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Hydrology as a Determinant of Riparian Habitat Structure in Lowland River Floodplains

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Abstract: The objective of the study was to determine the relationship between the structure of phytocenoses in riparian wetland ecosystems and the hydrologic regime in a lowland river floodplain. The hydrobotanical study was conducted over three years—2017, 2018, and 2019—which differed in hydrological conditions (wet, average, and dry) in a middle section of the Supraśl floodplain (NE Poland) as a case study. The results showed that the structure and pattern of phytocenoses in the floodplain are primarily controlled by the hydrological regime of the river and the geomorphological features of the area. The reach and duration of the flood contributed to a specific pattern of riparian vegetation. Based on the plant community structure and riparian habitat indicators such as soil moisture, fertility, reaction pH, soil granulometry, and organic matter content, four habitat types were identified and supported by linear discriminant analysis (LDA): wet, semi-wet, semi-dry, and dry zones. The indicator species analysis (ISA) revealed species characteristic of the zones with the dominance of reed rush, reed canary grass, anthropogenic or partially natural herbaceous communities along watercourses or riparian meadows, respectively. Natural inundation of the river water is an important driver of site-specific vegetation elements and habitat types and determines habitat availability, biodiversity, and ecosystem functions of wetlands. This knowledge can serve as the basis for conservation efforts, sustainable management practices, and decision-making processes aimed at maintaining the biodiversity and ecological integrity of riparian ecosystems in similar regions.

Keywords: lowland river; hydrology; riparian vegetation structure; floodplain; natural flow regime; riparian zonation

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1. Introduction

Natural floodplains are among the most productive and diverse ecosystems in the world. Due to increasing anthropogenic pressures and the influence of factors resulting from ongoing climate change, they are among the most threatened ecosystems [1].

Natural wet grasslands in the floodplains of lowland rivers are highly valuable for conservation [2,3]. They form important components of wetland habitats [4]. These grasslands provide multiple ecosystem services, including water regulation, carbon sequestration, landscaping, wildlife (native plants, birds, and invertebrates), recreation, and leisure [5]. In opinion of Grzybowski and Glińska-Lewczuk [6,7], traditional low-intensity management practices such as mowing or grazing are necessary to maintain their characteristic flora and promote species diversity. However, these semi-natural habitats have experienced rapid decline due to insensitive land use changes such as drainage, agricultural intensification, flood control, and neglect [5,8,9].

The structure of these dynamic environments, characterized by high diversity and habitat rotation [10,11], is primarily regulated by river flow regimes [12,13] and geomorphology [14]. Numerous studies have identified flood events as an important factor influencing plant distribution along elevation gradients in floodplains [15–17]. Therefore, floods and associated fluvial and geomorphic processes shape and maintain the spatial and temporal heterogeneity of floodplain areas and their plant communities [14,18,19].

The response of vegetation to hydrological changes depends on its ecophysiological characteristics [20]. Changes in habitat structure are influenced by species' environmental tolerance and the ability to compete with other species [21,22]. Plant species respond differently to direct flood or drought impacts, and these differences are reflected in species' zonation along elevation gradients in floodplains [17]. Species that are highly competitive under dry conditions [23] may not tolerate prolonged flooding and are easily damaged [24], whereas species characterized by greater resilience benefit from flooding [25]. Species tolerance to flooding determines their distribution in river valleys [26,27]. Studies by Van Eck et al. [28] have shown that species with more tolerant traits dominate at lower, more frequently flooded sites, while a greater number of less tolerant species are found at higher elevations that are flooded less frequently. Ultimately, survival to flooding depends on the timing, frequency, depth, and duration of the flood events [29,30]. Casanova and Brock [31] indicate that the duration of floods plays a critical role and is the most important factor in wetland plant community composition. Flooding events contribute to connectivity between patches of plant communities. Water can transport seeds from habitats in upper parts of the river network [32,33], altering local species composition [24,34]. Longitudinal fragmentation prevents the normal downstream transport of nutrients, fauna, flora, and organic matter, leading to the development of different environmental conditions along the river channel [35].

Regular droughts are seasonal environmental changes that are predictable and, when combined with regular flood events, increase ecosystem productivity (*flood pulse concept*) [36,37]. However, as climate changes, characterized by the increasing frequency and magnitude of extreme weather events [38], disruptions to natural processes are occurring, leading to a decrease in river water levels and posing a significant threat to the wetland ecosystems. Declining water levels in rivers disrupt lateral connections, causing water to retreat from floodplains [39]. This disruption of hydrological connectivity between riparian habitats and the increasing heterogeneity of the river channel result in changes in the species composition of the habitats.

The objective of our study was to evaluate the relationship between the species composition of vegetation in riparian meadow habitats and to determine the importance of environmental variables, particularly hydrologic variables, that determine it. Through changes in the ecological indicator values of vascular plants: soil moisture, fertility, pH, soil granulometry, and organic matter content, we investigated whether specific moisture zones determine the vegetation structure. We hypothesized that the reach and elevation of flooding influences the abundance and distribution of plant species, which is reflected in the structure and pattern of riparian habitats.

2. Materials and Methods

2.1. Study Site

The study was conducted on the lower course of the Supraśl River in NE Poland (Figure 1). To determine the different indicators of wetland biophysical habitats in relation to water level, we selected a fragment of the floodplain (2 km^2) adjacent to the main river.

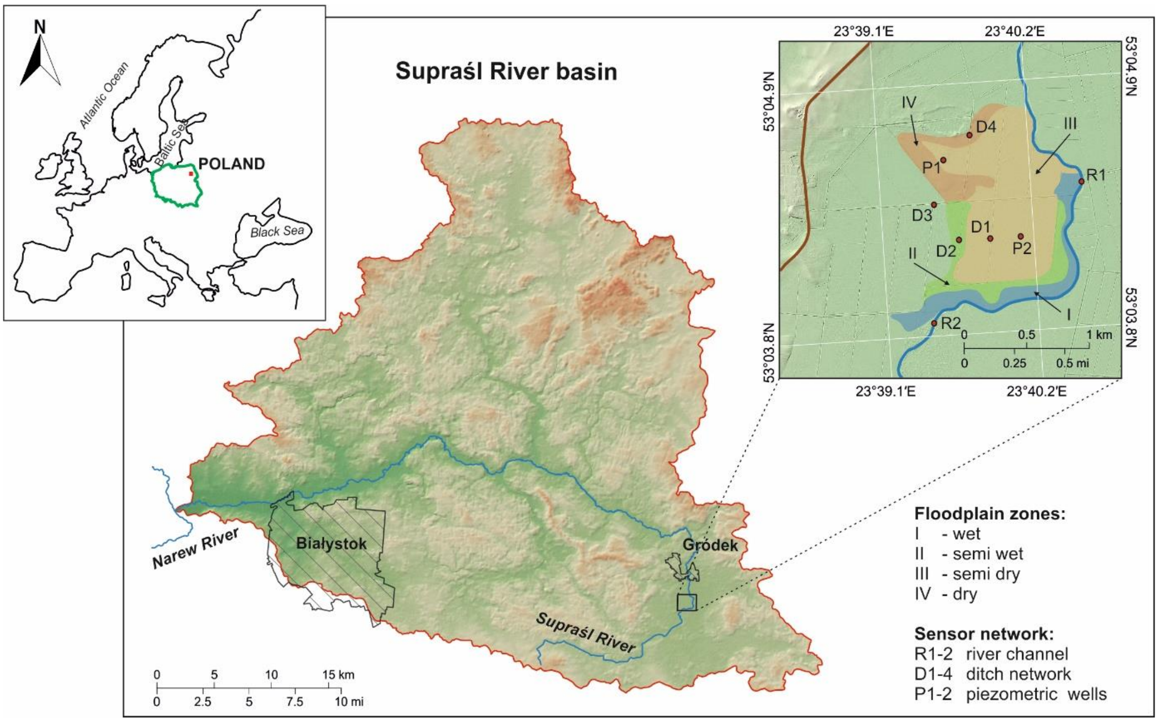


Figure 1. Location of the Supraśl River in northeastern Poland and study area.

The Supraśl River is one of the semi-natural ecosystems and therefore plays an important role in maintaining biodiversity in the region. The area hosts many bird species that are strongly linked to specific hydrological conditions and habitat types [40]. For these reasons, the upper part of the Supraśl floodplain was included in the Natura 2000 network as the "Puszcza Knyszyńska" Special Protection Area for birds (PLB 200003) and the "Ostoja Knyszyńska" (PLB 200006). In the wetlands of the study area, wading bird species such as black-tailed godwit (*Limosa limosa*), redshank (*Tringa totanus*), lapwing (*Vanellus vanellus*), snipe (*Gallinago gallinago*) and jack snipe (*Gallinago media*) breed.

The floodplain of the river is between 0.5 and 1.5 km wide and is characterized by a flat bottom and gentle slopes as it cuts through the frontal moraine zone. The geology of the valley is related to the Pleistocene glaciation, which shaped the area of the Białystok Upland and the Sokółka Foothills. As a result of terrain evolution, sandy depressions and extensive peat accumulations were formed in basin-like meltwater areas. The valley is characterized by organic soils such as peat, peat–marsh, and marsh–mineral soils. In the study area, the floodplain is well developed. The presence of peat–fibrous soils formed by the presence of near-surface groundwater plays an important role in shaping the hydrological regime in the study area, as they greatly increase groundwater retention. The hydrological regime plays an important role in structuring the habitat types in the floodplain. There is a certain spatial hydro-pedological pattern typical of natural central European floodplains that determines the biogeochemical relationships between the river hydrological regime, soil formation, and the corresponding plant communities [41]. Disturbance of this system, particularly by limiting flooding, can adversely affect the quality of wetland habitats.

The Supraśl is a third-order river and the largest right-bank tributary of the Narew River, belonging to the Vistula River basin. It has a length of 93.8 km and a catchment area of 1844.4 km^2. The Supraśl is a lowland river with a low channel gradient of 0.76‰, which is fed by numerous springs and groundwater [42]. This river exhibits a moderate hydrological regime characterized by a seasonal pattern of water flow. The highest flows occur in spring due to snowmelt and rainfall, while the lowest flows occur in summer due to evaporation and transpiration. Flow rates at Nowosiółki gauge (2009–2020) varied throughout the year, averaging between 0.23 and 2.18 m^3 s^{-1}. The high water retention in the river basin is reflected in the absence of sudden floods and in the relatively low ratio between the highest and lowest average monthly flows, which range from 10 to 12.

The qualitative and quantitative seasonality of water flow is influenced not only by morphological parameters or the size of the catchment area but also by the climatic conditions of the region. According to the climate classification of Koeppen and Geiger [43], the study area is located in the western part of the Dfb (Dfb: D = Continental; f = Fully humid; b = Warm summer) zone. The study area is characterized by a humid continental climate with certain subboreal features, resulting in long frosty winters, short early springs, a relatively short growing season, and warm summers. The average annual air temperature is 6.5 °C, and the growing season lasts 192 days. Winds from westerly (20.4%) and southwesterly (17.5%) directions prevail. The average annual precipitation in the region from 1971 to 2022 is 589 mm with a minimum of 456 mm and a maximum of 748.9 mm. Precipitation is not evenly distributed throughout the year. The highest rainfall occurs from May to August and peaks in August, while the lowest rainfall occurs between January and March. Snowfall accounts for about 21% of the annual precipitation. The average number of days with rainfall above 0.1 mm is 169, including about 63 days with snowfall. The study period (2017–2020) was characterized by variable moisture conditions. The year 2017 was exceptionally wet with a total precipitation of 935 mm. The years 2018 and 2019 were classified as dry with precipitation totals of 536 mm and 517 mm, respectively.

The Supraśl River valley is characterized by low population density and low levels of agricultural fertilization [44]. Although the riverbed follows a natural course, its hydrographic network was significantly modified by the introduction of a dense system of drainage ditches. These measures were aimed at adapting the area for agricultural use as pastures and meadows. The drainage system is currently used to irrigate the meadows through an extensive groundwater infiltration system. Currently, approximately 65% of the floodplain area in this section is occupied by wet meadows. These habitats have high ecological value and serve as important habitats for bird fauna. The dominant plant communities here belong to the *Molinio-Arrhenatheretea* class, which includes semi-natural or anthropogenic meadow and pasture communities of meso- and eutrophic habitats occurring on mineralizing and drying peatlands of low-lying peat [45].

2.2. Hydrological and GIS Data Sources

Hydrological conditions and spatial analysis of floods in the study area were performed with the help of a geographic information system (GIS) using QGIS 3.22.14 software (Białowieża). This allowed the visualization of data and simulation of water-level changes. The extent of river flooding in the valley delineating the river recharge zone was determined based on a digital elevation model (DEM) with a spatial resolution of 1 m, which was obtained from the resources of the Main Office of Geodesy and Cartography in Poland. A data set of surface and groundwater levels from hydrological years 2017–2019 was used for the hydrological analyses. The data were obtained from automatic pressure sensors programmed to record water levels with an accuracy of 1 cm per hour. The sensor network consisted of two devices installed in the river channel monitoring sites (R1-R2), four in the ditch network (D1-D4), and two in the piezometric observation wells (P1-P2), (Figure 1). Hydrological data were compared with water levels and flow rates of the Supraśl River measured at the nearest gauge in Nowosiółki by the Institute of Meteorology and Water Management (IMGW-PIB). Due to the long distance between the gauge and the study area, a data correction was applied. The determination of the extent of inundation was combined with the measurement of the height of the water table using GPS RTK (Real-Time Kinematic), which determines the coordinates of points in real time directly in the field.

2.3. Field Observations and Riparian Habitat Classification

The fieldwork included three survey cycles in 2017, 2018, and 2019 with surveys conducted from June to August. Initially, 4 types of riparian wetland habitats were distinguished based on an analysis of orthophoto maps (Geodesy and Mapping Center), field surveys, and hydrological data: I wet, II semi-wet, III semi-dry, and IV dry in the studied section of the floodplain (Figure 1).

To assess whether the four identified riparian habitat zones, corresponding to the influence of the duration and frequency of river floods, affect the distribution and composition of vegetation communities, we applied ecological indicator values as the most common and sufficiently effective method [46]. Thus, indicator values for soil moisture (SM_E), fertility (F_E), reaction pH (R_E), soil granulometry (SG_E), and organic matter content (OM_E) were adopted from Zarzycki et al. [47]. Indicator values were calculated based on in situ observations of plant species distribution/occurrence and assigned to a 5-point scale (weighted average). For species for which Zarzycki et al. [47] provided ranges of values, the average values from these ranges were taken. Only average indicator values from plots where at least three species with known indicator values were present were considered in the analysis. At each point where zone-specific vegetation was present, survey plots (10 $\times$ 10 m) were located to within 1 m using a GPS receiver. A total of 25 phytosociological relevés (vegetation plots) were conducted in 2017 and 25 phytosociological relevés (vegetation plots) were conducted in 2019. In the assemblages of *Agropyro-Rumicion crispi*, 16 phytosociological relevés (vegetation plots) were created, while *Phragmitetum australis*, *Phalaridetum arundinaceae*, and *Lysimachio vulgari—Filipenduletum* all had 3 plots each. A list of plant species was compiled for each plot, including a rating of the plants using a modified Braun–Blanquet 9-point scale. Plant community diversity was analyzed in four riparian habitat zones of the Supraśl floodplain using the species richness index (S), Shannon–Wiener diversity index (H') [48,49], Margalef index (R) [49], Simpson dominance index (D), and Pielou evenness index (J') [50]. The names of plant taxa were adopted after Szwed et al. [51]. The syntaxonomic nomenclature was adopted according to Ratyńska et al. [52].

It should be noted that the designated riparian habitat zones were also used as pastures for the Konik Polski, also known as the Polish horse (Konik means short horse), a semi-wild breed used mainly for conservation grazing. The studied section of the river floodplain is adjacent to extensively used cropland (cereals).

2.4. Statistical Analyses

Statistical analyses were performed to evaluate the effects of hydrologic factors on plant species distribution. The normality and homogeneity of variance assumptions were evaluated using Shapiro–Wilk and Levene's tests. For comparison between the means of biodiversity parameters in wet and dry years as well as riparian moisture zones, we performed an analysis of variance (one-way ANOVA) with Student's *t*-test and Tukey's HSD test as a post hoc procedure, respectively. Correlation analysis was used to evaluate the relationship between water level and vegetation occurrence.

To evaluate whether plant species could quantitatively represent different riparian habitat types (moisture zones) along a lateral moisture gradient, we ordinated riparian herbaceous vegetation data using linear discriminant analysis (LDA) in statistic package PAST 4.03 (Natural History Museum—University of Oslo, Norway) [53]. Major vegetation types were applied to establish the discriminant functions, and then the samples were classified into predicted vegetation zones. Based on the comparisons between a priori groups and predicted groups, riparian moisture zones were introduced to quantitatively interpret the results.

To identify vegetation communities with an affinity for a particular habitat type, indicator species analysis (ISA) [54] was used. The ISA value is calculated as the product of relative species abundance and frequency of occurrence to obtain a maximum indicator value (IV) for each species. Each species is then assigned to the group for which it has the highest indicator value. Indicator values range from 0 to 100, with a value of 100 representing a perfect indicator species, i.e., a species that occurs exclusively in one group, is found in all samples in that group, and has a high relative abundance within that group. A value of zero represents a species that has no indicator value for any group, is generally either rare in the data set, or occurs with a nearly uniform distribution in all or most groups [55]. Statistical significance of ISAs is assessed by a randomization procedure with 999 random permutations. Taxa that were significant at the 0.05 level were considered indicator species. The ISA was performed in PC–ORD version 6.0 developed and distributed by MjM Software (Gleneden Beach, OR, USA) [56].

3. Results

3.1. Hydrological Characteristics

Analysis of long-term hydrological data (2006–2020) for the Supraśl River showed a typical flood pulsing system (Figure 2). Due to intensive precipitation and snow melt, the year 2017 was characterized by extremely wet conditions, while 2018 was average and 2019 was classified as a dry year.

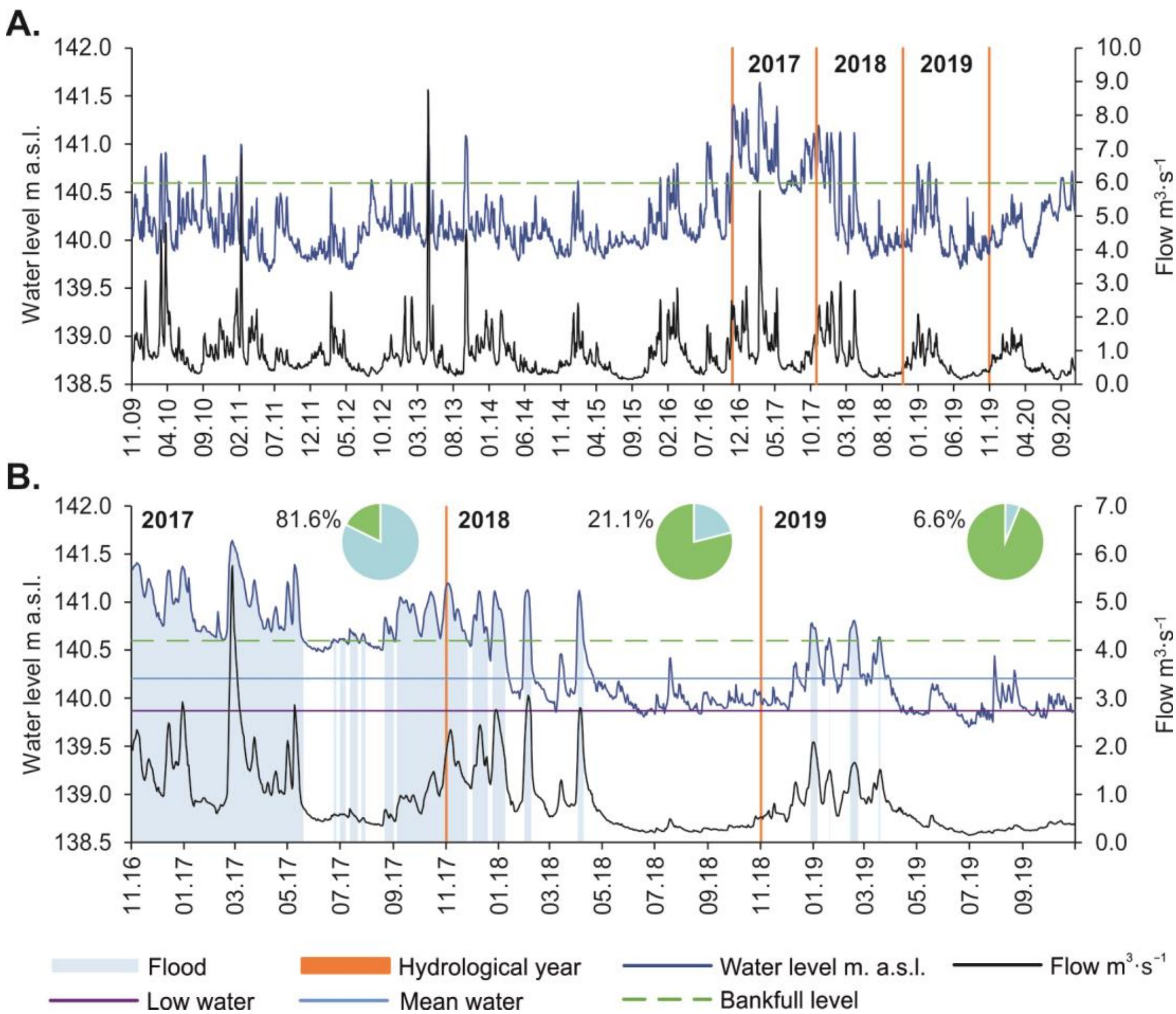


Figure 2. Hydrograph of pulsing water table of the Supraśl River: (**A**) 2010–2020, (**B**) 2018–2020. Low water = environmental flow. Blue slices in the circles denote % of days with floods, while green with no floods (below bankfull level).

Water levels of the Supraśl River exceeded the bankfull level in the wet year 2017 for almost 81.6% of days, while in 2018, it was 21.1%, and in the dry year 2019, they were only exceeded 6.6% of days. During 2017, the flood covered the entire study area and reached a maximum stage of 109 cm above the edge of the riverbed. In 2018, the maximal water stage was 64 cm above the riverbanks, and in 2019, it was only 26 cm.

3.2. Riparian Habitats

Within the study area, the dominant species were floodplain grasslands represented by species from the *Agropyro–Rumicion crispi* alliance. On the fringes of a large complex of floodplain grasslands, riverside herbaceous plants with *Filipendula ulmaria*—anthropogenic or partially natural herbal communities along watercourses developed. These are ecotone areas between the watercourse, which are moderately used for agriculture. Their species structure was unstable and most often corresponded to the characteristics of the *Lysimachio vulgaris–Filipenduletum* association. In the southern part of the area, the *Phalaridetum arundinaceae* rush was developing on marshy soils, touching the extensive *Phragmitetum* reed rush. Depending on the water conditions, they accompany the main species, mostly mud species from the *Calthion* alliance or herbaceous species from the *Filipendulion* alliance.

Various reaches and durations of the water table during flood pulsing across the naturally flat bottom of the Supraśl River valley contributes to specific riparian diversity patterns. The lateral zonation of vegetation formed by the reach of floods is presented in Figure 3.

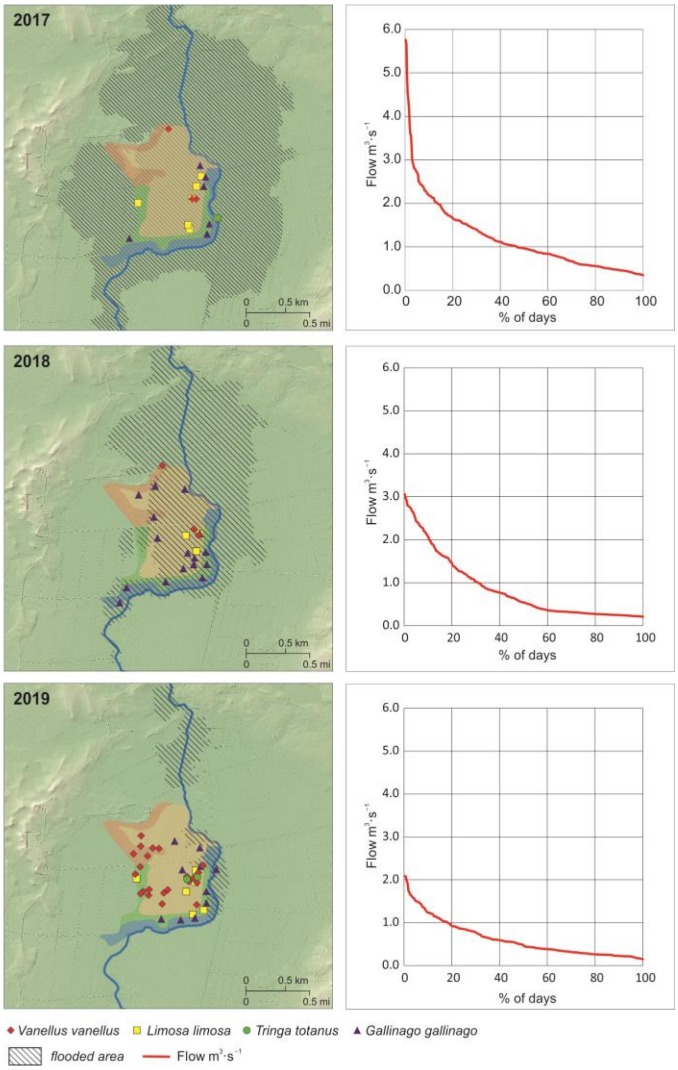
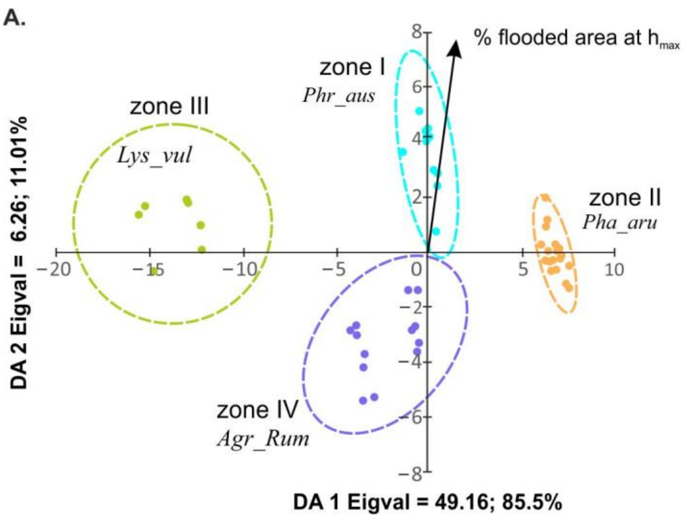


Figure 3. Left panel shows floodplain area flooded in 2017, 2018, and 2019 with the reach of riparian vegetation types and distribution of waterfowl species detected. Right panel shows diagrams with flow duration curves for the years of study, respectively. Data from 2017 to 2019 on the occurrence of valuable avifauna species are taken from the materials of the Polish Society for the Protection of Birds (PTOP, not published) and are included as a background characterizing the natural values of the studied section of the Supraśl River.

In consecutive years, flow duration curves for the wet 2017, average 2018 and dry 2019 years showed that the vegetation zone adjacent to the river bed is the most vulnerable to floods with flows as low as 2 $m^3 s^{-1}$, as noted in 2019. During the years of average conditions, when flow rates are as high as 3 $m^3 s^{-1}$ (2018), water covers the flat bottom. Flows as high as 3–6 $m^3 s^{-1}$ cause inundations of not only the flat floodplain area but also local convex forms as local sand bars. Under such conditions, certain phytocoenoses have adapted to wet and dry periods.

Based on the bird data for the study area provided by the Polish Society for the Protection of Birds (PTOP), we were able to determine a specific distribution of avifauna in relation to the reach of flood and vegetation zones (Figure 3). For example, during floods in 2017, when water depth exceeded 1.0 m, tall vegetation in zones I and II (shrubs and trees) was preferred by snipe (*Gallinago gallinago*), while black-tailed godwit (*Limosa limosa*) or lapwing (*Vanellus vanellus*) tended to prefer shallow waters in zone III. Waterfowl species were more widespread in the dry years of 2018 and 2019.

Based on hydrological and botanical data, four moisture habitat zones in the Supraśl river floodplain have been determined based on linear discriminant analysis (Figure 4a,b). LDA ordination yielded significant results when fitted with the percentage of flooded area at maximum inundation depth (h_{max}). The LDA best described the separation between moisture habitat zones. It indicated that the phytocenoses were distributed across the lateral floodplain gradient and the reach of floods, whereby zone I is more associated with riverbeds, zone II dominated by reed canary grass is associated with flat lands with shallow depressions that are flooded, zone III is principally overgrown by anthropogenic or partially natural herbaceous communities along watercourses and is associated with ditch networks, and zone IV creates floodplain riparian meadows on uplands flooded on extremely wet occasions.



B.

Confusion matrix

Given groups	Predicted groups: 4	3	2	1	Total
4	13	0	0	0	13
3	0	19	0	0	19
2	0	0	7	0	7
1	1	0	0	10	11
Total	14	19	7	10	50

100% correctly classified
98% jackknified

Figure 4. Linear discriminant analysis biplot (**A**) and confusion matrix (**B**) for plant species distribution in moisture habitat zones in the Supraśl River floodplain. Denotations of dominant communities: *Agr_Rum: Agropyro-Rumicion crispi*; *Phr_aus: Phragmitetum australis*; *Pha_aru: Phalaridetum arundinaceae*; *Lys_vul*: *Lysimachio vulgari—Filipenduletum*. Zone: I moist (reed rush), II semi-moist (reed canary grass), III semi-dry (anthropogenic or partially natural herbaceous communities along watercourses), IV dry (floodplain riparian meadows) in the studied section of the Supraśl floodplain.

Biodiversity indicators showed statistical differences between zones (Figure 5) apart from the number of taxa and evenness. The highest differences in biodiversity were stated among the most remotely located zones I (H′ = 0.6) and IV (H′ = 1.45). In zone I, a clear dominance of the rush vegetation was observed and supported with dominance index D = 0.7. Differences between zones were also shown for indicator values of SM_E, F_E, R_E, SG_E, as well as OM_E, and they are attached in the Supplementary Materials (Tables S1 and S2).

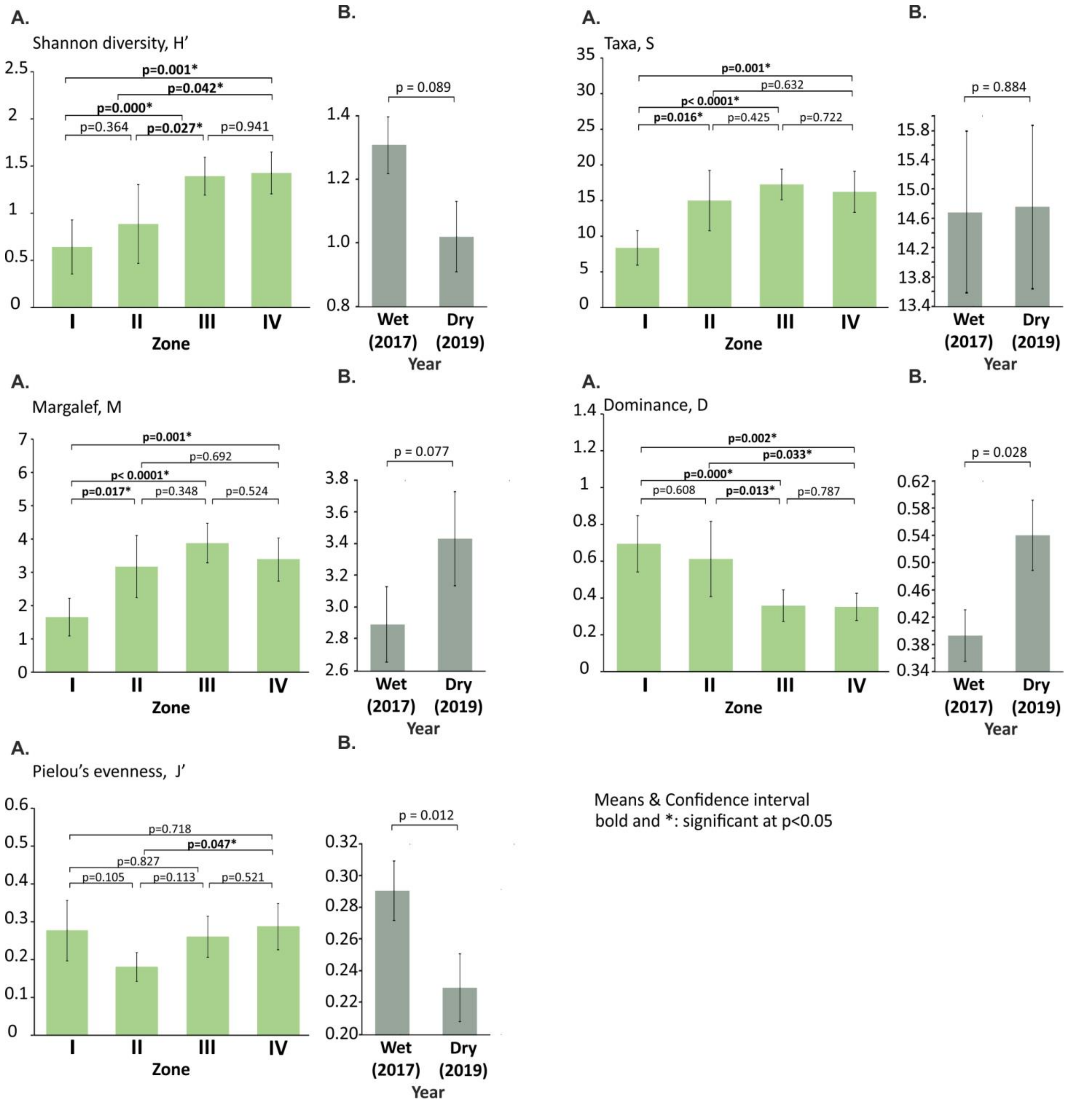


Figure 5. Biodiversity indices (mean ± SEM) of vegetation communities for (**A**) moisture zones and (**B**) wet and dry years in the Supraśl River floodplain (one-way ANOVA): (**A**) the Tukey's test as a post hoc procedure; (for (**B**) Student's *t*-test); *p*-value—Monte Carlo method after Bonferroni correction.

3.3. Indicator Species

Considering the relative abundance of 87 species in the four zones, we found species that indicate changes in moisture conditions (Table 1). The highest number of indicator species (9) was found in the dry zone (IV), representing floodplain herbaceous meadows and in the ecotone zone formed by semi-wet (II), which is represented by reed canary grass rushes. The number of indicator species was lower in the other two zones where the water conditions were more stable.

Table 1. The indicator species analysis (ISA). List of plant species characteristic for the different moisture conditions in the Supraśl river floodplain. Moisture riparian zones were defined by hydrology and plant communities criteria [54].

Moisture Riparian Zone	Species *	Observed Indicator Value (IV)	IV from Randomized Zones		*p*-Value **
			Mean	±SD	
I Wet	*Phalaris arundinacea*	80.5	32	8.98	0.0002
	Phragmites australis	55.3	16.7	7.3	0.0016
	Symphytum officinale	45.5	12.2	6.63	0.0008
	Urtica dioica	34.9	13.3	6.89	0.0132
	Alisma plantago-aquatica	27.3	10	5.48	0.0304
	Galium palustre	27.3	9.6	5.6	0.0112
	Carex rostrata	18.2	8.9	4.8	0.0720
II Semi-wet	*Filipendula ulmaria*	88.6	21.7	7.33	0.0002
	Galium palustre	71.4	11.9	6.49	0.0004
	Cirsium rivulare	70.4	16.4	6.88	0.0002
	Potentilla erecta	53.6	15.3	7.46	0.0010
	Veronica scutellata	52.7	13.7	6.83	0.0006
	Agrostis capillaris	42.9	9.6	5.55	0.0018
	Galium mologo	34.7	19.8	7.4	0.0444
	Achillea monticola	28.6	8.5	4.6	0.0204
	Galium aparine	28.1	9.9	5.5	0.0106
III Semi-dry	*Deschampsia caespitosa*	70.3	39.6	11.53	0.0134
	Festuca arundinacea	61.5	30.3	9.82	0.0092
	Lythrum salicaria	51.8	29.8	10.13	0.0296
	Epilobium palustre	44.5	21.1	7.25	0.0132
IV Dry	*Anthoxanthum odoratum*	76.1	22.7	9.03	0.0002
	Achillea millefolium	72.3	26.7	9.71	0.0010
	Lychnis flos-cuculi	56.5	23.9	6.76	0.0012
	Juncus compressus	52.1	23.2	7.4	0.0052
	Festuca pratensis	50.9	29.4	7.06	0.0114
	Potentilla anserina	49.2	23.9	7.28	0.0066
	Vicia cracca	41.6	16.1	7.55	0.0096
	Taraxacum officinale	30.8	10.1	5.68	0.0132
	Leontodon autumnalis	68	27.9	8.04	0.0002

Note(s): * only statistically significant species are presented; Monte Carlo test of significance of observed maximum indicator value for variable after 4999 permutations. ** proportion of randomized trials with indicator value equal to or exceeding the observed indicator value *p*-values = (1 + number of runs ≥ observed)/(1 + number of randomized runs). Zone = group identifier for group with maximum observed II and IV.

ISA analysis (Table 1) showed that among indicator species with high water requirements, *Phalaris arundinaceae* (IV = 80.5, p = 0.0002) and *Phragmites australis* (IV = 55.3, p = 0.0016) dominate. Both species in wet zone I form well-developed and low-impacted riparian galleries. At the other extreme (IV dry zone), remotely located from the riverbed were phytocoenoses composed of simpler communities characterized by species adapted to dry conditions and with occasional flood disturbances such as *Anthoxanthum odoratum* (IV = 76.1, p = 0.0002), *Achillea millefolium* (IV = 72.3, p = 0.001), *Leontodon autumnalis* (IV = 68.0, p = 0.0002), and *Lychnis flos-cuculi* (IV = 56.5, p = 0.0012). For semi-wet zone II, ISA produced the highest values for *Filipendula ulmaria* (IV = 88.6, p = 0.0002), *Cirsium rivulare* (IV = 70.4, p = 0.0002) or *Galium palustre* (IV = 71.4, p = 0.0004), while semi-dry zone III showed the highest values for *Deschampsia caespitosa* (IV = 70.3, p = 0.013), *Festuca arundinaceae* (IV = 61.5, p = 0.009), or *Lythrum salicaria* (IV = 51.8, p = 0.030).

4. Discussion

4.1. Patterns of Vegetation Diversity in Riparian Zones of Rivers

River floodplains are among the areas with the highest biodiversity, as these areas represent habitats with high levels of structural and functional dynamics, which are mainly induced by a hydrological regime [57]. Natural riparian landscapes are covered by mosaics of habitats differing in age, moisture, sediment characteristics, productivity, biota diversity, abundance, composition and successional status [58].

Considering the dynamic nature of river floodplains, we defined a tool that allows for understanding the relationship between the structure and functioning of a wetland ecosystem and hydrological changes in the river. The obtained results allowed us to simplify the complex ecosystem of river wetlands into a concept, combining the structure and pattern of wetland plants controlled mainly by both hydrological regime of the river and a pattern of hydrogeomorphic features of riparian area, as shown in Figure 6.

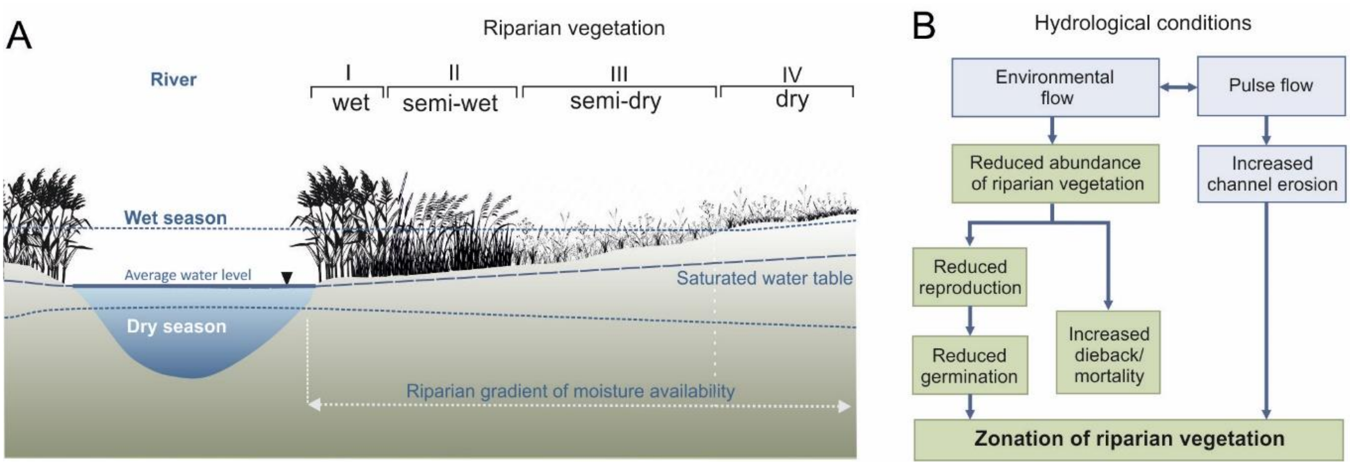


Figure 6. A sketch of riparian zonation in relation to river stage in a lowland river floodplain (**A**). Effects of hydrological conditions on vegetation in riparian area (**B**).

This concept takes into account both physical and biological elements that influence the dynamics and patterns of inundation along the river. Additionally, we considered various biological aspects of the wetland ecosystem, such as vegetation types, habitat types, and their interrelationships. Based on these data, we are able to forecast how changes in river water levels affect habitat availability, biological diversity, and the functions of the wetland ecosystem.

The natural decrease in the degree of hydration, determined by the relief of the terrain and the efficiency of the drainage network, resulted in variations in the floristic composition of floodplain grasslands. Within the river floodplain, flood disturbance and water availability vary along lateral gradients; over the length of the river, the intensity and frequency of flood disturbance decreases with increasing distance from (and above) the active channel, paralleling the increase in floodplain elevation resulting from sediment aggradation and riverbed incision processes [59]. Thus, changes in the hydrological regime set up patterns of plant species diversity in river riparian zones, which is in line with the works of other authors [60–62]. Our hydroecological analysis performed on the example of the Supraśl River floodplain (NE Poland) presents significant results by coupling the wetland landscape ecology into hydrological units.

Based on them, the composition of wetland communities in riparian biophysical habitats varies along a lateral hydrological gradient. The distribution, extent, and abundance of wetland communities increase progressively from herbaceous communities through marshes within the riverine zone, reflecting a moisture gradient. Simultaneously, the predominant patch area and quantity shift as transitional meadow communities replace them beyond the riverine zone. Floodwater plays a pivotal role in regulating the distribution of wetland communities within the studied floodplain. The typical marsh communities in the saturated zone give way to a broader distribution of wet meadows in the seasonally saturated zone, which is eventually supplanted by the predominant presence of wet meadows in the yearly unsaturated zone. Additionally, a cluster analysis of quantitative spatial characteristics reveals numerical distinctions between marshes and non-marshes in the core of the floodplain, further emphasizing the influence of hydrological factors on wetland community composition.

Vegetation locally reduces stream gradient stress across the floodplain. Disturbance regimes influence plant species diversity at local scales [63] through increasing groundwater depth and decreasing the replenishment of shallow soil moisture by overbank floods [64]. A zonal vegetation in floodplains is shaped by broad hydrological gradients, periodic flooding [65] and, to a lesser extent, soil composition [66]. Species that prefer wet microhabitats grow and survive longer compared to those in dry microhabitats [66].

4.2. Changes in Vegetation Cover Due to Hydrological Variations

Our results (Figure 5) confirmed that riparian vegetation is a suitable environmental change indicator that responds directly to the flow regime in an inter-annual timeframe [67,68]. We have shown that vegetation cover changes as a result of flooding and subsequent drying in the higher parts of the floodplain, which is consistent with the results of Kleinhans et al. [59].

The intermediate intensity or frequency of disturbance (or length of time since disturbance) should result in the highest levels of diversity by allowing a mixture of species adapted to stable environments and species adapted to frequent disturbance to coexist, although the magnitude of the effect may be small [69,70]. Plant indicator systems in the riverbed are well known [71–73]; however, they do not cover the vegetation of the flood zones of the river valley. This is due to the limitations of river monitoring systems, which do not include assessments of river valley biodiversity. As a result of our research, we have also identified a set of indicator species that represent the variability of the river’s impact on floodplain vegetation. Low flows were mostly regarded as negative both for aquatic organisms [74] and for riparian vegetation [75]. It could be proven that the species is able to outlast unsuitable conditions as long as seeds are remnant in the seed bank and that the negative effects of the new floodplain stream on the target species can be compensated sufficiently. Literature data [66,76] indicate that the duration of the withdrawal period must be long enough (here, germination is observed after 3 weeks, and there is at least another 3 weeks for rooting) to ensure successful establishment of the target species. If this period is too short, or if the water level rises significantly again, the seedlings may be fatally damaged [76] and the seed bank may be depleted without new seeds being produced. On the other hand, if the period of drought is too long, more competitive reed species may become established and outcompete the target species. Vegetation is in a fluctuating equilibrium that changes over time [77]. In a dry year, there may be large areas of typical terrestrial vegetation, whereas in wet years, reed species or aquatic plants may dominate [78]. Floodplain vegetation is able to recover from disturbances (floods or dry years), and a resilient system needs even these extreme events from time to time to reduce strong competitors [79,80]. Thus, if humans want to restore floodplains that suffer from static water conditions, dynamically changing water conditions need to be restabilized at irregular intervals, just as nature would do. If the release of water into the floodplain is controlled by humans through sluices (rather than automatically through spillways in the embankment; [81]), the hydrological objectives and target habitats and species must be clearly defined. Plant species characteristic of the various moisture conditions in the floodplain (Table 1) should be monitored to evaluate the effectiveness of potential restoration efforts.

4.3. Impact of Unstable River Valley Environment on Other Natural Values

The unstable environment of the river floodplain, combining the high dynamics of plant succession with frequent habitat restoration due to flooding, is inhabited by unique bird communities adapted to such conditions (Figure 6). Changes in the river environment, which limit the extent and frequency of flooding, are usually associated with climate change or anthropogenic transformations [6,7]. We observed that changes in the moisture content of the Supraśl Valley and the introduction of the Konik polski population in 2019 caused a reconstruction of meadow-breeding waders. Horses on a pasture influence the grass not only by grazing but also by trampling, rolling and leaving droppings. The year-round grazing of Konik polski horses, kept at a low stocking rate in the Supraśl Valley, has little effect on the grassland communities. The impact of the presence of horses was mainly manifested by changes in the structure of the sward and a reduction in the sward cover [82]. The droughts in the Supraśl Valley favored the growth of the populations of lapwing and black-tailed godwit, but they did not cause changes in the use of the Supraśl Valley by redshank, and they reduced the abundance of snipe. The black-tailed godwit and the redshank seem to have special needs, i.e., large wet meadows with large areas flooded in spring, where extensive cattle grazing takes place and where no additional fertilizer is used [83]. Our studies show that the lapwing has the highest tolerance to changes in meadow moisture, while the snipe has the lowest, which is also confirmed by field observations of other authors [84–86].

The results of this study provide valuable information regarding the relationships between wetland vegetation structure and hydrological changes in rivers. Riparian wetland ecosystems play a crucial role in maintaining biological diversity. By examining the impact of water level changes in rivers on habitat availability and the biological diversity of wetland ecosystems, we aim to better understand the complex interactions between riparian ecosystems and river hydrology. Our research, as well as that of Osmundson et al. [87] and Obolewski et al. [88], suggests that river valley restoration should begin with the identification of physical and biological pathways linking flow changes with ecological functions and species responses.

This knowledge can serve as a basis for conservation efforts, sustainable management practices, and decision-making processes aimed at preserving the biological diversity and ecological integrity of riparian ecosystems in similar regions. Monitoring and detailed solutions for the use of the floodplain should be included in the management of nature conservation forms (in case of the Supraśl floodplain, the task plan for the protection of the Natura 2000 site) after public consultation and then implemented in the water management plan (a mandatory document for water management authorities). By understanding the dynamics of riparian wetland ecosystems and their response to hydrological changes, we can work toward the conservation and sustainable management of these important ecological systems.

5. Conclusions

The results of our study on the impact of hydrological conditions on the functioning of wetland ecosystems, using the example of the Supraśl floodplain located in central Europe, show that the natural flow regime, defined as flood pulse, is responsible for the development of site-specific phytocenoses adapted to local hydrological conditions. Maintaining the river's natural flow regime with seasonal and annual water changes is crucial to ensure optimal preservation of biodiversity in wetland ecosystems. The spatial heterogeneity of flooding along rivers and streams affects local species diversity. The composition of riparian vegetation depends on the extent and timing of flooding and, as such, can indicate the development of strategies for riparian area management, biodiversity conservation, and planning actions.

The example of the Supraśl River shows that dynamically fluctuating water conditions, floods and droughts that occur at irregular time intervals require a long-term observation period for reliable ecological monitoring of riparian wetlands. Therefore, a thorough understanding of the functioning of such ecosystems and the relationships within them is essential. Therefore, it is important to select and clearly define target groups from among the many competing floodplain habitat types. All these factors make the Supraśl River floodplain an important natural area that requires special protection and sustainable management. Preserving biodiversity, maintaining appropriate hydrological conditions, and using natural resources wisely are crucial for effective conservation and meeting the needs of current and future generations.

Then, the intended measures have to be conducted, and the resilient system will react. This approach should further minimize detrimental effects on other habitats which are not of first priority (in case of groundwater drawdown the aquatic habitats) but whose conservation is also compulsory, e.g., due to the EU Water Framework Directive. All stakeholders should be involved in this process in order to avoid discussions or even the suspension of measures during appropriate periods (e.g., natural floods or low water conditions).

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/w16010164/s1, Table S1: List of ecological indicators and plant species; Table S2: Analysis of variance (two-way ANOVA: year and zone) for ecological indicator values.

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