021)), 85 new plots were randomly allocated to represent the diversity of vegetation units and environmental conditions across the study area. The selection emphasized mesic zones, while also capturing the wet and dry zones within the flood gradient, following the approach by Burkart (1998). In two areas, plots were positioned to reflect the flood troughs created by (NABU n.d) (Fig. 2), ensuring a short spatial distance between elevation gradients.

Vegetation was surveyed in all 85 plots using the Braun-Blanquet method (Dierschke 1994), employing a consistent plot size of 2 × 5 m. Each plot was oriented with the 2 m extent to the north. To facilitate long-term monitoring, new plots were permanently marked with buried magnets at their centers, with their positions recorded via GPS. For each plot, vascular plant species and bryophytes were recorded, alongside additional parameters such as plant cover and height.

The survey commenced in May 2020 with the drier regions, as access to the wetter areas was not possible due to flooding. In June, efforts were redirected to surveying the wetter areas as access improved. The vegetation survey was suspended after June 15th when the whole area was mowed. Three remaining plots were surveyed after the regrowth of vegetation

Table 2 Summary of species information and indicators for diversity, rareness, representativity, hemeroby and mean Ellenberg Indicator Values (EIV)

		TOTAL	Fischer_82		Burkart_95		Wesche_08		Kra_20	
Dataset			Total	GL	Total	GL	Total	GL	Total	GL
Plot size [m ²]			3-400	3-25	5-25	5-25	15-25	15-25	10	10
Number of plots		407	239	26	61	30	22	20	85	33
Sum of plot size [m ²]			7495	339	677	324	365	335	850	330
Plant diversity	Number of species	308	246	135	148	111	123	117	181	119
	Chao Index		273	232	166	121	166	144	243	160
	Bootstrapped Index		267	161	162	123	139	132	204	135
	Mean Shannon Diversity Index		1.39*	1.47*	1.85	2.15	2.73*	2.79*	1.87	1.92
rareness	Number of Red List species	102	78	38	39	32	35	35	47	29
	Number of plant species occurring exclusively in that survey		81	19	9	8	11	8	35	9
representativity	Number of river corridor plants	36	23*	15	18	16	19	18	19	11
	Number of plots with <i>Selinum dubium</i> (<i>Cnidium dubium</i> ; percent)		0 (0)	0 (0)	11 (18)	11 (36)	13 (59)	13 (65)	21 (25)	11 (33)
	Number of plots with <i>Holcus lanatus</i> (percent)		14 (6)	2 (8)	4 (6)	4 (13)	10 (45)	10 (50)	48 (56)	25 (75)
hemeroby	Number of neophytes	7	2	2	3	2	3	3	5	2
Ellenberg Indicator Values	Mean EIV_N		5.8	6.1	5.7	5.8	5.6	5.6	5.1	5.4
	Mean EIV_R		6.4	6.4	6.2	6.3	6.3	6.3	6.1	6.3
	Mean EIV_F		7.3	6.6	7.1	6.7	6.6	6.6	6.4	6.5

The table includes data for all four surveys and for the entire dataset (Total) as well as for the stratified grassland dataset (GL – bold values)

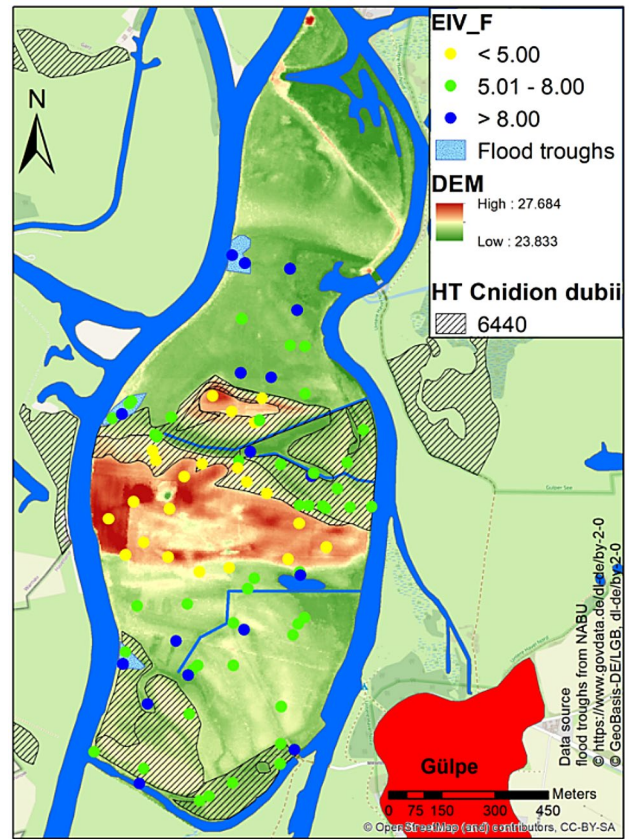
Values marked with an asterisk (*) indicate significant differences from the other surveys (significance calculated at plot level using Kruskal–Wallis H-test with Bonferroni-adjusted pairwise Mann–Whitney U-tests, $p < 0.05$)

in August 2020, and plots previously recorded were revisited with the aim of identifying previously undetermined plant species.

Data processing and analysis

The vegetation tables and analogous vegetation unit maps from Fischer_82 and Burkart_95 were

Fig. 2 Map of the 85 plots of the Kra_20 survey illustrates the differentiation according to Ellenberg Indicator Value for moisture (EIV_F) and the visualization of the HT *Cnidion dubii* (shaded areas) based on the DEM of the state of Brandenburg (LGB 2021)



digitized. The maps were geo-referenced in the ESRI geo-information system ArcGIS (Version 10.3). Vegetation data from all past and current vegetation surveys, encompassing a total of 407 plots, were stored in the TurboVeg 2.0 database software (Hennekens and Schaminée 2001). R version 4.2.2 was used for all statistical analyses. The taxonomy of the data was standardized to the universal electronic reference list for the German flora, GermanSL (Jansen and Dengler 2008), using the R-package vegdata (Jansen and Dengler 2010). Nevertheless, several plant names still required manual adjustment. The vegetation tables from Fischer_82, Burkart_95, and Kra_20 required conversion of values from cover abundance scales (Braun-Blanquet) to percentage cover. EIV were also obtained from GermanSL, and mean values were calculated for each plot to describe the habitat function. Here, EIV_F reflects soil moisture preferences, EIV_N nutrient preferences, and EIV_R soil pH preferences. EIV were used to capture the environmental conditions at the time of the vegetation surveys.

Species accumulation curves (Rosenzweig 1995; Hill et al. 1994; Dengler 2009) were generated using the "specpool" function in R (package vegan) to facilitate comparisons of species richness across the four vegetation surveys with varying plot numbers and sizes (Fig. 6a, Appendix).

To further address the issue of differing plot sizes and environmental conditions, the cumulative plot area for each survey with EIV_F values between 5 and 8 was calculated to facilitate comparisons of the same habitat types. Among the surveys, Burkart_82 had the smallest cumulative area (324 m²). To ensure comparability, plots from the other datasets (restricted to ≤ 25 m²) were randomly selected until the total area matched that of Burkart_82. This standardization minimized the influence of plot size differences on subsequent analyses and led to the creation of a stratified grassland (GL) dataset.

With this refined dataset, detailed analyses of changes in vegetation were conducted, providing robust comparisons across all four vegetation surveys (Fischer_82, Burkart_95, Wesche_08 and Kra_20).

Comprehensive analyses were performed using both the total dataset and the GL dataset. Since the data on plot base were non-normally distributed, the vegetation data were analyzed using Kruskal–Wallis H- tests with pairwise comparisons using Mann–Whitney U tests. Probability values from pairwise comparisons were adjusted using Bonferroni correction, with a significance threshold set at $p < 0.05$.

To reveal the quality and change of the habitat function, further indicators for diversity (1), rareness (2), representativity (3), and hemeroby (4) were considered.

1. Number of species per plot and the Shannon Diversity Index (R vegan package, Oksanen et al. 2022), were used to determine the extent of changes in the plant diversity over the past 40 years as well as the current status (research questions 1 and 2). Additionally, expected number of species in the regional pool in each survey period were computed following the approach of Chao et al. 1987 and a bootstrap-based approach using the "specpool" function in R's vegan package.
2. Rareness was analyzed by the changes in the number of Red List species (Brandenburg: Ristow 2006, and Saxony-Anhalt: Frank et al. 2020) and, of these, endangered species. In this study, Red List species also include those categorized at the "Near Threatened" warning level, while excluding species without direct threats or those with insufficient data. Additionally, the number of plant species occurring exclusively in only one survey was determined.
3. Representativity of the Gülpe floodplain vegetation was compared with river corridor plants (Burkart 2001) to get a more detailed impression of vegetation composition changes and the importance of floodplains as a habitat for plant species adapted to dynamic moisture conditions. Therefore, the river corridor plant *Selinum dubium* (*Cnidium dubium*) was investigated as a representative species for the regular flooding. In contrast, the Poaceae *Holcus lanatus* was studied, as it is not a river corridor plant and thus is less representative of floodplain ecosystems and more indicative of areas with lower flood frequency. The occurrence of both *Selinum dubium* (*Cnidium dubium*) and *Holcus lanatus* can also provide information on changes in the mowing regime (intensive vs. extensive agricultural use) during the study period.
4. Hemeroby and the associated risk to native species were assessed by the number of neophytes according to Ristow (2006).

To analyze changes in the Shannon Diversity Index, the number of Red List species and river corridor plants, 95% confidence intervals were calculated for each survey period. The confidence intervals were based on the sample mean and standard error, using the t-distribution to account for sample size and variability. Calculations were performed separately for the total dataset and the stratified GL dataset.

In addition, the temporal development of the vegetation composition (research question 2) was investigated using non-metric multidimensional scaling (NMDS) ordination. The ordination was performed using the "metaMDS" function in R in the vegan package (Oksanen et al. 2022) with two dimensions and a maximum of ten iterations. For the ordination, all species with only one occurrence were omitted from the analysis to reduce noise. Ordinations were based on Bray–Curtis distances with a random starting configuration. Three-dimensional solutions were chosen by visually checking the decrease in stress values with an increasing number of dimensions, according to the method described by (Leyer and Wesche 2008). To explore underlying ecological gradients in the dataset, we included vectors of the number of species, Shannon Diversity Index, as well as EIV showing a significant association with a p-value of 0.001. Furthermore, a NMDS was performed for each plant species recorded in at least two plots within the study site during the four surveys. In this way, species occurrence with certain EIV characteristics could be assessed.

To analyze how water availability has changed over the past 40 years (research question 3), daily precipitation data from the nearest gauge in Scholene and daily water levels of the upper Garz gauge, compare Fig. 1a, were examined five years prior to each of the four vegetation surveys. Groundwater data provided by the State Office for the Environment (LFU data on request 16 May 2024) only started in July 1998 and were not included in the analysis. The sum of summer (May to September, relevant for the survey periods) and winter precipitation (January to April and October to December of the same year) was

compared with the number of days with high and low water levels of Garz OP by graphical representations of confidence intervals. The number of days with high water levels was calculated based on the mean high water ($MHW \geq 294$ cm). For low water levels, a threshold ≤ 200 cm was chosen instead of the mean low water ($NHW \leq 187$ cm), as water levels rarely fell below 187 cm. This adjustment provides a more practical and relevant basis for identifying dry periods, reflecting expert judgment.

Graphical representations of confidence intervals of EIV_N, EIV_R as well as EIV_F statistically explore the changes in the habitat functions regarding nutrient levels, climate and water availability. Therefore, average monthly precipitation sums were analyzed separately for summer and winter across the four survey periods. For the number of days with low water and high water levels, no distinction was made between summer and winter, as the number of days with low water levels was too low to test a statistical difference. For each survey the year of the survey itself was excluded from the analysis, as it has limited influence on plant occurrence due to most surveys being conducted in spring and early summer.

Results

Changes in plant diversity

Altogether, within the plots 308 vascular species were recorded in the Gülpe floodplain over the past 40 years (Table 2). Almost 80% of all species (246 species) were recorded by Fischer_82. The number of species, the Chao Index and the Bootstrapped Index were higher in the total dataset compared to the GL dataset. The highest values were recorded in the first survey period (Fischer_82), followed by a decline in the second (Burkart_95) and third (Wesche_08) periods, and increased again in the Kra_20 survey, though not reaching the level of the first survey. In contrast, the mean Shannon Diversity Index showed an opposite trend, increasing over time, with the highest values recorded in the third survey (Wesche_08) followed by the survey of Kra_20. Shannon Diversity was consistently higher in the GL dataset compared to the total dataset (Table 2, Fig. 3a), also reflecting the highest number of species per plot in medium-wet

plots (EIV_F=5 to 8), which represent the GL dataset.

The lowest species counts per plot, with only three or four different species, were found in Fischer_82, Burkart_95, and Kra_20 in very wet habitats (EIV_F>9). The species composition of these plots varied considerably, with *Agrostis stolonifera* dominating in Burkart_95, *Phalaris arundinacea* in Kra_20, and the more sporadic occurrence of *Typha latifolia* in Fischer_82.

Indicator of rareness – changes over time

A total of 102 Red List species were identified within the study site, representing approximately one third of all observed plant species. Fischer_82 recorded the highest number of Red List species (78), whereas Kra_20 recorded 47 Red List species, which is higher than the two previous surveys for the total dataset (Burkart_95: 39, Wesche_08: 34, see Table 2). The most frequent Red List species assessed in 2020 were *Galium palustre* agg., *Lychnis flos-cuculi*, and *Selinum dubium* (*Cnidium dubium*, Table 3a), all plants adapted to humid/wet areas (EIV_F=8–9). The number of Red List species per plot is highest in the Wesche_08 survey (Fig. 3b). The number of Red List species per plot differs between the total and the GL dataset: while Kra_20 has the lowest number in the GL dataset, its number in the total dataset is higher than those of Burkart_95 and Wesche_08. 35 plant species were recorded in the total area for the first time in the Kra_20 survey (i.e. *Anthemis ruthenica*, *Erigeron canadensis*, *Solidago canadensis*), which is much higher than in the Burkart_95 and Wesche_08 surveys. Considering the GL dataset, these first-time observations are similar for Kra_20, Wesche_08 and Burkart_95. However, the numbers observed in these surveys are considerably lower than those recorded by Fischer_82, which was conducted 40 years ago.

Indicator of representativity – changes over time

Altogether, 36 river corridor plant species were identified in the four surveys, of which 18–23 were found in all surveys (Table 2, Table 3b). Although the total number of river corridor plants was highest in Fischer_82, the mean number of river corridor plants per

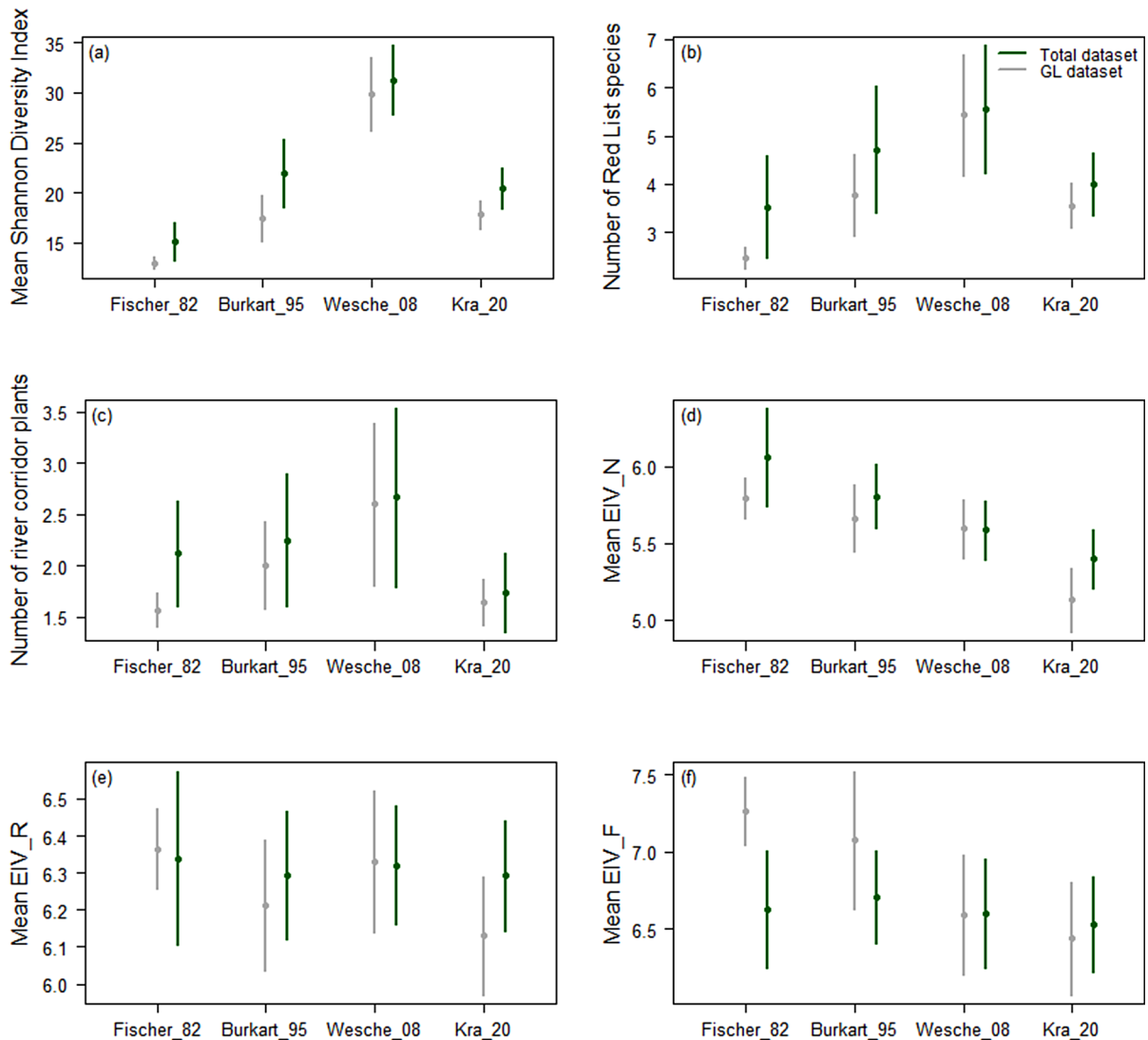


Fig. 3 Confidence interval plots comparing the total dataset (grey) and the stratified grassland dataset (GL, green) for the following variables on a plot level: Shannon Diversity Index

(a), number of Red List species (b), number of river corridor plants (c), and mean Ellenberg Indicator Values for nutrients (EIV_N; d), reaction (EIV_R; e), and moisture (EIV_F; f)

plot was the lowest (Table 2, Fig. 3c). Similar to the number of Red List species in Kra_20, the number of river corridor plants in the GL dataset was lowest, whereas the total dataset did not exhibit this pattern. *Selinum dubium* (*Cnidium dubium*), a river corridor plant indicating longer periods of inundation, was not recorded by Fischer_82, but has appeared since the 1990s with occurrences in 11 plots and 21 plots in 2020 (total dataset, Table 2). However, only for Kra_20 is the number of plots with *Selinum*

dubium (*Cnidium dubium*) higher in the total dataset than in the GL dataset whereas for Burkart_98 and Wesche_08 the number is the same. The occurrence of *Holcus lanatus* increased progressively across the four survey periods, rising from 6% in the total dataset to 25%, and from 8 to 75% in the GL dataset, rendering *Holcus lanatus* the most dominant species in the Kra_20 survey.

Indicator of hemeroby – changes over time

Over the past 40 years, seven neophytes were identified in total at the study site (Table 2, Table 3c). Previous surveys documented only two or three neophytes, whereas the most recent survey, Kra_20, recorded five (total dataset), whereas in the GL dataset the value remains relatively constant with two or three species. The most frequent neophytes in Kra_20 were *Rumex thyrsiflorus*, *Arrhenatherum elatius*, and *Anthemis ruthenica*. Additionally, *Erigeron canadensis* and *Solidago canadensis*, which each appeared in only one plot in drier sites of Kra_20 ($EIV_F < 5$), were recorded for the first time at the study site (Table 3c).

Changes in EIV – changes over time

Mean EIV_N values declined from Fischer_82 to Kra_20, with the 2020 survey diverging significantly from all previous surveys (Table 2, Fig. 3d), for both the total dataset and in the stratified GL dataset. Significant differences in EIV_R were found only between Fischer_82 and the surveys of Burkart_95 and Kra_20, with no clear trend (Fig. 3e). Regarding EIV_F , a decrease in moisture was observed in the total dataset, with significant changes between Fischer_82 and Wesche_08, as well as between Burkart_95 and Wesche_08 (Fig. 3f). The GL dataset was stratified using EIV_F between 5 and 8, which indicates that EIV_F are, by logical inference, within the same range for this particular dataset.

Temporal changes: NMDS

The temporal changes in species composition, including the selected species *Selinum dubium* (*Cnidium dubium*) and *Holcus lanatus*, were evaluated using NMDS for both the total dataset and GL dataset. For the total dataset, there was considerable overlap between the Burkart_95 (green) and Kra_20 (orange), whereas Fischer_82 (blue) exhibited several plots not covered by later studies (Fig. 4a). All plots surveyed in Wesche_08 (black) were centrally located in the ordination and were covered by the other vegetation surveys (Fig. 4a). Axis one of the NMDS (NMDS1) correlated negatively with EIV_F (NMDS1 = -0.92), EIV_R , and EIV_N and positively with the Shannon Diversity Index, and the number of species, with

all p-values ≤ 0.001 (Fig. 4g). The highest correlation was observed for EIV_F ($R^2 = 0.91$) followed by EIV_R and EIV_N (both $R^2 = 0.51$), indicating that these environmental values had the strongest influence on species composition.

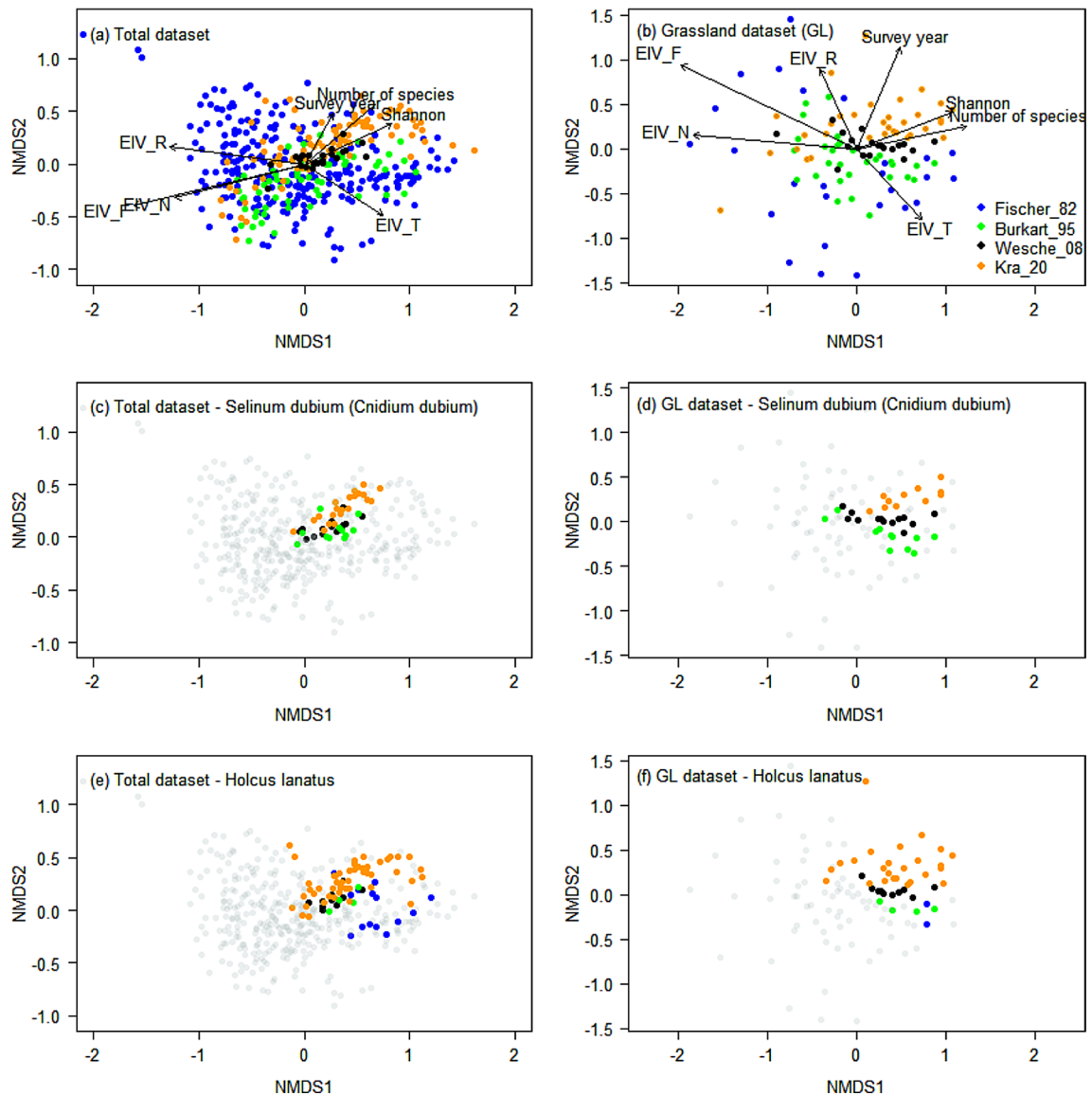
For the GL dataset, the NMDS ordination highlighted clear distinctions compared to the complete dataset. EIV_F remained the most influential variable, strongly associated with NMDS1 (NMDS1 = -0.91, $R^2 = 0.76$), followed by EIV_N ($R^2 = 0.54$). NMDS2 was most strongly correlated with EIV_R (NMDS2 = 0.91), and survey year showed a positive correlation with NMDS2 (NMDS2 = 0.91), reflecting temporal shifts in vegetation structure. NMDS show that plant community composition differs mainly in terms of species moisture, nutrients, and soil reaction preferences.

A closer look at two species with remarkable development in the study area is presented in NMDS in Fig. 4c to f in the total and the GL dataset on a plot basis: The appearance of the river corridor plant *Selinum dubium* (*Cnidium dubium*) in the total dataset (Fig. 4c) is close to the center of the ordination, representing medium EIV_F and EIV_N values, directing to the vector representing a high number of species. In contrast, *Holcus lanatus* shows a remarkable variability in distribution across the different survey periods (Fig. 4e). While Burkart_95 and Wesche_08 have a similar distribution of *Holcus lanatus* in semi-humid plots, its occurrence is limited to drier plots in Fischer_82. Moreover, in Kra_20, *Holcus lanatus* exhibits distribution across both dry and wet areas and emerges as the dominant species, being present in 48 out of 85 plots (56%, see Table 2).

In the GL dataset, plots with *Selinum dubium* (*Cnidium dubium*) distinguishes itself on the NMDS2 axis, showing separation between the surveys of Burkart_95, Wesche_08, and Kra_20 (Fig. 4d). This separation aligns with the environmental values represented by the Shannon Diversity Index and the number of species. For *Holcus lanatus*, the differentiation is likewise most pronounced along the NMDS2 axis, with a much greater frequency and broader distribution in Kra_20 compared to earlier surveys (Fig. 4f).

Changes in hydrology

There is a clear difference in the hydrological conditions of the four surveys due to man-made water



(g)	Total dataset			Grassland (GL) dataset		
	NMDS1	NMDS2	R ²	NMDS1	NMDS2	R ²
Variables						
EIV_F	-0.92	-0.24	0.91	-0.91	0.43	0.76
EIV_R	-0.71	0.09	0.51	-0.42	0.91	0.15
EIV_N	-0.70	-0.15	0.51	-0.99	0.08	0.54
Number of species	0.41	0.34	0.29	0.98	0.20	0.25
Shannon Diversity Index	0.48	0.22	0.28	0.93	0.36	0.25
EIV_T	0.31	-0.33	0.20	0.67	-0.73	0.18
Survey year	0.15	0.28	0.10	0.40	0.91	0.25

Fig. 4 NMDS ordination of all plots comparing composition of the total dataset (a, c, e) and the grassland (GL) dataset (b, d, f), colored per survey period. Stress=0.176, 0.198 respectively. Panels (a) and (b) show the general vegetation patterns, with biplot arrows derived from envfit analysis indicating environmental and supplementary variables. Panels (c) and (d) illustrate the distribution of plant species *Selinum dubium* (*Cnidium dubium*); and panels (e) and (f) illustrate the distribution of plant species *Holcus lanatus*. Results of envfit analysis, indicating the correlation of the variables with the NMDS axes (NMDS1, NMDS2) are presented as table (g). Variables are sorted by their R^2 values of the total dataset

regulation and climatic conditions: Precipitation in the five years preceding each survey varied and showed considerable interannual variability (Fig. 5). The highest precipitation sums were recorded in the winters of 1981, 1992, 1994 and 2008, the four years before the Kra_20 survey were the driest for both, summer and winter (Fig. 5a and b).

To facilitate prolonged agricultural use of the floodplain while still accommodating commercial shipping, water levels were maintained at a relatively balanced level through regulation until the 1990s. Despite this, the highest mean water levels and days with high water levels (≥ 294 cm) occurred more frequently, especially until 1995. Particularly the number of days with high water levels per month were higher during the first two survey periods (Fig. 5c). A notable observation from the Kra_20 study is the absence of days with high water levels during the four years preceding the survey. The largest flooding events did not occur in the period considered in Fig. 5c, but rather in August 2002, Spring 2003, Spring 2006, and June 2013 (Fig. 1). However, the hydrological preconditions for all four surveys varied in terms of dry and wet periods, with the driest periods occurring before the Wesche_08 survey and the most recent survey Kra_20 (Fig. 5d).

Discussion

Changes in plant diversity

The study demonstrates that the Havel floodplain near Gülpe has been supporting a high level of plant diversity over the past 40 years. The importance of grassland floodplains in providing habitats for a wide range of plant species is highlighted by extracting the GL dataset, which, despite comprising fewer plots, still

includes a high number of species. These medium-humid areas have been shown to be particularly species-rich in all four surveys, a finding that is consistent with results from former studies, such as Wilson et al. (2012). The Shannon Diversity Index was highest in Wesche_08; however, as this index is calculated on a plot level, the result should be interpreted with caution. Wesche_08 included the largest plots among the surveys, and larger plot sizes tend to yield higher Shannon Diversity values due to the increased likelihood of capturing more species. Among the surveys, Kra_20 exhibited the highest number of species, as well as the highest Chao and Bootstrapped Indices compared to Burkart_95 and Wesche_08. However, the total number of species has declined over the past 40 years. This unclear outcome aligns with findings from other authors who observed a notable decline in species richness in other lowland and grassland floodplains in Germany (Wesche et al. 2012; Diekmann et al. 2014). However, this is in contrast to studies on the Lower Havel (Wesche et al. 2012; Kaiser and Ahlborn 2021) which did not find a significant decline in the number of species.

Since the study area has been designated as a nature reserve since 2004, utilizing the land for intensive agricultural purposes is prohibited and might lead to the recovery of floodplain vegetation. Studies show that intensive agricultural use is often a major factor contributing to biodiversity loss in Central Europe (i.e. Ellenberg and Leuschner 2010; Krause et al. 2011).

Evaluation of indicators for rareness, representativity, and hemeroby in the context of hydrological, climatic, and agricultural changes

Using Red List species to determine the conservation status of species is a widely accepted method to evaluate their relevance for nature conservation (i.e. Harvolk et al. 2015; Kaiser and Ahlborn 2021; Stammel et al. 2022), and was used in this study as an indicator for rareness. The number of Red List species increased in the Kra_20 survey (total dataset) in comparison to both Burkart_95 and Wesche_08 (Table 2). This demonstrates that the implemented conservation measures, such as water management and the extensive agricultural management aligned with Natura2000 goals, are effective in terms of rareness. Regular but regulated mowing (Eriksson 2021; Žuna

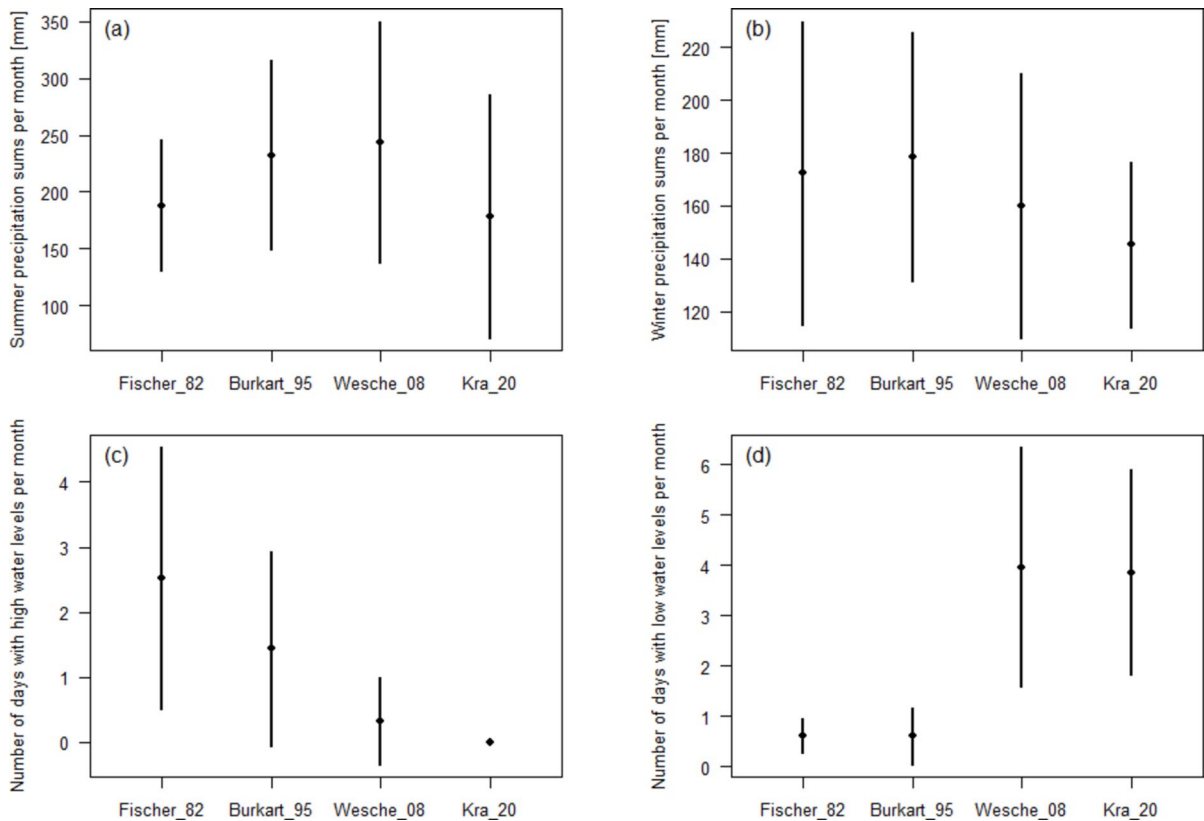


Fig. 5 Confidence intervals across the survey periods (Fischer_82, Burkart_95, Wesche_08, and Kra_20). **a** Summer precipitation sums [mm] per month. **b** Winter precipitation

sums [mm] per month. **c** Number of days with high water levels per month. **d** Frequency of days with low water levels per month. Error bars represent 95% confidence intervals

Pfeiffer et al. 2017), along with an intermediate disturbance caused by flooding (Slezák et al. 2022), creates habitats within this cultural landscape that provide suitable conditions for endangered plant species.

The spatial distribution and environmental extent of river corridor plants has, thus far, received only limited attention in the literature (Nobis et al. 2017). However, understanding their distribution is important, as river corridor plants serve as indicators for evaluating the habitat function of floodplains. The number of river corridor plants declined in Kra_20 when comparing the GL dataset which represents exactly this mid-humid habitat. The number of *Selinum dubium* in the plots was established as an indicator of the representativity of the Gülpe floodplain

as a species-rich floodplain with the presence of HT *Cnidion dubii*. Comparing the total and the GL dataset reveals the spread of *Selinum dubium* (*Cnidium dubium*) into areas with different environmental conditions than the typical mid-humid areas. This is exactly what (Geißler 2007) observed: *Selinum dubium* (*Cnidium dubium*) exhibits tolerance to both severe flooding events (as occurred in August 2002) and prolonged summer drought as witnessed in 2003. Other studies conducted in various floodplains, however, indicate a drought-related weakening of *Selinum dubium* (*Cnidium dubium*) and that it tends to benefit from summer floods (Dullau et al. 2021). Nevertheless, the sustained proliferation of *Selinum dubium* (*Cnidium dubium*) in the Kra_20 survey suggests

that it is capable of withstanding prolonged summer droughts of 2018/19 as long as winter water levels remain at a certain level and agricultural management is adapted. In contrast to *Selinum dubium*, *Holcus lanatus* is considered to be intolerant to flooding (Hellberg 1995). The dominance of *Holcus lanatus* in the Kra_20 survey indicates prolonged dry conditions in the floodplain, characterized by extended periods of low water levels and limited flooding events (Fig. 5c and d). *Holcus lanatus* is not a good forage plant, with low feed value (AGFF 2024), and thus it is generally controlled in agricultural practice by early mowing. However, this is again not possible in the area due to the protection of ground-nesting birds. Thus, the ecosystem service of fodder production for livestock in this area has likely decreased, but deserves further investigation.

Although the protection status of the area is effective, the increase in neophytes indicates that ongoing threats and constant changes are occurring in the floodplain, reflecting an increase in hemeroby. The first occurrence of *Solidago canadensis* in the study site during the Kra_20 survey (total dataset), which has been listed on the BfN management list since 2013 (Nehring et al. 2013), illustrates this issue. As it is included on this management list, further spread of *Solidago canadensis* should be prevented, and controlled by manual extraction to prevent further spreading. The introduction of species outside their natural range is widely acknowledged as a major cause of biodiversity loss. In particular, invasive species such as *Solidago canadensis*, represent a significant threat to native ecosystems, habitats, and species, constituting a critical challenge for conservation efforts (Rabitsch et al. 2013).

Changes of habitat functions exemplarily illustrated by HT *Cnidion dubii*

The ordination (Fig. 4a and b) indicates the significant influence of soil moisture (EIV_F) on vegetation composition. This emphasizes the importance of regular flooding for species composition in the area, as well as for the occurrence of the HT *Cnidion dubii*, with *Selinum dubium* (*Cnidium dubium*) as an indicator species, which is adapted to regular flooding.

Despite the low water levels prior to the Kra_20 survey (after the flood in 2013), *Selinum dubium* (*Cnidium dubium*) was widespread in the study area. This may indicate that the adjusted water regime and the implemented restoration measures have prevented a drastic lowering of groundwater levels. EIV_F, EIV_R, and EIV_N were correlated (Fig. 4a) suggesting that wetter areas tend to also be nutrient-richer and alkaline. These findings are consistent with Bridgham et al. (1998), who observed higher nutrient availability in moist conditions. The decline in EIV_N (Fig. 3d) may reflect the extensification of agriculture in the study area due to its designation as a Natura2000 site. Since 1999/2000, grazing by cattle has ceased, resulting in the absence of animal manure on the managed land. Additionally, the area has not been fertilized since that time. On the one hand, the habitat function changed in favour of HT *Cnidion dubii* because inundation is possible on large areas during winter time and the prohibition of fertilization favours typical floodplain meadow plants. On the other hand, threats to HT *Cnidion dubii* meadows still occur. The abandonment of mowing or grazing, (BfN 2024) initially benefit some species by reducing disturbance; however, long-term effects often lead to a decline in species richness due to encroachment by competitive species. In this study, this is exemplified by the spread of *Holcus lanatus*, which tends to dominate drier areas. Furthermore, Gerard et al. (2008) proved statistically that only the combination of frequent flooding and annual mowing clearly increased species richness of temperate lowland floodplain meadows – which is exactly what is found in the Gülpe floodplain.

In accordance with the guidelines set forth by BfN (2024), HT *Cnidion dubii* meadows are to be mowed at least once a year. In the study area, however, this is only feasible from mid-June onwards, due to the protected status afforded to ground-nesting birds. *Selinum dubium* (*Cnidium dubium*) exhibits a high tolerance to grazing (Heimes et al. 2010), which resulted in the detection of this species at the study site during the Burkart_95 survey (grazing until 1999/2000). The absence of *Selinum dubium* (*Cnidium dubium*) in 1981/82 is presumed to be the result of intensive agricultural utilization and hydraulic engineering measures that were in place back then.

Protected floodplains, such as the study site, which are characterized by frequent flooding and a low influence of (nitrogen) fertilizers, can serve as valuable control sites for further studies investigating the biodiversity of extensively used grassland floodplains in lowland areas of Central Europe. Thus, despite the prolonged drought that has characterized the area since 2013, river corridor plants that depend on regular flooding have been able to survive or even, in the case of *Selinum dubium* (*Cnidium dubium*), spread more widely in the area. This development probably shows the influence of the Natura2000 management plan, which includes measures to conserve the HT *Cnidion dubii* habitat type and the implementation of restoration measures. Thus, flooding of certain areas of the floodplain is likely possible than in previous years, indicating the effectiveness of conservation efforts and restoration projects in maintaining the ecological integrity of the floodplain ecosystem.

Limitations

The database comprises non-random vegetation samples, which strictly prohibits the application of statistical analysis (Lájer 2007). Nevertheless, statistical tests were employed, as they can provide valuable information when superior-quality data sets are not available (for a similar argument, see Oksanen 2001). Historical surveys of vegetation not based on permanent plots face the risk of introducing bias. One challenge in the statistical analysis of the data lies in the different data bases and methodologies employed in the vegetation surveys. In this study, the plot design and plot size were based on the survey by Burkart (1998). The differing plot sizes and the sampling design of Fischer_82 (with markedly disparate plot sizes, a high number of plots, and an unclearly defined location of the study area) and Wesche_08 (with a research question limited exclusively to grasslands) represent an additional difficulty for the comparison of the vegetation surveys in the area (Dengler 2009). It is well established that plot-size effects can become problematic when the size range spans several orders of magnitude (Duprè et al. 2010). The plot sizes employed in this study are below the commonly used 16–20 m² range typically observed in Central European grassland studies (Bruehlheide and Chytrý 2000). However, this difficulty could

be overcome by applying a species accumulation curve (Fig. 6a and b, Appendix) to standardize the sampling effort, and the resulting GL dataset, which served as a comparable dataset. Another source of uncertainty lies in the use of EIV as environmental values. While they offer insights when direct measurements are unavailable, their use involves circularity, as both ordination and EIV values stem from species presence, potentially reinforcing their correlation.

It is also relevant to consider the temporal aspect of the four vegetation surveys, as this may have been conducted at different stages of the vegetation period; thus, earlier studies examined how the intra-seasonal variability of vegetation influences the pattern of species richness and species composition, (Vymazalová et al. 2012). Furthermore, it is important to consider the possibility of an observer bias, which may be caused by individual differences in plant identification and data collection. This bias could lead to variations in the survey results. Nevertheless, the four surveys enable crucial and unique insights into the dynamics of biodiversity in managed floodplain grasslands and their habitat function, providing an exceptional opportunity to better comprehend this ecosystem.

Conclusion

The study examines the habitat function, plant diversity and composition of the vegetation in a 110-hectare study site along the Lower Havel near Gülpe, Germany, which is used extensively as a grassland and is designated as a nature reserve. Data from four surveys conducted over four decades provide a valuable basis for analyzing influence of agricultural management and hydrology on the plant composition and plant diversity of the Gülpe floodplain. Relating our results to the discussion of ES in floodplains, we observed that changing environmental conditions have enhanced the habitat function in some areas, as seen in the establishment of the HT *Cnidion dubii* in temporally inundated zones. However, increasing droughts and the permanent removal of nutrients may threaten species richness in more elevated areas.

The study confirms the importance of the Gülpe floodplain in terms of plant diversity, particularly the

habitat function of these unique environments. These habitats are subject to constant change due to fluctuating water levels, providing refuge for many Red List species and river corridor plants. Comparative studies of biodiversity in Central European lowland grassland floodplains have demonstrated a general decline in the number of species. However, this trend does not appear in the Havel floodplain near Gülpe. Moreover, quantitative studies of reference datasets on long-term changes in grassland vegetation covering four decades or more are extremely rare. Therefore, it is advisable to establish permanent plots in the study site for a quantitative analysis of the change in vegetation composition in the Lower Havel floodplain. In the future, new challenges will arise due to climate change with regard to protecting these unique habitats and protected habitat types such as HT *Cnidion dubii*. The ongoing vegetation survey in the Gülpe floodplain is important to show the changes in plant diversity in a protected, extensively used lowland floodplain – especially under the influence of climate change and possibly longer lasting droughts in summer.

Further research should aim to model the relationship between the observed increase in *Selinum dubium* and factors such as flooding and drought durations and frequencies as well as mowing management. Additionally, studies like Detrended Correspondence Analysis (DCA) ordination to explore community composition dynamics and an analysis of functional traits should be conducted to gain a comprehensive understanding of ecological processes, dynamics, and services besides the habitat function.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Appendix

See Fig. 6 and Table 3.

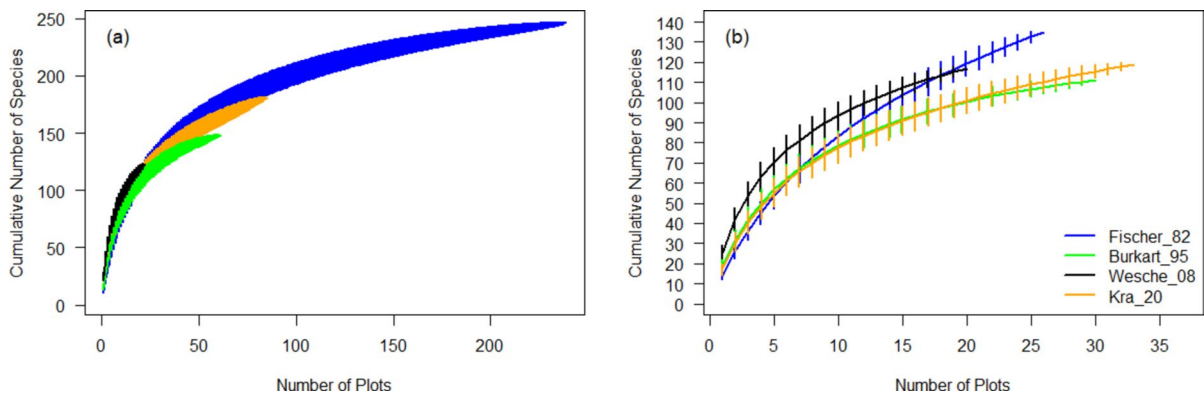


Fig. 6 Species accumulation curves of the total dataset (a) and of the grassland (GL) dataset (b)

Table 3 **a** Proportion and absolute frequency of Red List species, **b** River corridor plants and **c** Neophytes over the past 40 years at the study site

(a) Red List species	Absolute Frequency	Fischer_8 2 (%)	Burkart_9 5 (%)	Wesche_0 8 (%)	Kra_20 (%)
<i>Galium palustre</i> agg.	100	15.9	27.87	50	40
<i>Lychnis flos-cuculi</i>	72	7.11	19.67	45.45	38.82
<i>Selinum dubium</i>	45	0	18.03	59.09	24.71
<i>Cardamine pratensis</i> agg.	42	6.28	11.48	18.18	18.82
<i>Mentha arvensis</i>	43	3.77	21.31	22.73	18.82
<i>Stellaria palustris</i>	49	5.86	21.31	31.82	17.65
<i>Carex vulpina</i>	39	5.02	19.67	18.18	12.94
<i>Festuca ovina</i> s. str.	27	7.95	0	0	9.41
<i>Sanguisorba officinalis</i>	32	5.86	8.2	22.73	9.41
<i>Centaurea jacea</i> agg.	20	3.77	1.64	13.64	8.24
<i>Ranunculus auricomus</i> agg.	35	5.86	18.03	13.64	8.24
<i>Rhinanthus minor</i>	9	0.84	0	0	8.24
<i>Saxifraga granulata</i>	13	0.42	6.56	4.55	8.24
<i>Ranunculus bulbosus</i>	9	0.42	3.28	0	7.06
<i>Thalictrum flavum</i>	25	5.02	6.56	13.64	7.06
<i>Viola stagnina</i>	17	2.93	4.92	4.55	7.06
<i>Butomus umbellatus</i>	30	7.11	11.48	4.55	5.88
<i>Cardamine parviflora</i>	8	0	4.92	0	5.88
<i>Serratula tinctoria</i> s. l.	11	0.42	4.92	9.09	5.88
<i>Carex disticha</i>	16	2.51	3.28	18.18	4.71
<i>Inula britannica</i>	32	9.21	3.28	18.18	4.71
<i>Vicia lathyroides</i>	7	0	4.92	0	4.71
<i>Juncus gerardi</i>	4	0	0	4.55	3.53
<i>Lathyrus palustris</i>	20	5.44	3.28	9.09	3.53
<i>Veronica scutellata</i>	13	0.42	13.11	4.55	3.53
<i>Achillea salicifolia</i>	2	0	0	0	2.35
<i>Alisma lanceolatum</i>	3	0	1.64	0	2.35
<i>Iris sibirica</i>	5	0	4.92	0	2.35
<i>Myosotis discolor</i>	4	0	3.28	0	2.35
<i>Oenanthe fistulosa</i>	16	2.51	9.84	9.09	2.35
<i>Polygala vulgaris</i> s. l.	3	0.42	0	0	2.35
<i>Scutellaria hastifolia</i>	6	1.26	0	4.55	2.35
<i>Stachys palustris</i>	27	8.79	3.28	9.09	2.35
<i>Achillea ptarmica</i>	35	10.04	1.64	40.91	1.18
<i>Allium angulosum</i>	1	0	0	0	1.18
<i>Caltha palustris</i>	36	12.13	8.2	4.55	1.18

Table 3 (continued)

(a) Red List species	Absolute Frequency	Fischer_8 2 (%)	Burkart_9 5 (%)	Wesche_0 8 (%)	Kra_20 (%)
<i>Carex nigra</i>	2	0.42	0	0	1.18
<i>Centaurium erythraea</i> s. l.	1	0	0	0	1.18
<i>Eleocharis uniglumis</i>	1	0	0	0	1.18
<i>Epilobium palustre</i>	4	1.26	0	0	1.18
<i>Gentiana pneumonanthe</i>	1	0	0	0	1.18
<i>Persicaria lapathifolia</i> s. l.	3	0.42	1.64	0	1.18
<i>Ranunculus aquatilis</i>	7	2.51	0	0	1.18
<i>Senecio aquaticus</i> s. str.	5	0	3.28	9.09	1.18
<i>Teucrium scordium</i>	1	0	0	0	1.18
<i>Veronica catenata</i>	4	0	4.92	0	1.18
<i>Viola canina</i> agg.	3	0.42	0	4.55	1.18
<i>Ajuga genevensis</i>	1	0.42	0	0	0
<i>Aphanes arvensis</i>	1	0.42	0	0	0
<i>Bidens cernua</i>	1	0.42	0	0	0
<i>Bidens connata</i>	1	0	0	4.55	0
<i>Bidens tripartita</i>	21	5.86	9.84	4.55	0*
<i>Briza media</i>	2	0.84	0	0	0
<i>Campanula patula</i>	2	0.84	0	0	0
<i>Carex cespitosa</i>	1	0.42	0	0	0
<i>Carex pallescens</i>	2	0.84	0	0	0
<i>Carex pseudocyperus</i>	1	0.42	0	0	0
<i>Carex vesicaria</i>	4	1.26	0	4.55	0
<i>Carum carvi</i>	1	0.42	0	0	0
<i>Cyperus fuscus</i>	2	0.42	1.64	0	0
<i>Dianthus carthusianorum</i>	2	0.84	0	0	0
<i>Dianthus deltoides</i>	9	3.35	1.64	0	0*
<i>Eleocharis acicularis</i>	3	1.26	0	0	0
<i>Eryngium campestre</i>	5	2.09	0	0	0
<i>Euphorbia palustris</i>	2	0.84	0	0	0
<i>Festuca arundinacea</i>	25	10.46	0	0	0
<i>Fragaria viridis</i>	1	0.42	0	0	0
<i>Galium boreale</i>	1	0.42	0	0	0
<i>Galium uliginosum</i>	5	2.09	0	0	0
<i>Gnaphalium uliginosum</i>	4	1.67	0	0	0
<i>Gratiola officinalis</i>	9	3.77	0	0	0*
<i>Hieracium laevigatum</i>	1	0.42	0	0	0
<i>Hippuris vulgaris</i>	5	2.09	0	0	0*
<i>Hydrocotyle vulgaris</i>	1	0.42	0	0	0
<i>Inula salicina</i>	3	1.26	0	0	0*
<i>Juncus atratus</i>	1	0	0	4.55	0
<i>Koeleria macrantha</i>	1	0	1.64	0	0
<i>Littorella uniflora</i>	1	0.42	0	0	0
<i>Lysimachia thyrsiflora</i>	4	1.67	0	0	0
<i>Mentha pulegium</i>	1	0	0	4.55	0

Table 3 (continued)

(a) Red List species	Absolute Frequency	Fischer_8 2 (%)	Burkart_9 5 (%)	Wesche_0 8 (%)	Kra_20 (%)
<i>Myosurus minimus</i>	1	0.42	0	0	0
<i>Peplis portula</i>	4	1.67	0	0	0
<i>Peucedanum oreoselinum</i>	2	0.84	0	0	0
<i>Phleum phleoides</i>	2	0.84	0	0	0
<i>Pimpinella saxifraga</i>	2	0.84	0	0	0
<i>Potentilla erecta</i>	3	1.26	0	0	0
<i>Potentilla verna</i>	2	0.84	0	0	0
<i>Ranunculus lingua</i>	4	1.67	0	0	0
<i>Ranunculus peltatus</i> subsp. <i>peltatus</i>	3	0	4.92	0	0
<i>Ranunculus reptans</i>	1	0	0	4.55	0
<i>Scleranthus perennis</i>	9	3.77	0	0	0
<i>Scleranthus polycarpus</i>	1	0	1.64	0	0
<i>Scrophularia umbrosa</i>	1	0.42	0	0	0
<i>Sedum rupestre</i>	1	0.42	0	0	0
<i>Selinum carvifolia</i>	5	2.09	0	0	0
<i>Senecio erraticus</i>	4	0	0	18.18	0
<i>Senecio paludosus</i>	5	2.09	0	0	0
<i>Silaum silaus</i>	15	5.86	1.64	0	0
<i>Silene otites</i>	1	0.42	0	0	0
<i>Trifolium fragiferum</i>	2	0.84	0	0	0*
<i>Veronica anagallis-aquatica</i>	2	0.84	0	0	0*
<i>Veronica maritima</i>	3	0.84	0	4.55	0

(b) River corridor plants	Absolute Frequency	Fischer_82 (%)	Burkart_95 (%)	Wesche_08 (%)	Kra_20 (%)
<i>Rumex thyrsiflorus</i>	46	0.84	18.03	22.73	32.94
<i>Selinum dubium</i>	45	0	18.03	59.09	24.71
<i>Carex vulpina</i>	39	5.02	19.67	18.18	12.94
<i>Sanguisorba officinalis</i>	32	5.86	8.2	22.73	9.41
<i>Thalictrum flavum</i>	25	5.02	6.56	13.64	7.06
<i>Viola stagnina</i>	17	2.93	4.92	4.55	7.06
<i>Butomus umbellatus</i>	30	7.11	11.48	4.55	5.88
<i>Cardamine parviflora</i>	8	0	4.92	0	5.88
<i>Inula britannica</i>	32	9.21	3.28	18.18	4.71
<i>Lathyrus palustris</i>	20	5.44	3.28	9.09	3.53
<i>Achillea salicifolia</i>	2	0	0	0	2.35
<i>Alisma lanceolatum</i>	3	0	1.64	0	2.35
<i>Oenanthe fistulosa</i>	16	2.51	9.84	9.09	2.35
<i>Scutellaria hastifolia</i>	6	1.26	0	4.55	2.35
<i>Allium angulosum</i>	1	0	0	0	1.18
<i>Bolboschoenus maritimus</i> s. str.	7	0.84	4.92	4.55	1.18
<i>Carex praecox</i> s. str.	6	0.42	6.56	0	1.18
<i>Teucrium scordium</i>	1	0	0	0	1.18

Table 3 (continued)

<i>Urtica kioviensis</i>	5	1.67	0	0	1.18
<i>Barbarea stricta</i>	1	0.42	0	0	0
<i>Bidens connata</i>	1	0	0	4.55	0
<i>Bidens frondosa</i>	28	10.46	4.92	0	0
<i>Eryngium campestre</i>	5	2.09	0	0	0
<i>Euphorbia palustris</i>	2	0.84	0	0	0
<i>Galium boreale</i>	1	0.42	0	0	0
<i>Gratiola officinalis</i>	9	3.77	0	0	0
<i>Juncus atratus</i>	1	0	0	4.55	0
<i>Juncus compressus</i>	4	1.26	1.64	0	0
<i>Koeleria macrantha</i>	1	0	1.64	0	0
<i>Lindernia dubia</i>	1	0	0	4.55	0
<i>Mentha pulegium</i>	1	0	0	4.55	0
<i>Rorippa anceps</i>	1	0	0	4.55	0
<i>Senecio erraticus</i>	4	0	0	18.18	0
<i>Senecio paludosus</i>	5	2.09	0	0	0
<i>Silaum silaus</i>	15	5.86	1.64	0	0
<i>Veronica maritima</i>	3	0.84	0	4.55	0

(c) Neophytes	Absolute Frequency	Fischer_82 (%)	Burkart_95 (%)	Wesche_08 (%)	Kra_20 (%)
<i>Rumex thyrsiflorus</i>	46	0.84	18.03	22.73	32.94
<i>Arrhenatherum elatius</i>	10	0	1.64	4.55	9.41
<i>Anthemis ruthenica</i>	3	0	0	0	3.53
<i>Erigeron canadensis</i>	1	0	0	0	1.18
<i>Solidago canadensis</i>	1	0	0	0	1.18
<i>Bidens connata</i>	1	0	0	4.55	0
<i>Bidens frondosa</i>	28	10.46	4.92	0	0

The proportion for each survey period was determined by calculating the percentage of plots (see Table 1) where the species was present, then ranking these proportions relative to species occurrences in Kra_20. Absolute frequency was calculated as the total number of plots (out of 407) where the species appeared across all survey periods.

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