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Environmental Drivers of Functional Structure and Diversity of Vascular Macrophyte Assemblages in Altered Waterbodies in Serbia

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Abstract: There is a gap in the knowledge about how environmental factors affect functional diversity and trait structures of macrophyte communities in altered waterbodies. We used macrophyte and environmental data collected from 46 waterbodies; we extracted data on 14 traits with 43 attributes for 59 species and calculated seven functional diversity indices. We used redundancy analysis (RDA) to investigate the response of functional diversity indices to the environmental variables. To relate traits to environment we performed the analysis on three data matrices: site by environmental variables (R), site by species (L), and species by traits (Q)—the RLQ analysis, and the 4th corner analyses. The RDA showed that the environmental variables explained 47.43% of the variability in the functional diversity indices. Elevation, hemeroby (integrative measure of the impact of all human intervention) of the land cover classes on the banks, and water conductivity were correlated with all diversity indices. We found that the traits characteristic of floating and emergent plants represents a strategy to increase efficiency in light interception under high nutrient concentrations in lowland waterbodies, while submerged plants dominate nutrient-poorer waterbodies at higher altitudes. Future investigations should be focused on the role of functional diversity and the structure of macrophyte communities in the indication of tradeoffs and/or facilitation between ecosystem services that altered waterbodies provide, in order to guide their adequate management.

Keywords: heavily modified waterbodies; artificial waterbodies; macrophytes; ecological processes

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1. Introduction

Three types of ecological processes, or filters (i.e., dispersal, abiotic environment, and biotic interactions), shape local species assemblages by progressively filtering species from the regional species pool to local communities, producing non-random patterns in community structure, by acting on species traits rather than on species themselves [1–5]. Species traits are morphological, physiological, and phenological characteristics, measurable at the species or individual level [2]. Dispersal influences the community structure by selecting species according to their ability to disperse to a site [6]. The abiotic environment acts as filter that selects species with suitable traits that can persist in the given habitat, leading to convergent traits and reducing functional diversity [7,8]. Biotic interactions (niche differentiation) are ecological processes prevailing on a finer scale where coexisting species have small overlaps in their functional niches due to competitive exclusion, leading to divergent traits and increased functional diversity [9]. The interactions of these three filters are complex and can lead to shifts in the community structure, changing the abundance and presence of species [10]. It is suggested that environmental filtering is important under disturbed conditions, while biotic interactions prevail in less-disturbed environments [5,11,12].

Macrophytes are key elements of freshwater ecosystems, playing a central role in biogeochemical processes, and as primary producers, they constitute an important food resource [13,14]. Due to their ecological importance, macrophyte species are formally recognized as one out of four biological quality elements used in the monitoring of surface water ecosystems [15]. Macrophyte communities are strongly influenced by hydrology, reflecting both anthropogenic and natural disturbances, with hydrology having a stronger effect on the trait composition than on the species composition of the community [16–19].

There is a growing body of literature dealing with the relationships between environmental factors and functional diversity and trait distributions of macrophyte communities in altered waterbodies (e.g., [4–6,13–18,20–23]). The methods applied to investigate these relationships include the use of multivariate characterization of functional assemblage structures, functional diversity measures, and/or specific trait–environment correlations. In general, all these studies supported the conclusion first drawn by Baattrup-Pedersen et al. [4] that trait-based rather than species-specific approaches might provide better insight into the biological mechanisms underlying the changes in macrophyte communities induced by habitat disturbances.

When analyzing trait–environment relationships in European lowland streams, Baattrup-Pedersen et al. [4] found that eutrophication affected macrophyte community trait characteristics by filtering species with efficient light utilization, indicating that light is a limiting factor for growth in nutrient-enriched environments. Lukács et al. [5] also found that the mechanisms underlying the changes in stream plant communities are mostly related to light capture and utilization, although their results indicated that the plant traits showed stronger associations with carbon gradient than with nutrient gradients.

It was suggested that the functional trait composition of aquatic plants can distinguish hydromorphological degradation from eutrophication in streams [20]. Mouton et al. [22] demonstrated that native and non-native stream macrophyte assemblages responded differently to habitat disturbances, with riparian shading and hydromorphological conditions being the strongest variables shaping the macrophyte functional structure by selecting the species with suitable traits related to colonization and competition strategies. They found that disturbances such as a lack of riparian shading and eutrophication increase functional diversity. A study carried out in permanent and intermittent streams in Cyprus [14] revealed that hydromorphological factors, primarily flow duration patterns, shape macrophyte communities by filtering species with traits related to population resistance and resilience. Comparing channelized and un-channelized streams, Paz et al. [6] showed that macrophyte communities in channelized streams were dominated by emergent species and had lower functional diversity.

Previous studies conducted in the Danube River section in Serbia showed that both species and functional diversity increased along the anthropogenic pressure gradient (i.e., damming and loss of forest cover in the riparian zone) [24,25]. Since similar pressures operate in the altered waterbodies analyzed here, we hypothesized that a similar functional diversity response of macrophyte communities will be found. We expected a significant influence of the water chemistry, particularly nutrient content, on the functional diversity indices and on the individual traits. A higher nutrient content should favor a higher number of strategies (i.e., traits) to exploit these resources [5,26], leading to higher functional diversity. Similarly, species in nutrient-poor environments are constrained to a smaller range of these strategies [5], which will lead to a decrease in functional diversity.

Therefore, here, we evaluated the functional response of macrophyte communities to the environmental drivers in the waterbodies with altered hydromorphological features, using both functional diversity indices and trait–environment correlations. Our main objectives were: 1. to investigate the effects of water chemistry and river habitat features on macrophyte functional diversity indices; and 2. to identify macrophyte traits that respond to the analyzed environmental factors.

2. Materials and Methods

Original data on the abundance and distribution of macrophytes were collected during the surveys conducted between 2017 and 2019, under the WFD scheme in order to achieve the ecological classification of waterbodies in Serbia. We sampled 72 altered bodies of running water (Figure 1). The macrophytes were surveyed according to EN 14184:2014 Standard [27], using a five-level scale metric for the estimation of their abundance (1—very rare, only single plants, up to 5 specimens; 2—rare, approximately 6 to 10 single plants, loosely scattered over sampling unit, or up to 5 single plant stocks; 3—frequent, cannot be overlooked, but not frequent; 4—abundant, occurring frequently, but not in masses, with incomplete cover, exhibiting large gaps; 5—very abundant, dominant, found more or less everywhere, cover markedly more than 50%) in relation to the volume and length of the sampling unit. The survey of macrophytes was carried out over the whole length of the sampling unit visually and/or by raking, using a small boat. The sampling units were 100 m, 500 m, and 1000 m long, depending on the size and characteristics of the waterbody [27]. In each waterbody, a minimum of three sampling units were surveyed on the left and on the right riverside, and the collected data were averaged for later use. The macrophytes were not recorded in 26 out of a total of 72 surveyed waterbodies. Further analyses included data from the remaining 46 waterbodies.

Figure 1. Map of surveyed altered waterbodies in Serbia.

The environmental data analyzed here were divided into two groups: water chemistry and river habitat features (Table 1). We used time- and space-specific data on water chemistry and water temperature published in yearly reports available on the Serbian Environmental Agency website (www.sepa.gov.rs (accessed on 27 April 2022)) as well as in the European Environmental Agency Central Data Repository—EIONET (https://cdr.eionet.europa.eu/rs/eea (accessed on 13 June 2022)). For the purposes of this study, the annual average values were calculated. Data on the bank slope (1—flat, gentle slope; 2—intermediate; 3—very steep slope) and CORINE Land Cover classes were estimated in the field, according to the guidelines provided by the Copernicus Land Monitoring Service (https://land.copernicus.eu/pan-european/corine-land-cove (accessed on 12 September 2022)). The mean width of the riparian zone and the mean width of the waterbodies (i.e., channel width) were measured using landscape images from Google Earth. Data on the CORINE Land Cover classes were used to extract the number of land cover classes (No_LUt) and average degree of hemeroby (avg.hemeroby) of land cover classes along the banks of the waterbody. To measure hemeroby, we applied the approach used by Walz and Stein [28], where CORINE Land Cover classes were assigned to seven degrees of hemeroby, between degree 1—land cover with almost no human impact (e.g., CORINE class 332—bare rocks), and degree 7, assigned for land cover with excessively strong human impact (e.g., 111—continuous urban fabric, 121—industrial or commercial units, etc.). We treated the degrees of hemeroby as numerical values, and for each waterbody we calculated the average degree of hemeroby.

Table 1. Environmental variables used in data analyses, with the grouping applied in the Variation Partitioning (VarPart) procedure: Wchem—water chemistry; habitat—river habitat parameters.

VarPart	Environmental Variable	Unit	Code	Mean	Std.Dev	Min	Median	Max
Wchem	dissolved oxygen	mg/L	dis_O	8.55	1.55	5.21	8.93	11.29
	pH	-	pH	8.03	0.18	7.56	8.01	8.39
	conductivity	µS/cm	cond	404	164	126	395	1234
	ammonium	mg/L	NH4_N	0.15	0.18	0.03	0.11	1.14
	nitrite	mg/L	NO2_N	0.02	0.01	0.01	0.01	0.09
	nitrate	mg/L	NO3_N	0.70	0.34	0.23	0.66	1.53
	total nitrogen	mg/L	total_N	1.48	0.72	0.64	1.45	4.57
	orthophosphate	mg/L	PO4_P	0.07	0.08	0.01	0.05	0.37
	total phosphorus	mg/L	total_P	0.14	0.09	0.04	0.12	0.46
habitat	water temperature	°C	w_t	15.08	2.16	7.95	15.35	18.79
	channel width	m	chn_w	357	364	9	220	1622
	elevation	m a.s.l.	elev	180	185	32	80	832
	bank slope degree	0–3	bnk_slp	1.98	0.69	1.00	2.00	3.00
	riparian width	m	rip_w	116	253	0.00	5	1140
	average degree of hemeroby	1–7	avg_hmrb	3.63	1.10	1.50	3.84	6.00
	number of land cover classes	-	No_LUt	2.80	1.44	1.00	3.00	7.00

For 59 recorded vascular macrophyte species, data on 14 traits with 43 trait attributes were extracted from the literature [29–31] (Table 2). These encompassed morphological traits including growth forms and traits important for species dispersal, reproduction, and survival. The trait attributes had values of 0 for absence, 1 for occasional, but not general presence, and 2 for general presence of the attribute [20,31]. We also included ecological preference traits in form of Ellenberg's indicator values on a nine-level scale for temperature, reaction, nitrogen, and light; and a twelve-level scale for water [29,30].

Table 2. List of 14 plant species traits and their attributes included in the analyses.

Trait	Attribute	Code
Ellenberg Temperature	1–9	TB
Ellenberg Water	1–12	WB
Ellenberg Reaction	1–9	RB
Ellenberg Nitrogen	1–9	NB
Ellenberg Light	1–9	LB
Growth form:	free-floating, surface	Ffl_srfc
	free-floating, submerged	Ffl_sbm
	floating leaves, anchored	Ac_fllv
	submerged leaves, anchored	Ac_sbmlv
	emergent leaves, anchored	Ac_emglv
	heterophylly, anchored	Ac_htrlv
Vertical shoot architecture:	single apical growth point	snglapgr
	single basal growth point	snglbsgr
	multiple apical growth point	mltpapgr
Leaf type:	tubular	tblr
	capillary	cplr
	entire	entr
Leaf area:	small (<1 cm^2)	LA1
	medium (1–20 cm^2)	LA2
	large (20–100 cm^2)	LA3
	extra-large (>100 cm^2)	LA4

Table 2. *Cont.*

Trait	Attribute	Code
Morphology index (score):	<1	MI1
	1–10	MI2
	10–40	MI3
	40–100	MI4
	>100	MI5
Mode of reproduction	rhizome	rhzm
	fragmentation	frgm
	budding	bdng
	turions	trns
	stolon	stln
	tubers	tbrs
	seeds	sds
Perennation:	annual	annl
	biennial	bnnl
	perennial	prnnl
Body flexibility:	low (<45°)	BF1
	intermediate (45–300°)	BF2
	high (>300°)	BF3
Leaf texture:	soft	lfsft
	rigid	lfrgd
	waxy	lfwx
	non-waxy	lfnwx

Based on the plant abundance dataset and trait dataset, we computed seven distance-based multi-trait alpha diversity indices: FRic—functional richness, representing the amount of functional space filled by a community; FEve—functional evenness, measuring the regularity of the species abundance distribution along the minimum spanning tree that links the species points in multidimensional functional space; FDiv—functional divergence, relating to how species abundances are distributed within the functional trait space; FDis—functional dispersion, representing the mean distance of individual species to the centroid of all species in the multidimensional trait space, taking into account the species relative abundances; RaoQ—the sum of the dissimilarities between all possible pairs of species, weighted by the product of species proportions; FD—functional diversity, an index based on the Rao quadratic entropy, representing the sum of dissimilarities in functional traits between all possible pairs of species weighted by the product of species proportions; and Fred—functional redundancy, index based on the Rao quadratic entropy, representing the difference between maximum functional diversity—the inverse Simpson taxonomic diversity—and FD [32–36]. Since the trait attribute values were not quantitative and continuous, Principal Coordinate Analysis (PCoA) of the Gower dissimilarity matrix computed on trait attributes matrix was used to obtain the functional trait space [35]. To explore the correlations between functional diversity indices, linear correlation coefficients were calculated and the correlations between paired samples were tested. Analyses were conducted using R package "FD" [37].

To analyze the relations between the functional diversity indices and environmental variables, we applied redundancy analysis (RDA). We chose RDA because: (a) linear relationships between functional diversity indices and environmental variables were indicated in a number of previous studies, e.g., [6,22,23,38,39]; (b) during the data exploration procedure (not shown here), detrended correspondence analysis (DCA) of the functional diversity indices matrix gave gradient lengths <3 standard deviations for the longest axis, indicating that a linear response would adequately fit the data [40]; (c) this method allows the extraction and summarization of variation in the whole set of components of functional diversity, in form of functional diversity indices, explained by the environmental variables. Prior to the analysis, both the functional diversity indices and the environmental variables were standardized. The statistical significance of the final RDA model and of the individual canonical axes was tested using permutation tests. An unbiased amount of variation in the response data (functional diversity indices) explained by environmental variables was measured as an adjusted R^2 and was used later in the Variation Partitioning (VarPart). To explore the correlations between the functional diversity indices and environmental variables, linear correlation coefficients were calculated and the correlations between paired samples were tested. VarPart was applied to distinguish between the amount of variation in the response data explained by water chemistry, by river habitat features, and by their joint effect (Table 1). The analyses were carried out using the R package "vegan" [41].

To evaluate the relationships between the species traits and environmental data, mediated by the species abundance data, two complementary methods were applied: RLQ and fourth-corner analysis [21,42–44]. RLQ analysis was performed on three data matrices: site by species (L), site by environmental variables (R), and species by traits (Q). RLQ analysis is an ordination method allowing the visualization of the joint structure resulting from the three data tables, based on the coefficients for the environmental variables and species traits. It is followed by single global test [42]. Fourth-corner analysis is a series of statistical tests of individual trait–environment relationships. Since the fourth-corner method involves multiple testing, the overall rate of type I error is increased, and therefore correction for multiple testing should be performed [21,40,43,44]. Here, the false discovery rate (FDR) method with $\alpha = 0.05$ was applied [41,43–47]. RLQ and fourth-corner analysis were carried out using the "ade4" R package [48,49].

3. Results

We recorded 59 plant species (Supplementary Material Table S1) in 46 out of the 72 surveyed waterbodies. Based on the species traits (Table 2), seven distance-based functional indices were calculated (Table 3).

Table 3. Functional diversity indices used in the analyses.

Index	Abbreviation	Mean	Std.Dev	Min	Median	Max
Functional Richness	FRic	0.38	0.28	0	0.37	0.92
Functional Evenness	FEve	0.73	0.3	0	0.83	0.99
Functional Divergence	FDiv	0.69	0.28	0	0.79	0.88
Functional Dispersion	FDis	5.63	1.12	0	5.88	6.85
Rao Quadratic Entropy	RaoQ	33.8	9.68	0	35.91	47.76
Functional Diversity	FD	1.37	0.12	1	1.38	1.56
Functional Redundancy	FRed	6.36	5.14	0	4.86	19.06

All linear correlation coefficients between functional diversity indices were statistically significant (Table S2). The highest correlation coefficient was found between Rao quadratic entropy and Rao-based diversity, while the lowest value was found between evenness and redundancy.

The RDA model explained 47.43% of the variation in the response data (Figure 2). According to the permutation tests, both the whole RDA model and the first canonical axes were highly statistically significant ($p < 0.001$). The first two RDA axes explained 45.42%, and the first RDA axis alone explained 40.16% of the unbiased variation in the response data. Therefore, the major trends were well modeled in the RDA. Furthermore, the first unconstrained eigenvalue (PC1) is relatively small (1.207) compared to the first constrained eigenvalue (3.919), indicating that any dominant residual structure is not displayed in the RDA model. Variables: the elevation ($r = 0.822$), average hemeroby ($r = -0.665$), and conductivity ($r = -0.531$) were strongly correlated with the first RDA axis, whereas the strongest correlation with the second RDA axis was detected for the width of the riparian zone ($r = 0.551$).

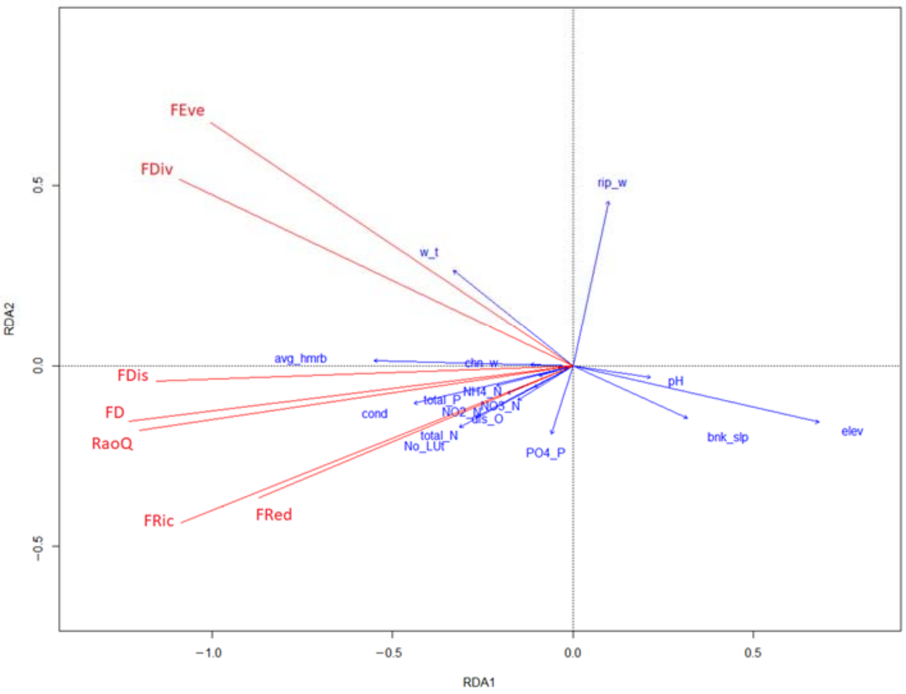
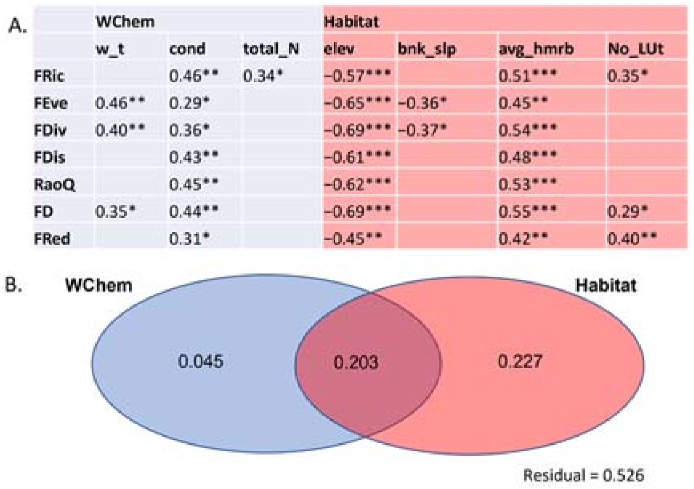


Figure 2. RDA plot of the environmental predictors and functional diversity indices as response variables, with scaling 2 applied. The abbreviated names of the environmental variables are given in Table 1, and those of functional diversity indices in Table 3.

Conductivity and average degree of hemeroby had significant positive correlations and elevation a negative correlation with all functional diversity indices (Figure 3A). a negative correlation was found between bank slope and functional evenness and divergence. These two indices, as well as functional diversity, had a positive correlation with water temperature. The number of CORINE land cover classes had a positive correlation with functional richness, diversity, and redundancy. The coefficients of correlation between the other environmental variables and functional diversity indices were not statistically significant.


A.

	WChem			Habitat			
	w_t	cond	total_N	elev	bnk_slp	avg_hmrb	No_LUt
FRic		0.46**	0.34*	−0.57***		0.51***	0.35*
FEve	0.46**	0.29*		−0.65***	−0.36*	0.45**	
FDiv	0.40**	0.36*		−0.69***	−0.37*	0.54***	
FDis		0.43**		−0.61***		0.48***	
RaoQ		0.45**		−0.62***		0.53***	
FD	0.35*	0.44**		−0.69***		0.55***	0.29*
FRed		0.31*		−0.45**		0.42**	0.40**

Figure 3. (**A**) Statistically significant coefficients of linear correlation between functional diversity indices and environmental variables ($p < 0.001$—***; $p < 0.01$—**; $p < 0.05$—*). (**B**) Venn diagrams of variation partitioning. The abbreviated names of the environmental variables are given in Table 1, and those of the functional diversity indices in Table 3.

The fraction of the variation in the functional diversity indices explained only by river habitat features was the highest at 22.7% (Figure 3B). The joint effect of both subsets of environmental variables on the variability in functional diversity indices was 20.3%, while water chemistry alone had the smallest effect on the response variables, explaining only 4.5% of their variability.

The RLQ analysis (Figure S1) yielded a combined p-value < 0.001, which means that the links between the matrices sites by species (L) and species by traits (Q), and between site by environmental variables (R) and site by species (L) were significant. The fourth-corner analysis revealed eleven positive and seven negative associations (Figure 4). Positive associations were found between the concentration of dissolved oxygen and ecological indicator value for light; water conductivity and extra-large leaf area; nitrite concentration and "surface free-floating" growth form, and low body flexibility; nitrate concentration and low body flexibility, and waxy leaf texture; and altitude and "anchored with submerged leaves" growth form, soft leaf texture, and non-waxy leaf texture. Negative associations were found between the concentration of dissolved oxygen and non-waxy leaf texture; nitrite concentration and "anchored with submerged leaves" growth form, and soft leaf texture; nitrate concentration with ecological indicator value for water, multiple apical growth, and non-waxy leaf texture; and average hemeroby of the land use types on the banks and morphology index between 40 and 100.

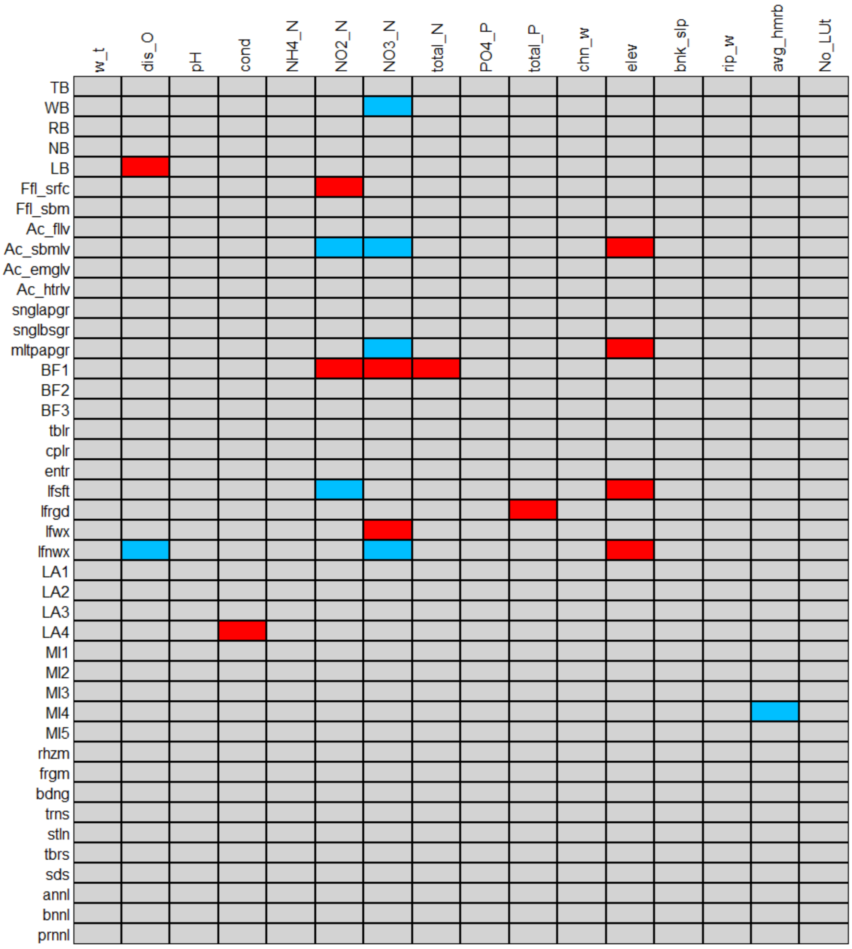


Figure 4. Results of the fourth-corner tests, corrected for multiple testing using FDR procedure. At $\alpha = 0.05$ level, significant positive associations are represented by red cells and negative ones by blue cells. The abbreviated names of environmental variables are given in Table 1, and those of functional traits in Table 2.

4. Discussion

We investigated the effects of environmental factors—water chemistry and river habitat features—on the functional diversity and trait structure of vascular macrophyte assemblages in canals and heavily modified rivers in Serbia.

4.1. Correlations between Macrophyte Functional Diversity Indices

We found significant positive correlations between all functional diversity indices, since they measure different aspects of the same facet of diversity. Notably, a strong positive correlation was observed between RaoQ and FDis. That was expected, since both indices, although different, estimate the dispersion of species in trait space, weighted by their relative abundances [34]. Similarly, a strong positive correlation was found between RaoQ and Rao-based FD. We also found a strong positive correlation between FDiv and FEve, indices that measure two components of functional diversity—divergence and evenness. A high FDiv indicates a high degree of niche differentiation and low resource competition, while a high FEve indicates a high degree to which the biomass of a community is distributed in niche space to allow the effective utilization of the entire range of available resources [50]. Therefore, in the altered waterbodies analyzed here, as the degree of niche differentiation increases, the abundance distribution degree of the macrophyte communities in niche space tends to be even, allowing the effective utilization of resources, with low resource competition. This tends to increase the productivity and reliability of the ecosystem, decreasing the opportunity for invaders [50].

4.2. Effects of Water Chemistry and River Habitat Features on Macrophyte Functional Diversity Indices

The environmental constraints analyzed here were able to explain nearly half of the variability in functional diversity indices. River habitat features, compared to water chemistry, were responsible for the largest part of that variability. Our results showed similar responses of all functional diversity indices to the three main gradients: positive correlations with the essentially related factors—average degree of hemeroby and conductivity; and negative correlations with the elevational gradient, indicating an increase in all components of functional diversity towards the lowland waterbodies that are under stronger anthropogenic influence.

Notably strong negative correlations between elevation and all the analyzed components of functional diversity suggested that species with similar traits were filtered along the elevational gradient. Elevational gradient is a gradient of natural variability [22] and was found to be an important predictor of macrophyte vegetation in lakes and rivers [15,22,51–55]. It reflects changes in slope, type of substrate, water temperature, nutrient load, and the intensity of agricultural pressures typical for lowland reaches. Along the elevational gradient, all factors contributing to the increase in the diversity of vascular macrophyte vegetation are decreasing. Several studies have shown an opposite pattern, suggesting that the observed response of macrophyte communities to altitude might depend on the analyzed range of the elevational gradient [52,53,56,57].

In the studied waterbodies, the water temperature was related to the elevational gradient, with higher values at lower altitudes. Our results showed that a higher water temperature leads to an increase in functional evenness, functional divergence, and Rao-based FD, which measures both components [50]. Although all components of functional diversity shift along the elevational gradient, changes in temperature along this gradient particularly influence niche differentiation and the abundance distribution degree of macrophyte communities in niche space (i.e., functional evenness). At lower altitudes, the abundance distribution in niche space tends to be even, allowing the effective utilization of resources with low resource competition [50].

Functional evenness and divergence were also related to the littoral slope degree. They were found to be lower in waterbodies with a steep littoral slope, indicating the filtering of species with similar traits allowing them to occupy deeper water, with a low degree of niche differentiation, high resource competition, uneven abundance distribution in niche space, and the underutilization of resources [50]. In this case, the average degree of hemeroby was significantly positively correlated to all aspects of functional diversity. Hemeroby represents an integrative measure of the anthropogenic impact on ecosystems [58,59]. Different human activities have shaped the area surrounding the studied waterbodies, decreasing their naturalness [28] and directly and/or indirectly influencing other environmental factors. Similarly, a positive relationship between anthropogenic disturbances and diversity, both taxonomical and functional, was found for macrophytes in the Danube River [24,25,60] and in Slovakian ponds [54]. The intensity of human impact on the waterbodies studied here, reflected mainly in the deforestation of regions in the riparian zone, the reduction in flow velocity, the increase in transparency, sediment accumulation, as well as the subsequent higher nutrient supply, can promote an increased abundance of functionally distinct species, providing niche diversification for the establishment of diverse assemblages of macrophytes [23]. It was suggested that the functional response of the communities depends on the intensity of stress (both natural and anthropogenic), and that ecosystems that are under intensified stress will exhibit functionally homogeneous communities [61]. Our results indicate that the anthropogenic stressors are not intense enough to lead to the functional homogenization of macrophyte communities, while the intensity of natural stressors operating at higher altitudes (shading, bedrock in littoral areas, oligotrophic environment, lower temperatures, etc.) leads to trait convergence and functionally more homogeneous communities.

An additional possible explanation for the observed positive correlation between functional diversity and the intensity of human impact (i.e., hemeroby) might be (often anthropogenically induced) habitat heterogeneity, expressed here as the number of land cover classes along the banks of the waterbodies. The number of land cover classes was found to be significantly positively correlated to functional richness, the Rao-based diversity index, and functional redundancy. Larger number of land cover classes on banks provide habitat heterogeneity offering a more heterogeneous range of niches (open, shaded, different littoral slope, nutrient supply, etc.) and favoring plants with different resource utilization strategies, increasing productivity and stability, since the number of species with the same traits (i.e., functional redundancy) is also increasing [5,50].

Like the average hemeroby, water conductivity was also significantly and positively correlated to all functional diversity indices. Conductivity has frequently been reported as a key driver of richness and diversity of macrophyte communities [52,53,55,61–65], where high conductivity was indicative of waters disturbed by anthropogenic processes [52,53,55,63].

We found that the amount of niche space filled by species in the community (i.e., functional richness) increased in waterbodies with higher nitrogen concentrations. Previous studies reported nitrogen having a positive effect on species richness and diversity [55]. However, it was also documented that some species, particularly submerged macrophytes, may be lost when nitrogen concentration exceeds a certain threshold, and when the phosphorus concentration is high enough [66,67]. At high or very low nutrient levels, species and functional richness is expected to be lower, since low nutrient concentrations filter species with similar traits adapted to it, while competitive interactions usually increase when nutrient levels increase, and the highest diversity is expected at intermediate nutrient levels [68]. Therefore, we can assume that the nitrogen concentrations in the waterbodies with high functional richness are in the intermediate range.

4.3. Effect of Water Chemistry and River Habitat Features on Macrophyte Functional Trait Structure

Our results confirmed the conclusions of previous studies [4,6] that floating and emergent plants represent strategies to increase the efficiency of light interception under high nutrient concentrations, while submerged plants dominate in nutrient-poorer waterbodies at higher altitudes. A similar shift from more productive and eutrophic waterbodies dominated by emergent and floating plants to nutrient-poorer waterbodies dominated by submerged macrophytes was found in a cascade series of reservoirs at the medium and low Tietê River in Brazil [69]. This shift between two dominating growth forms is the consequence of competition for resources, primarily nitrogen and light. It was reported that floating plants have primacy for light, while submerged plants can grow at lower nutrient concentrations in water and can reduce nutrient concentrations in water to lower levels [70,71].

5. Conclusions

The simultaneous use of functional diversity indices and trait–environment correlations applied here allow us to draw several conclusions regarding the community changes along the environmental gradients, and the traits that are related to those changes. The shift from low to high functional diversity along the gradient of anthropogenic stressors, and the opposite trend of functional diversity along the elevational gradient, might indicate the prevailing processes that structure macrophyte communities. Our results confirm the previous findings that biotic filters, competition, and niche differentiation play a role in aquatic ecosystems under high anthropogenically induced productivity [72,73]. In contrast, the functional diversity indices were found to decrease with elevation, indicating the shift to predominating abiotic environmental filtering and more stressful conditions for vascular macrophytes along the elevational gradient. Trait–environment analyses indicated the change in community structure, from emergent and floating macrophytes dominant in more productive and eutrophic lowland waterbodies to submerged macrophyte-dominated waterbodies at higher altitudes with lower nutrient load and conductivity.

Our results indicate that both functional diversity indices and functional traits might prove to be useful diagnostic tools to guide the choices of relevant management measures in altered waterbodies in Serbia. We found that the current intensity of anthropogenic stressors is low enough to prevent functional homogenization and the decline of macrophyte communities. However, the high productivity and dominance of emergent and floating plants in lowland waterbodies might indicate the eutrophication-related process [4] that will, in the future, impair the ecosystem services that these waterbodies were designed to provide. This is particularly important for waterbodies designed to store water for the water supply, where in many cases, intensive land use close to the shoreline was observed (pastures, farming, summer cottages, villages, agriculture and plantations, beaches, camping areas). Therefore, in these waterbodies, management efforts should be directed toward the reevaluation of land use decisions and the reduction of nutrient inputs. Although altered waterbodies are designed to provide different services for human wellbeing, they might be harboring biota of conservational value [74]. Future investigations of altered waterbodies must include more detailed biodiversity studies and the selection of sites of conservational importance, as well as the application of adequate measures for their protection. Moreover, it is important to focus further investigation on the role of functional diversity and the structure of macrophyte communities in the indication of possible tradeoffs and/or facilitation between the ecosystem services that those altered waterbodies provide in order to direct their adequate management.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15020231/s1, Table S1: Species list; Table S2: Linear correlation coefficients between functional diversity indices; Figure S1: Results of the RLQ analysis.

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