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Response of Aquatic Plants to Extreme Alterations in River Morphology

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Abstract: In this study, we aimed to identify the macrophyte pattern and diversity under exposure to substantial hydromorphological degradation in rivers, taking into account the water quality factor. The study was based on 190 small and medium lowland rivers in Poland that had experienced channel alterations. The number of taxa identified (153 species) was consistent with natural/seminatural rivers, and the average species richness for the survey site was 16. Nevertheless, nearly 25% of the survey sites were poor in species for which ten or fewer taxa were noted. The most common species were emergent *Phalaris arundinacea*; free-floating *Lemna minor*; heterophyllous *Sparganium emersum*; filamentous algae *Cladophora* sp.; and some amphibious species, including *Agrostis stolonifera*. The surveyed sites represented a wide diversity gradient, from sites poor in species and with low diversity based on relative abundance to highly diverse river sites in less transformed rivers. Our results revealed that macrophyte species were mostly determined by hydromorphological degradation, as well as other distinguished environmental factors, such as water trophy (e.g., *Lemna gibba*, *Bidens tripartita*, and *Ceratophylum demersum*) and channel dimensions (e.g., *Nuphar lutea*, *Sagittaria sagittifolia*, and *Typha latiflolia*).

Keywords: hydromorphological degradation; macrophytes; rivers; water quality

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1. Introduction

Hydromorphological modifications are one of the main pressures that influence aquatic biota and the ecological quality of freshwaters [1]. The importance of hydromorphological conditions for aquatic ecosystem health was recognised by the Water Framework Directive (WFD). Since then, heavily hydromorphologically modified water bodies have been required to be identified as ecosystems with specific conditions for the development of aquatic biota [2]. Therefore, the proper recognition of the relationship between biotic and abiotic components of an ecosystem is required for the effective monitoring of ecological status. It is also needed for the implementation of mitigation programs that are crucial for achieving compliance with water quality goals [3,4]. This is an ambitious challenge considering the underlying assumptions of ecosystem functioning, the practicalities and costs of its implementation, and the societal expectations that usually only extend to the short term [5,6]. Although pollution control, especially in terms of point sources, is being dealt with, the mitigation of hydromorphological pressures is much more challenging, and they are less prone to direct responses from biotic factors [7,8].

The impact of the hydromorphological modification of rivers on aquatic organisms has been the subject of many studies. Their results have demonstrated the influence of habitat quality on macrophytes [9–12] and other groups of aquatic organisms, such as fish and macroinvertebrates [13–16]. The response of aquatic biota to hydromorphological conditions depends strongly on the group of organisms, the specific type of alterations, and the scale of pressure and responses [13,17,18]. Fundamental changes in channel morphology may lead to the disappearance or merging of available habitats, alter the patterns of flow, and reduce the development of flora and fauna [19,20]. In altered and artificial substrates, only adapted organisms can exist [10,21–24]. Hydromorphological alterations also refer to changes in the hydrological conditions, including the energy and velocity of flowing water. In channelised, over-deepened reaches, the flow velocity increases, which affects both aquatic plants and animals [12,13]. Riparian cutting changes light conditions by reducing shade and affects shade-tolerant species [25] while benefiting species that prefer full sunlight (heliophiles) [10,26,27]. Other consequences of hydromorphological alterations include the appearance of synanthropic species typical of anthropogenic habitats, the loss of rare and sensitive taxa, and an increase in the abundance of tolerant species [28].

Natural or anthropogenic attributes of a river channel and habitat complexity and heterogeneity affect the development of specific macrophytes species, including their abundance, richness, and biodiversity [12,18,29–31]. Many studies indicate that the physical and chemical characteristic of water, and in particular eutrophication, are major factors determining macrophyte development [32–36]. Furthermore, aquatic vegetation development is also affected by hydromorphological conditions, including physical alterations [37]. Some macrophyte metrics used in ecological status assessment were found to respond to hydromorphological conditions [9,18]. It has been demonstrated that multiple stress situations, rather than single stressors, occur in most river systems [32]. Hydromorphological alterations and eutrophication are both related to human activity (e.g., settlement and agriculture) and very often occur together [38]. Meanwhile, it can be challenging to separate the individual impact of pressures on aquatic organisms in multi-stress situations [39]. Although the responses to hydromorphological alterations and eutrophication are frequently entangled, in heavily modified riverine water bodies, hydromorphological alterations may prevail [14].

Hydromorphologically modified rivers, through the simplification of the habitat structure, the introduction of artificial features, and hydrological alterations, constitute specific habitat conditions for the development of macrophytes [13]. This type of habitat is also often influenced by pressures related to anthropogenic changes in the catchment, including pollution from agricultural and urban areas [7,39]. Previous studies often lacked a clear indication of the individual taxa of macrophytes that developed in artificially modified rivers and their relationships with the major factors affecting macrophytes in this type of ecosystem. Therefore, this study was based on a comprehensive database covering details related to morphological habitats, hydrochemical parameters, and biological records. The research goals were to investigate the impact of hydromorphological degradation on macrophyte communities and to identify specialist species that can thrive in heavily modified rivers. Moreover, we attempted to estimate the variability of macrophyte metrics under extensive hydromorphological alterations. We hypothesised that in heavily modified rivers, hydromorphological conditions stimulate the development of particular plant communities that disturb the bioindicative signals based on botanical indices.

2. Material and Methods

This study was based on 190 study sites located in 177 rivers. They were surveyed in the years 2007–2014 and provided a broad representation of Polish rivers (Figure 1). All surveyed rivers were small and medium lowland rivers characterised by low habitat quality and the implementation of channel alterations (mainly straitening, resectioning, and strengthening), thus lacking natural hydromorphological features due to the current or prior alterations. In the sites analysed, there were no elements causing strong flow regulation (e.g., impoundments). All sites were located mostly in urban or suburban areas, as well as in intensively used agricultural land. Study sites represented a broad range of water quality conditions, particularly in terms of water trophy (Table 1).

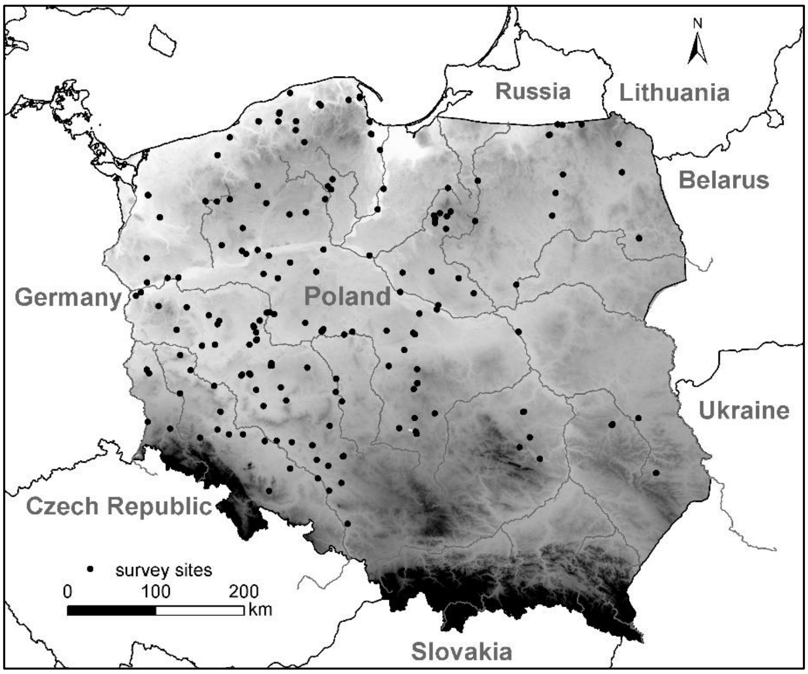

Figure 1. Location of the surveyed sites.

Table 1. Details of hydromorphological and physicochemical parameters used in the study.

Variable	Shortcut	Unit	Minimum	Maximum	Mean	Median
Conductivity	Cond.	µS/cm	150	2250	606	531
Alkalinity	Alkal.	mg $CaCO_3$/L	50	490	192	175
Reactive phosphorus	PO_4-P	mg PO_4/L	0.02	4.40	0.34	0.19
Total phosphorus	TP	mg P/L	0.03	2.56	0.38	0.28
Nitrate nitrogen	NO_3-N	mg N/L	0.02	5.74	0.92	0.60
Ammonia nitrogen	NH_4-N	mg N/L	0.01	7.75	0.45	0.21
Total nitrogen	TN	mg N/L	0.71	26.77	3.85	3.23
Dissolved oxygen	DO	mg 0_2/L	0.80	22.32	8.17	8.18
Channel width	Width	m	0.65	15.00	5.12	4.00
Channel depth	Depth	m	0.05	3.50	0.66	0.50
Habitat Quality Assessment	HQA	-	6	52	27	27
Habitat Modification Score	HMS	-	11	108	62	59

2.1. Hydromorphological Survey

Detailed hydromorphological studies based on the River Habitat Survey (RHS) were conducted in each study site spanning 500 m along the river [40]. Variables characterising all sites were calculated based on data obtained from the field surveys. These variables included two synthetic hydromorphological indices: Habitat Quality Assessment (HQA), which provides information on the degree of naturalness of a river; and Habitat Modification Score (HMS), which reflects the degree of anthropogenic changes in a river channel. Both indices were used to classify the studied sites into one of five classes of hydromorphological status. One hundred and ninety analysed river sites were in the 4th (poor status) or 5th (bad status) classes according to RHS method. In addition, data on the river size (depth and width) were considered.

2.2. Water Quality Survey

Water samples were collected during the summer season from each sampling site. Conductivity and dissolved oxygen were determined using portable equipment (*Elmetron CPC-105* and *Elmetron GO-105k*). Other parameters were determined in the laboratory of

Poznan University of Life Sciences within 24 h of collection. Alkalinity was measured with sulphuric acid to an endpoint of pH 4.5 in the presence of methyl orange. Concentrations of phosphate (molybdenum blue method), total phosphorus (molybdenum blue method after microwave mineralisation in MARS 5X), nitrate nitrogen (cadmium reduction method), and ammonium nitrogen (Nessler's method) were determined using a HACH-LANGE DR/2800 spectrophotometer.

2.3. Macrophyte Survey

Aquatic vegetation studies were carried out following the Macrophyte Index for Rivers (MIR) method, which was developed in Poland for assessing ecological status under the WFD requirements [36]. This method is based on a qualitative and quantitative inventory of all macrophytes identified in 100 m stretches along the river within the RHS survey areas. Each species that grew in the water for at least 90.0% of the vegetation season was recorded during the survey. The botanical survey in the rivers included all groups of aquatic plants: monocotyledonous and dicotyledonous plants, pteridophytes, mosses, liverworts, and filamentous algae. Groups of plants that were difficult to identify in the field, such as bryophytes, macroscopic algae, *Potamogeton* sp., or *Ranunculus* sp., were collected and then identified in the biological laboratory using a microscope. The abundance of each taxon was estimated using the following nine-point scale: <0.1%, 0.1–1%, 1–2.5%, 2.5–5%, 5–10%, 10–25%, 25–50%, 50–75%, and >75%. Based on the field data, species richness (N) and the total abundance of macrophytes defined as the coverage of the channel surface (p_i) were calculated. Moreover, two metrics containing the relative abundance of species (the Shannon index (H) [41] and the Simpson index (D) [42]) were calculated proposed by Jost (Shannon exponential—^{1}H; Simpson concentration—^{2}D) [43]. This correction changed the entropy represented by both indices into diversity (the effective number of species).

2.4. Statistical Analysis

A group of the most common taxa was selected based on frequency analysis. The environmental characteristics consisting of 16 variables (Table 1) covering water quality parameters and hydromorphological variables were treated by factor analysis (FA) [44]. Based on a scree plot, the dimensionally of the dataset was reduced to four constructed FA gradients, revealing the main directions of habitat variability in the modified river stretches. The effect of habitat factors on the development of the most frequent macrophytes (frequency $\geq$10.0%) was evaluated by canonical correspondence analysis (CCA) [45]. This analysis utilised FA gradients (eigenvalues) as environmental variables. The variance explanation of all variables was carefully determined. The full model of the Monte Carlo permutation test (499 permutations) was used to evaluate the significance of the selected environmental variables. The macrophyte indices responses to different environmental variables were analysed by Pearson's correlation coefficient. Each environmental variable was separately correlated to macrophyte metrics, including the MIR index, macrophyte abundance, and diversity indices.

3. Results

In total, 153 taxa were identified among all surveyed sites. An average of 16 species were found per standard 100 m survey site; however, the number of macrophytes varied significantly, from 2 to 40. Almost half of the study sites (n = 90) were poor in terms of species, and the number of macrophyte species ranged between 11 and 20 taxa. Regarding species richness, in nearly one fourth of the sites (n = 47) only ten or fewer taxa were noted. In another quarter of the sites (n = 48), 21–30 taxa were recorded, and 30 or more taxa were found for only five sites (Table S1).

Frequency analysis revealed a large group of plants that occurred occasionally. One third of the taxa occurred in only one or two sites, and the frequency for these plants was lower than 1.5%. The frequency of more than half of the plants identified (97 taxa) was lower than 10%. This meant that 64% of the taxa occurred in a maximum of 18 sites.

Only 20 taxa had a frequency ≥25% (Table 2). The analysis showed that the most frequent species were an emergent plant *Phalaris arundinacea*, which occurred in 73% of the surveyed sites, followed by the free-floating plant (pleustophyte) *Lemna minor* at a frequency of 66% and the heterophylly hydrophyte *Sparganium emersum* occurring at 55%. The fourth and final species exceeding a frequency of 54% was *Cladophora* sp., the first of the nineteen filamentous algae taxa. We did not find any submerged macrophyte species among the top ten species. We found seven emergent plants; two free-floating plants; and *S. emersum*, a species that may appear in multiple forms (emergent, submerged, and free-floating) due to its high morphological plasticity. The first two exclusively submerged species were *Callitriche cophocarpa*, which also showed a small proportion of floating leaves, and *Elodea canadensis*; these were followed by *Potamogeton pectinatus* at a frequency just above 30%. Among the most frequent macrophytes was the first of eleven identified bryophytes, *Leptodictyum riparium*, which was present in a quarter of sites.

Table 2. List of the most frequent species occurring in the studied modified river stretches (frequency ≥25%).

Taxon	Group of Macrophytes	Number of Sites	Frequency
Phalaris arundinacea L.	emergent	138	73%
Lemna minor L.	free-floating	125	66%
Sparganium emersum Rehmann	emergent, submerged, floating leaved	105	55%
Cladophora sp. Kütz.	macroscopic algae	102	54%
Agrostis stolonifera L.	emergent, amphibious	86	45%
Myosotis palustris (L.) L. em. Rchb.	emergent, amphibious	84	44%
Sparganium erectum L. em. Rchb.	emergent	84	44%
Rorippa amphibia (L.) Besser	emergent, amphibious	84	44%
Spirodela polyrhiza (L.) Schleid.	free-floating	82	43%
Glyceria maxima (Hartm.) Holmb.	emergent	80	42%
Callitriche cophocarpa Sendtn.	submerged	62	33%
Elodea canadensis Michx.	submerged	62	33%
Mentha aquatica L.	emergent, amphibious	62	33%
Potamogeton pectinatus L.	submerged	61	32%
Ranunculus repens L.	emergent, amphibious	61	32%
Berula erecta (Huds.) Coville	emergent, submerged	59	31%
Sagittaria sagittifolia L.	emergent, submerged, floating leaved	55	29%
Veronica anagallis-aquatica L.	emergent, submerged	51	27%
Glyceria fluitans (L.) R.Br.	emergent, amphibious	47	25%
Leptodictyum riparium (Hedw.) Warnst.	bryophyte	47	25%

Based on the macrophyte survey list, four diversity indices were calculated (Table 3). The results showed a large variation in the biodiversity indices values between sites. Species richness in the studied sites ranged from 2 to 40 taxa. This differentiation was similar to that in the values of the corrected Shannon and Simpson indices, as well as the abundance of plants in the sites. This meant that, taking into account a certain variation in the hydromorphological quality of the study sites (Table 1), the prevailing conditions (the strongest transformations) resulted in a significant unification of the occurring plants; on the other hand, moderate transformations allowed not only the abundant development of macrophytes, but also their significant variety in terms of species composition and evenness.

Table 3. Variation in macrophyte diversity indices in the hydromorphologically altered river sites.

Variable	Symbol	Minimum	Maximum	Mean	Median
Abundance (cover)	p_i (%)	0.25	100.00	34.48	28.75
Shannon exponential	^1H	1.04	15.83	4.96	4.38
Simpson concentration	^2D	1.01	12.16	3.47	2.86
Species richness	N	2	40	16	16

A matrix of twelve habitat parameters was explored by factor analysis, identifying the major directions of variability in the modified river habitats (Table 4). The first four components explained over 60% of the total environmental variation within the river habitats. The first component was associated with water pollution, mostly phosphorus content. The second component was related to channel dimensions. The third factor was also associated with water quality parameters, nitrates, and total nitrogen. Hydromorphological quality, both naturalness (Habitat Quality Assessment) and modifications (Habitat Modification Score), was revealed as the fourth factor due to the fact that only modified rivers were analysed, and the hydromorphological gradient was relatively narrow.

Table 4. Factor analysis results for 16 environmental variables.

Variable	1st Factor	2nd Factor	3rd Factor	4th Factor
	Phosphorus Pollution	**Channel Dimensions**	**Nitrogen Pollution**	**Habitat Degradation**
Habitat Quality Assessment	−0.172	−0.095	−0.022	**−0.797**
Habitat Modification Score	−0.089	−0.162	−0.122	**0.762**
Conductivity	**0.648**	−0.199	0.113	0.037
Alkalinity	**0.726**	−0.115	−0.117	−0.027
Reactive phosphorus	**0.806**	0.028	−0.028	−0.047
Total phosphorus	**0.752**	0.090	0.082	0.113
Nitrate	−0.018	−0.047	**0.855**	−0.053
Ammonia	0.600	−0.020	0.285	0.009
Total nitrogen	0.336	0.069	**0.653**	−0.221
Dissolved oxygen	−0.042	−0.152	0.544	0.423
Channel width	−0.139	**0.893**	−0.057	−0.031
Channel depth	−0.008	**0.912**	−0.023	−0.066
% of explained variance	22.5%	14.6%	13.2%	12.2%

Figures in bold are factors higher than 0.6.

The canonical correspondence analysis (CCA) revealed the preferences of different indicator taxa reflecting the environmental variables. CCA was performed for the 56 taxa that occurred most frequently in the studied rivers (frequency $\geq$10.0%). The main factors identified via factor analysis were used as environmental variables in the CCA, and the results are shown in Figure 2. The chart covers the two axes of the CCA, which together explained 75.6% of the species–environment relationship (Table 5).

Table 5. Results of canonical correspondence analysis for species–environment relations.

Axes	1	2	3	4	Total Interia
Eigenvalues	0.132	0.070	0.047	0.018	3.653
Species–environment correlations	0.716	0.583	0.610	0.441	
Cumulative percentage variance					
of species data	3.6	5.5	6.8	7.3	
of species–environment relation	49.5	75.6	93.3	100.0	

Monte Carlo unrestricted permutations (499 permutations) proved that habitat quality and phosphorous pollution had a significant influence on macrophyte development (p = 0.002). Analyses showed that channel dimensions had the strongest influence (initial extra fit = 0.122), followed by habitat quality (0.072) and phosphorous pollution (0.50).

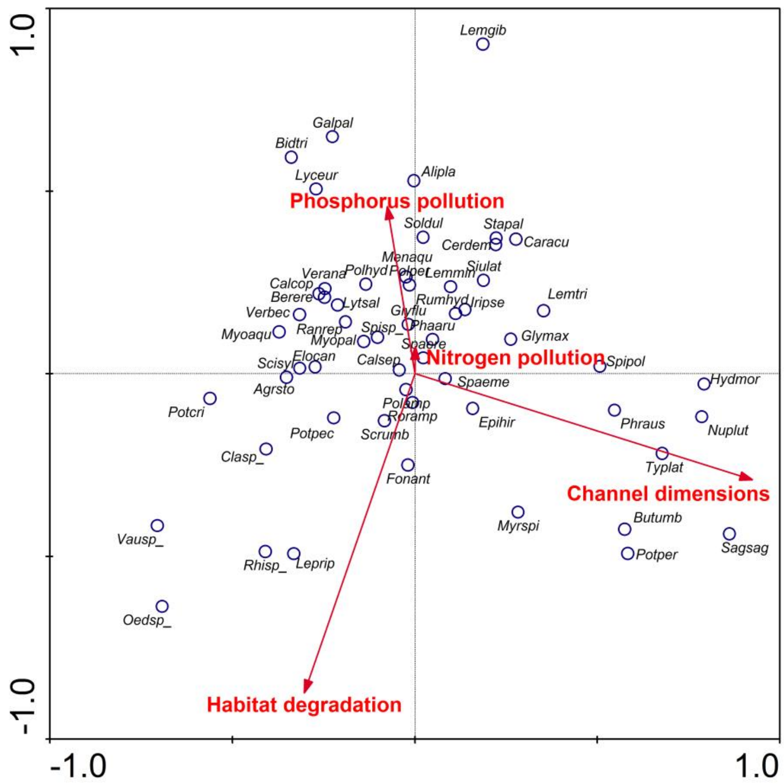

Figure 2. CCA of 56 most frequent species (frequency ≥10%) and environmental variables (PCA factors). A description of the abbreviations is provided in the Supplementary Materials (Table S1).

The CCA revealed a group of species with specific environmental preferences. Several species were found to be positively related to channel dimensions (channel depth and width). These macrophytes represented a diverse ecological group, including submerged *Potamogeton perfoliatus* and *Nuphar lutea* (with floating leaves), free-floating *Hydrocharis morsus-ranae*, emergent *Typha latifolia* and *Phragmites australis*, and heterophile *Sagittaria sagittifolia* and *Butomus umbellatus*. Analysis proved a clear positive relationship between habitat degradation (hydromorphological quality, represented by the two indices Habitat Quality Assessment and Habitat Modification Score) and three macroalgae taxa: *Rhizoclonium* sp. (in particular); *Vaucheria* sp.; and *Oedogonium* sp., which was also one of the most frequent taxa (occurring in about 20% of sites). In this group, we also found one moss species, *Leptodictyum riparium*, which demonstrated tolerance to habitat degradation. A higher level of nutrients (mainly a higher reactive and total phosphorus content) stimulated the development of *Lemna gibba*, *Bidens tripartita*, and *Ceratophylum demersum*. On the other hand, a higher water chemical quality (lower phosphorus concentrations) had a positive effect on the development of *Potamogeton perfoliatus*, *Myriophylum spicatum*, and *Fontinalis antipyretica*. The analysis also revealed a group of macrophytes located in the middle of the graph that were not associated with the two factors analysed. This group included numerous emergent helophytes, i.e., *T. latifolia*, *Sparganium erectum*, *P. arundinacea*, *Lythrum salicaria*, *Lycopus europaeus*, *Glyceria fluitans*, *Glyceria maxima*, and *Veronica beccabunga*; some submerged species, i.e., *Elodea canadensis* and *Potamogeton crispus*; and free-floating *Lemna trisulca*.

4. Discussion

During this nationwide research program investigating hydromorphologically transformed rivers, a total of 153 macrophyte taxa were identified. This number corresponded well to the overall river plant biodiversity resources of lowland rivers in Poland [46]. It was shown that almost all river macrophyte species occurring in Poland appeared in hydromorphologically transformed rivers, at least incidentally. The estimated average species richness of the survey site was 16, and this was consistent with other studies that have investigated hydromorphologically altered rivers [47]. This number is only slightly lower than that determined for non-modified rivers—the average species richness of lowland rivers in Poland has been estimated at 19 taxa per standard site [48,49].

On the other hand, the species richness under extensive modification was very variable, and the number of species in an extreme site was reduced to only two species. A species richness decline under hydromorphological disturbance was previously indicated for macrophytes [10], as well as other aquatic organisms such as fish and macroinvertebrates [19,50]. This tendency is a source of difficulty for the principal methods of biological monitoring for ecological river classification under the WFD. It is regarded that species-poor communities provide an uncertain assessment of ecological status [36,46]. In order to increase the accuracy of biological monitoring methods in species-poor rivers, the sampling effort should be increased by, for example, extending the distance of the surveyed river stretches.

The results indicated that low species richness was related to low values for the biodiversity indicators based on relative abundance. Other authors [39,51,52] have shown that the structure of the river habitat, including its heterogeneity, is a very important factor affecting the development of various groups of aquatic organisms, both plants and animals. On the other hand, the high values of biodiversity obtained for some sites indicated that macrophyte richness and diversity can be relatively high even in morphologically transformed rivers. This is contradictory to, e.g., Bączyk et al. [13], whose findings showed the clear negative impact of hydromorphological work on all major groups of aquatic biota. The differences are probably due to the type, intensity, and age of the modifications and the appearance of niches over time that could be colonised by different organisms [10]. Despite the clear relationship between aquatic plants and environmental factors, there is still a lack of direct information about the degree of environmental degradation indicated by biodiversity metrics based on relative abundance, such as evenness and, to some extent, the effective number of species represented by the Shannon exponential and Simpson concentration numbers [53,54].

The botanical analysis revealed the taxonomical pattern of the modified rivers. The most frequent species were *Phalaris arundinacea*, *Lemna minor*, *Sparganium emersum*, and *Cladophora* sp. (each having a frequency above 50.0%). It has already been shown that these taxa grow well in both natural and hydromorphologically modified watercourses [10,12]. This study confirmed their broad ecological tolerance towards physical habitats. Moreover, these species are also commonly found in highly eutrophic [36,55] and moderately eutrophic rivers [56]. This indicates that these species are extreme ecological generalists, which was also confirmed by the CCA results. Our study also highlighted a group of amphibious species tolerant to hydromorphological modifications, such as *Agrostis stolonifera*, *Myosotis palustris*, *Rorippa amphibia*, and *Mentha aquatica.* These species have also been documented in lowland rivers [57]. Amphibious macrophytes are rooted in the bank zone (e.g., on the edge of existing modifications or in cracks in reinforcements), and only their shoots and leaves sprawl into the water [58]; thus, their presence in hydromorphologically impacted rivers can be more frequent than most helophytes and hydrophytes.

The group of the most common species included another free-floating plant, *Spirodela polyrhiza,* in addition to *Lemna minor*. This was quite unexpected, given that the transformation of rivers is often followed by an increase in water flow [13], and L. minor and other pleustophytic plants develop well under low-flow conditions [59]. Our findings, however, can be explained by the specific habitats in the altered rivers, which in our case were favourable for pleustophytes. These habitats provided high nutrient availability (as pollution sources were often associated with the modifications), increased water temperature, and greater access to light (e.g., due to the lack of canopy under hydromorphological pressures) [60]. Moreover, lower water levels can be often observed in hydromorphologically degraded rivers during the summer period (low-flow period), causing the intensive development of free-floating species [59].

In the rivers studied, eleven species of bryophytes were recorded. The considerable development of bryophytes in modified rivers has previously been described [61]. Nevertheless, there is still a lack of comprehensive studies on the associations between this group of macrophytes and the hydromorphological status of rivers, especially when compared to studies on water quality. Aquatic bryophytes include a large group of rheophilic species that prefer fast-flowing river stretches with hard substrates [62,63]. The lack of natural hard substrates can limit bryophyte development in most lowland rivers, while artificial substrates such as concrete or brick and stones create suitable habitats for them [27]. Despite this, the successful development of bryophytes on these substrates is not always as common as might be expected [61]. On the other hand, river engineering leads to a reduction in the distribution of various habitats related to riparian trees (underwater tree roots, fallen trees, and woody debris), which are often inhabited by bryophytes [25,64]. In addition, mosses and liverworts have a definite dependence on the chemical characteristics of water, including its trophic conditions and pH [62,65]. Among the bryophytes, *Leptodictyum riparium* was one of the most frequent taxa. The presence of this species was clearly related to the environmental gradient represented by hydromorphological modifications, as shown in the CCA. The high frequency of this species was also previously reported in unimpacted lowland rivers [25] and Mediterranean watercourses [64]. Moreover, *L. riparium* is a species that prefers high-nutrient environments and develops well in eutrophic waters [36,56].

An important element of the plant pattern of hydromorphologically modified rivers is a high abundance of filamentous algae. Eighteen taxa were identified in this group of plants. The most common was *Cladophora* sp., which had an abundance of more than 50.0%, followed by *Oedogonium* sp., *Rhizoclonium* sp., and *Vaucheria* sp. It has been shown that due to rhizoids, filamentous algae are able to anchor to artificial substrates, and their high morphological plasticity enables their survival in modified habitats [11,24,65]. Th =e fast growth of algae may also be the result of their faster nutrient uptake compared to vascular plants [66]. Numerous studies on the ecology of *Cladophora* species and other filamentous algae have demonstrated the influence of nutrients on the robust growth of these organisms [65,67,68]. Furthermore, Birk and Willby [69] showed that a large group of macroscopic algae inhabit rivers degraded by high concentrations of nutrients. The abundance of macroscopic algae could also be associated with the rapid development of these organisms, from the overwintering filament in early spring [68] and effective reproduction by fragmentation [70]. This, combined with the lack of competition from other macrophyte groups that are not adapted to morphological alterations [11], allows for the productive development of algae under potentially unfavourable conditions.

5. Conclusions

Our research distinguished the macrophyte characteristics of hydromorphologically altered rivers and highlighted several environmental factors determining the development of individual taxa and groups of macrophytes. The overall number of taxa present in hydromorphologically altered rivers was large, comparable with the total macrophyte flora in lowland rivers. Moreover, the local richness of the modified watercourses was only slightly poorer than that of natural rivers. Nevertheless, the overrepresentation of species-poor rivers (ten or fewer taxa) was apparent under heavy modifications—nearly one fourth of the survey sites were poor in species richness and diversity. Moreover, the metrics based on relative abundance indicated a decline in biodiversity under hydromorphological degradation. On the contrary, several sites with smaller transformations allowed for the diverse development of macrophytes. The development of particular groups of aquatic plants was highlighted, including various plants that could attach to artificial substrates (algae, bryophytes) or could grow in unreinforced places and sprawl into the water. On the other hand, the limited development of typical hydrophytes in the modified rivers indicated the greater impact of modifications. Further research should, however, include an attempt to separate the variability of these two factors and accurately assess their individual effects on macrophytes.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w14223746/s1, Table S1: List of all aquatic plants found in the study sites with their frequency.

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Data Availability Statement: The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

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Conflicts of Interest: The authors declare no conflict of interest.

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