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Metaphyton contributes to open water phytoplankton diversity

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Abstract In contrast to pelagic and benthic realms of the aquatic ecosystems, studies on the metaphytic habitats remain underrepresented in the literature. However, this realm may have a potential impact on composition and diversity of the open water assemblages through metacommunity processes (source-sink dynamics, mass-effect) especially in small ponds with extended littoral zone. Using a limnocorral experiment we studied how metaphyton affects diversity and composition of open water phytoplankton in a small eutrophic pond in the vegetation period. The three habitats (metaphyton, isolated and non-isolated open water) showed considerable differences in their taxa and functional group composition. Abundance-based diversity measures did not reveal remarkable differences among the assemblages of the three habitats. However, taxonomic and functional richness of the metaphyton and the non-isolated part of the pelagial significantly exceeded that of the limnocorral. Incidence-based similarity index values also showed closer resemblance of the metaphyton and plankton samples compared to that of the limnocorral. In the case of several functional groups, their functional redundancy in the metaphyton exceeded that in the open water areas. These results suggest that the

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metaphyton provides a refuge for several euplanktic elements that survive in the littoral and occasionally enrich the phytoplankton of the open water areas, representing that a within–lake metacommunity processes shape the composition and functioning of the open water areas in standing waters.

Introduction

Understanding the rules of community assembly has long been of interest to researchers and inspired a number of studies on this subject (Hille Ris Lambers et al., 2012; Letten et al., 2017; Ellner et al., 2022). To reconcile the discrepancies among the various theories, Vellend (2010, 2016) proposed a framework that focuses on four basic processes of community assembly, namely: speciation, demographic stochasticity, selection and dispersal. Although, evolutionary processes can occur in a short period of time, especially in the case of microbes (Fussmann et al., 2003), speciation as community assembly rule might be important in phytoplankton communities only at large geographic scales. In contrast, demographic stochasticity is more important in the case of small populations at smaller spatial scales. According to the Baas-Becking view of microbial realm (Baas-Becking, 1934), environment selects the organisms best adapted to the conditions provided by the habitats; otherwise, everything could be found everywhere. Yet, according to several studies, assembly of local communities are primarily driven not only by niche processes but dispersal too (Borics et al., 2021). The relative importance of these processes mostly depends on the size and type of the observed water bodies (Várbíró et al., 2017). Leibold & Chase (2018) determined four basic paradigms of metacommunity assembly (patch-dynamics, species-sorting, mass- effect, neutral view) built around the concept of selection and dispersal, of which mass-effect (source-sink dynamics) has the greatest impact on phytoplankton assemblages. This paradigm states that propagule pressure from an abundant source population can maintain high diversity in the recipient habitat, even if it provides unfavourable conditions for the newcomers (Mouquet & Loreau, 2003). Several studies highlighted the importance of

this process in maintaining diversity across isolated habitats like lakes (Szabó et al., 2019) or in river–lake complexes (Bergström et al., 2008; Bortolini et al., 2017), but it has relevance also in within-lake dynamics of microorganisms (Rimet et al., 2023).

Aquatic habitats in general can be divided into pelagic and benthic realms, inhabited by free-floating and sessile creatures respectively. However, besides these two realms a third one, the metaphyton can also be distinguished. The term was used first by Behre (1956) who defined metaphyton as algae, which are associated with macrophytes but not attached to them. Later definitions: "group of algae found aggregated in the littoral zone, which is neither strictly attached to substrata nor truly suspended" (Hutchinson, 1975), or „loose collection of nonmotile or slightly motile algae without any obvious mode of attachment" (Round, 1981) are identical in the sense, that besides filamentous forms, flagellates and other components of the microflora (diatoms and desmids) have been also included. In recent publications the meaning of the term was restricted to unattached filamentous green algae (Howell et al., 1990; Kelly et al., 1995; Pikosz & Messyasz, 2015). These different definitions beside leading to terminological confusion, neglect an assemblage that has the potential to significantly contribute to the diversity and functioning of the littoral.

Metaphyton frequently develops in wetlands, or in sheltered areas of lakes' littoral zone, and is associated with good light conditions and warm waters (Goldsborough & Robinson, 1996). Parts of aquatic macrophytes below the water table together with the filamentous algae create a three-dimensional matrix, which impedes water movements and create lentic conditions that allow the development of various environmental gradients (Barko & Smart, 1986; Dvořák & Liskova, 1970; Alahuhta et al., 2013). Littoral vegetation reduces the gas exchange with the air and diffusion of oxygen to the sediment (Moore et al., 1994), furthermore nutrient uptake and release by the plants (Lu et al., 2018), and production of allelopathic substances (Gross, 2003) also contribute to the microheterogeneity of this environment. Heterogeneity of the littoral creates large habitat diversity allowing the coexistence of several metaphytic algal species (Borics et al., 2003). The metaphyton is not just a unique assemblage, but might serve as a refuge for many species and depending on hydrological conditions may inoculate the pelagic realm,

contributing and maintaining its high diversity (Görgényi et al., 2019; Naselli-Flores & Barone, 2012). The findings of Görgényi et al. (2019) suggest that metaphyton plays also pivotal role in the recruitment of phytoplankton in lakes with extended littoral zone, because metaphytic components of the phytoplankton do not show asymptotes during spatially and temporally intensive samplings. This finding implies that the contribution of metaphyton to the phytoplankton assemblage can be considered as mass-effect, which assumes that because of the propagule pressure (or source-sink dynamics) from the metaphyton, diversity of phytoplankton can be high even under unfavourable conditions (Leibold & Chase, 2018). In accordance with the above-mentioned arguments, we assumed that in eutrophic lakes a source-sink dynamic operates between the metaphyton and the pelagic phytoplankton, and thus within-lake metacommunity processes shape the phytoplankton diversity in these systems.

To test this assumption a study question was raised: how does the diversity and composition of the open water phytoplankton change with the exclusion of the source-sink dynamics in a macrophyte dominated standing water. While field studies provide sufficient information on the source-sink dynamics in natural conditions, its real impact can be studied exclusively in controlled environment. Therefore, we studied this question in a whole pond experiment, where a part of the pelagic region of a small eutrophic pond was isolated by limnocorral, and tested how the metaphytic algal assemblages differ from the isolated and non-isolated phytoplankton.

We had the following hypotheses:

(i) The taxonomic and functional composition (functional groups (FGs)—Reynolds et al., 2002) of the metaphyton will be different from the two phytoplankton assemblages, showing greater similarity between the metaphyton and the non-isolated phytoplankton, than between metaphyton and isolated phytoplankton.

(ii) The diversity of the metaphytic assemblage will be higher than that of the phytoplankton assemblages in terms of both taxa and functional groups.

(iii) The metaphyton has a more stable community structure than phytoplankton, therefore comparing to the other two habitats, less changes are expected in its composition during the vegetation period.

Materials and methods

Study site

The studied pond is located in the Tuzson János Botanical Garden, in Nyíregyháza, Hungary (WGS84: 21.710588; 47.973473—Fig. 1), which is a small eutrophic pond (Supplementary Table 1) with large amount of macrophytes [roughly 60% cover, dominated by *Nymphaea alba* L. and *Ceratophyllum demersum* L.]. The maximum depth of the pond is 2.2 m. The middle part of the open water area was isolated by plastic foil (limnocorral) in a cylindrical shape from the bottom to the surface. The limnocorral was installed at the 20th of March to have enough

Fig. 1 Location of the experimental pond in Hungary (WGS84: 21.710588; 47.973473) and the three sampling points on the schematic picture of the pond (*M* metaphyton, *P* the non-isolated phytoplankton and *L* the phytoplankton isolated by limnocorral)
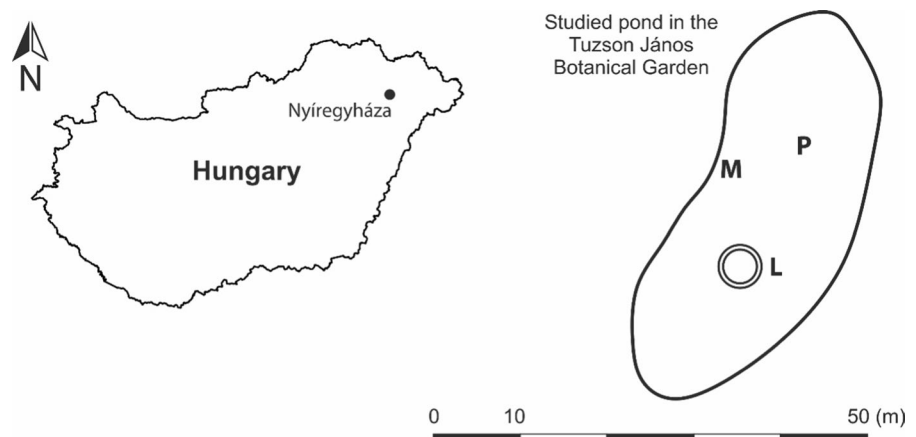
time for the development of differences between the communities in the different habitats. The bottom of the limnocorral was stabilized with concrete weights, and all seedlings of macrophytes were removed from the bottom of the isolated part. Area of the pond is approximately 600 m² of which 10 m² was isolated.

Sample collection, microscopic analysis and data processing

Metaphyton and phytoplankton samples were collected weekly from 13th of June to 10th of October in 2019. Altogether 51 samples were collected from 3 points (Figs. 1 and 2) during 17 weeks. Phytoplankton samples were taken by a tube sampler from the euphotic zone (2.5×depth of Secchi-disc) or from the whole water column from both the isolated (L) and non-isolated (P) part of the pond. Metaphyton (M) samples were collected with a plastic dish from the water among the macrophyte stands 10–20 cm below the surface. Water samples for abiotic variables (temperature, oxygen concentration, oxygen saturation, pH, conductivity, total nitrogen, total phosphorus) were collected at monthly intervals (Supplementary Table 1).

Samples were preserved with Lugol's solution in the field (CEN 13946, 2003). Counting of algal units (cells, colonies, or filaments) were performed according to the CEN 15204 (2006) standard using an inverted microscope (Leica DMIL) at ×100 and ×400 magnification. Estimating the biomass, the linear dimensions of 20 specimens of each taxon were measured and for calculating the phytoplankton biovolume realistic 3D models were used

following Borics et al. (2021). Based on the AlgaeBase (Guiry & Guiry, 2023) the currently accepted names of phytoplankton species were used.

Functional approaches in biodiversity studies provide extensive options to examine communities considering community assembly and ecosystem functioning (Mason et al., 2005; Abonyi et al., 2018). Since there are well established functional groups for phytoplankton in use by many algologists, identified taxa were classified into Reynolds' functional groups (FGs) (Reynolds et al., 2002; Borics et al., 2007; Padisák et al., 2009).

For richness metrics number of taxa and number of FGs were used. Richness metrics are easily interpretable indices of diversity and they are easy to use, however they do not consider relative abundance. Besides the richness metrics, Shannon diversity index (Shannon, 1948) was applied, which is a broadly used diversity metric that takes into account relative species and group abundances. Furthermore, Pielou's evenness (Pielou, 1966) and Berger–Parker diversity (Berger & Parker, 1970) were also used to express the dominance relations in the communities. To test the similarity of the three habitats Jaccard similarity index was applied (Jaccard, 1901). Furthermore, to test dissimilarity of changes within the sampling points, community change rate was calculated using Bray–Curtis dissimilarity (Bray & Curtis, 1957) values and 1-Jaccard similarity index (incidence based community change rate) values between consecutive samples in each habitat.

Fig. 2 The schematic view of the sampling points (represented with letters for the three habitats: *M* metaphyton, *P* the non-isolated phytoplankton and *L* the phytoplankton isolated by limnocorral) in the experimental pond
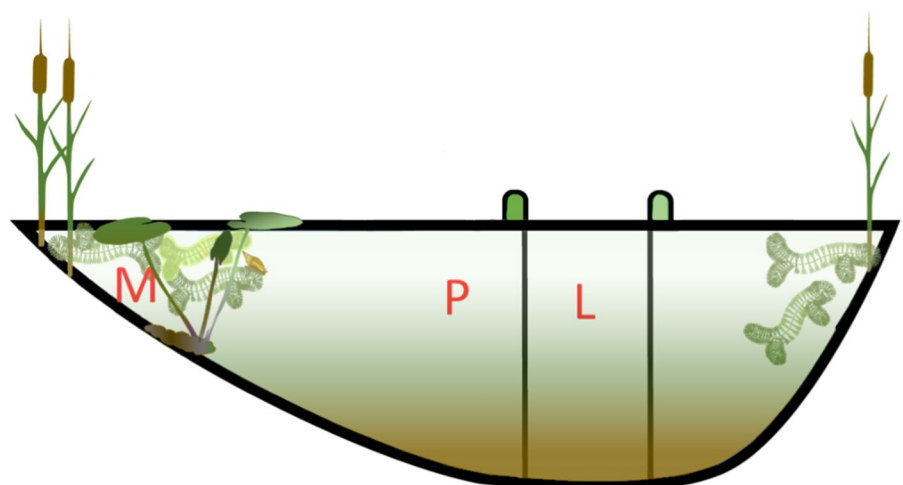
Statistical analyses

To visualize the differences of taxa and functional group composition between the sampling points (M, P, L) relative biomass data of taxa and FGs were applied using non-metric multidimensional scaling (NMDS). To test the statistical difference in the composition of the three habitats, analysis of similarity (ANOSIM) and permutational analysis of variance (PERMANOVA) were performed. To address pairwise comparisons between the habitats, pairwise.adonis function was used in R (R Core Team, 2022).

To test the similarity between the taxonomic and functional composition of the habitats, Jaccard similarity index was calculated for each sampling time between the habitat pairs (M–P, L–M, L–P) (PAST software, version 4.10; Hammer et al., 2001). For the calculation of community change rate values based on Bray–Curtis dissimilarity and 1-Jaccard similarity, PAST software was used (version 4.10; Hammer et al., 2001).

Taxa and functional group richness, Shannon diversity, Pielou's evenness and Berger–Parker diversity were also calculated by the PAST software (version 4.10; Hammer et al., 2001).

Statistical differences of community change rate, taxa and functional group richness, Shannon diversity, Pielou's evenness, Berger–Parker diversity and Jaccard similarity were tested with one-way ANOVA followed by Tukey post-hoc tests (in the case of normally distributed data). Kruskal–Wallis test was used with pairwise Wilcoxon test as a post-hoc pairwise comparison (in the case of non-normally distributed data). Analyses (NMDS, ANOVA, Kruskal–Wallis test, Tukey and pairwise Wilcoxon tests) were performed in R statistical environment (R Core Team, 2022).

To compare the functional redundancy in FGs between the habitats species saturation curves were fitted for each FGs using iNEXT R package (Hsieh et al., 2016).

Results

Number of taxa and functional groups in the three habitats

Altogether 225 taxa were found in the 51 samples, from which 177 occurred in the metaphytic habitat

Table 1 Number of taxa in FGs (Borics et al., 2007; Padisák et al., 2009; Reynolds et al., 2002) in the three habitats

FGs	Habitats		
	L	M	P
A	0	0	1
C	2	2	2
D	4	4	4
E	4	4	4
F	9	11	11
G	0	1	0
H1	5	1	3
J	24	28	28
K	8	8	6
Lo	8	10	11
M	1	0	1
N	0	2	1
P	0	4	3
Q	2	2	2
S1	6	5	4
T	1	3	2
TIB	6	21	11
TIC	0	1	0
TID	0	2	2
W0	3	3	4
W1	20	22	23
W2	4	5	4
WS	1	0	1
X1	26	24	25
X2	11	7	11
X3	4	4	4
Y	4	4	5

L limnocorral (isolated phytoplankton), *M* metaphyton, *P* non-isolated phytoplankton

(M), 172 in the non-isolated phytoplankton (P) and 152 in the isolated phytoplankton (L) (Supplementary Table 2). Number of shared taxa between the habitats was 118 and number of unique taxa were 28, 17 and 20 for M, P and L respectively (see Supplementary Table 2).

The observed taxa belonged to 27 FGs, from which 24 FGs were present in the M, 25 FGs in P and 21 FGs in L (Table 1). Only 7 FGs were present in all samples. Unique FGs were only found in M (FG: G and TIC) and in P (FG: A) (see Table 1).

Taxa and functional group composition of the habitats

Distribution of the samples of the three habitats showed an overlap in the NMDS plot (Figs. 3 and 4). While we observed a considerable scatter regarding the metaphyton (M) and the limnocorral (L) samples, an overlap could also be observed between them. The non-isolated plankton samples (P) showed overlap with both M and L, and these samples were more concentrated.

Despite the overlaps, the results of the ANOSIM showed significant differences among the composition of the three habitats for both taxa (R = 0.2012 and $P = 0.0001$) (Fig. 3; Table 2) and FGs (R = 0.1382 and $P = 0.0001$) (Fig. 4; Table 2). However, the R-values fell between 0.1 and 0.25 in both cases, indicating high similarity between the habitats.

Clusters found on the NMDS plot were also tested using PERMANOVA, which indicated significant compositional differences among the habitats ($P < 0.0001$) in the case of both taxa and FGs. The results of the pairwise comparisons (pairwise.adonis function) also showed significant differences between all habitat pairs (Table 2).
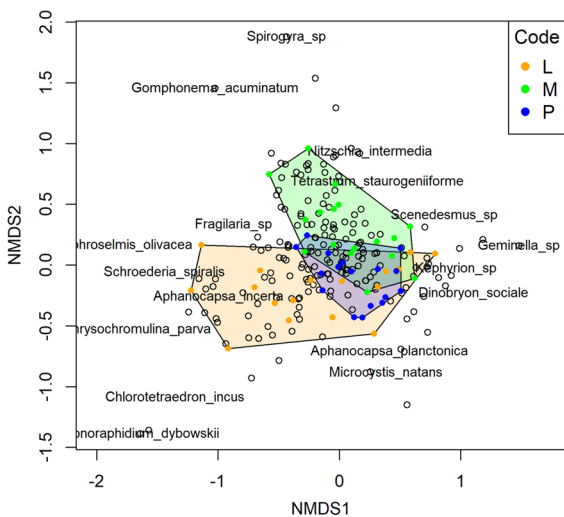

Fig. 3 NMDS plot of taxa composition in the three habitats [*L* limnocorral (isolated phytoplankton), *M* metaphyton, *P* non-isolated phytoplankton; stress = 0.1882203]
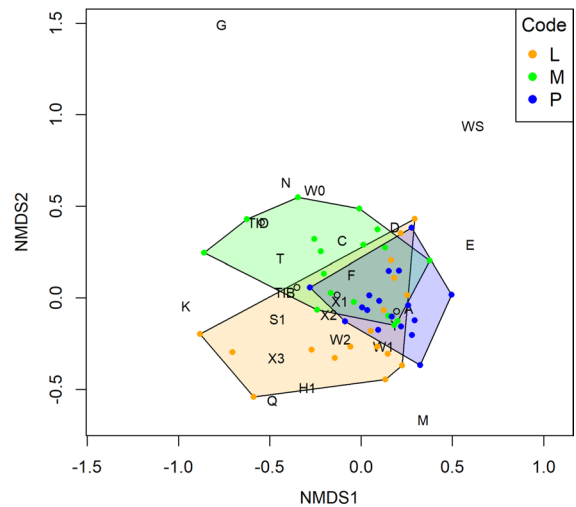

Fig. 4 NMDS plot of FG composition in the three habitats [*L* limnocorral (isolated phytoplankton), *M* metaphyton, *P* non-isolated phytoplankton; stress = 0.1856]

Similarity of habitats

The values of the Jaccard similarity index were the highest in the metaphyton and non-isolated phytoplankton relation (M–P) and the lowest in the metaphyton and isolated phytoplankton relation (L–M) in the case of both taxa and FGs (Fig. 5a, b). The ANOVA showed significant differences between the habitat pairs ($P = 0.00004$ for taxa and $P = 0.0178$ in the case of FGs; Table 3). The Tukey post hoc test showed the clear separation of the M–P pairs from the L–M pairs for both taxa and FGs (Table 3).

Functional redundancy in the different habitats

To study the differences in functional redundancy among the three habitats we created species saturation curves for each FG (Fig. 6). Functional groups with low redundancy (species numbers in the FG < 5; D, E, Y, K) showed no remarkable differences. In the case of most species rich groups (J, W1, TIB, F, Lo) functional redundancy was considerably higher in the metaphyton (M) and in the plankton of the non-isolated part of the pond (P) as compared to that in the limnocorral (L). An opposite tendency was found only for the X2 FG, where the functional redundancy of the limnocorral (L) and plankton (P) samples exceeded that of the metaphyton (Fig. 6k).

Table 2 Results of the ANOSIM, PERMANOVA and pairwise.adonis tests for taxa and FG composition in the three habitats

	ANOSIM		PERMANOVA	pairwise.adonis				
	R	P	P	Pairs	R^2	P value	P adjusted	Sig.
Taxa	0.2012	0.0001	0.0001	L–M	0.111366	0.001	0.003	*
				L–P	0.073186	0.005	0.015	
				M–P	0.08408	0.003	0.009	*
FGs	0.1382	0.0001	0.0001	L–M	0.104131	0.001	0.003	*
				L–P	0.08223	0.006	0.018	
				M–P	0.123044	0.001	0.003	*

L limnocorral isolated phytoplankton, *M* metaphyton, *P* non-isolated phytoplankton

In the pairwise.adonis test significance codes (sig) indicate marginal significance "."; and significance "*"

Temporal changes of diversity metrics in the three habitats

We also investigated how diversity metrics (species and FG richness, Shannon diversity, Pielou's evenness and Berger–Parker diversity) vary in the three habitats. Nearly all metrics (except community change rate based on 1-Jaccard similarity) showed a decreasing trend in diversity (increase in Berger–Parker diversity) with fluctuations throughout the study period (Figs. 7a, e, g, i, k and 8a, e, g, i, k).

Differences between diversity metrics in the three habitats

The mean values of the number of taxa and FGs were the highest in the metaphyton (M) and plankton (P) samples and the lowest in the limnocorral (L). The ANOVA showed significant differences in the case of both richness metrics ($P = 0.0003$ for the number of taxa; and $P = 0.0219$ for the number of FGs—Figs. 7f and 8f). The Tukey test highlighted that there were significant differences between L–P and L–M in the case of number of taxa, while in the case of number of FGs, significant difference appeared only in the L–M relation (Table 3).

We found the highest mean Shannon diversity values in the metaphyton samples (M) both for taxa (Fig. 7h) and FGs (Fig. 8h). The results of the ANOVA, however, did not indicate significant differences for taxon diversity ($P = 0.1340$; Table 3). In contrast, regarding FGs, it appeared to be significant ($P = 0.0406$; Table 3). Despite the result of the ANOVA for FGs, the Tukey test did not show significant differences between the habitats (Table 3),

only marginal significance was observed between metaphyton and the other two habitats ($P = 0.0746$ for M–P and $P = 0.0664$ for M–L).

Even though mean values of Pielou's evenness were the highest in the metaphyton (M) in the case of both taxa and FGs (Figs. 7j and 8j) there were no significant difference between habitats (Table 3).

Despite mean and median values of Berger–Parker diversity were the highest in the limnocorral (L) in the case of both taxa and FGs (Figs. 7l and 8l), no significant difference between the three habitats were observed ($P = 0.133$ for taxa (ANOVA); $P = 0.2937$ for FGs (Kruskal–Wallis test); Table 3).

Differences in community change rate between the habitats

The Bray–Curtis dissimilarity based mean community change rate values were the highest in the limnocorral (L) and somewhat lower in the metaphyton (M) and plankton (P) samples (Figs. 7b and 8b), but the ANOVA results did not show significant differences neither in the case of taxa ($P = 0.3910$), nor in the case of FGs ($P = 0.4140$; Table 3).

In contrast, there were significant differences in the incidence-based community change rate values (1-Jaccard similarity) (Table 3), indicating that the metaphyton (M) showed less changes than the isolated- (L) and non-isolated phytoplankton (P) in the case of taxa ($P = 0.0248$ for L–M and $P = 0.0065$ for M–P; Fig. 7d, Table 3). However, in the case of FGs the metaphyton (M) only showed significant difference from the non-isolated phytoplankton (P) ($P = 0.0296$ for M–P; Fig. 8d, Table 3).

A $F_{Welch}(2, 30.79) = 18.12$, $p = 6.27e{-}06$, $\widehat{\omega_p^2} = 0.50$, $CI_{95\%}$ [0.27, 1.00], $n_{obs} = 51$

B $F_{Welch}(2, 29.7) = 5.81$, $p = 7.44e{-}03$, $\widehat{\omega_p^2} = 0.23$, $CI_{95\%}$ [0.02, 1.00], $n_{obs} = 51$
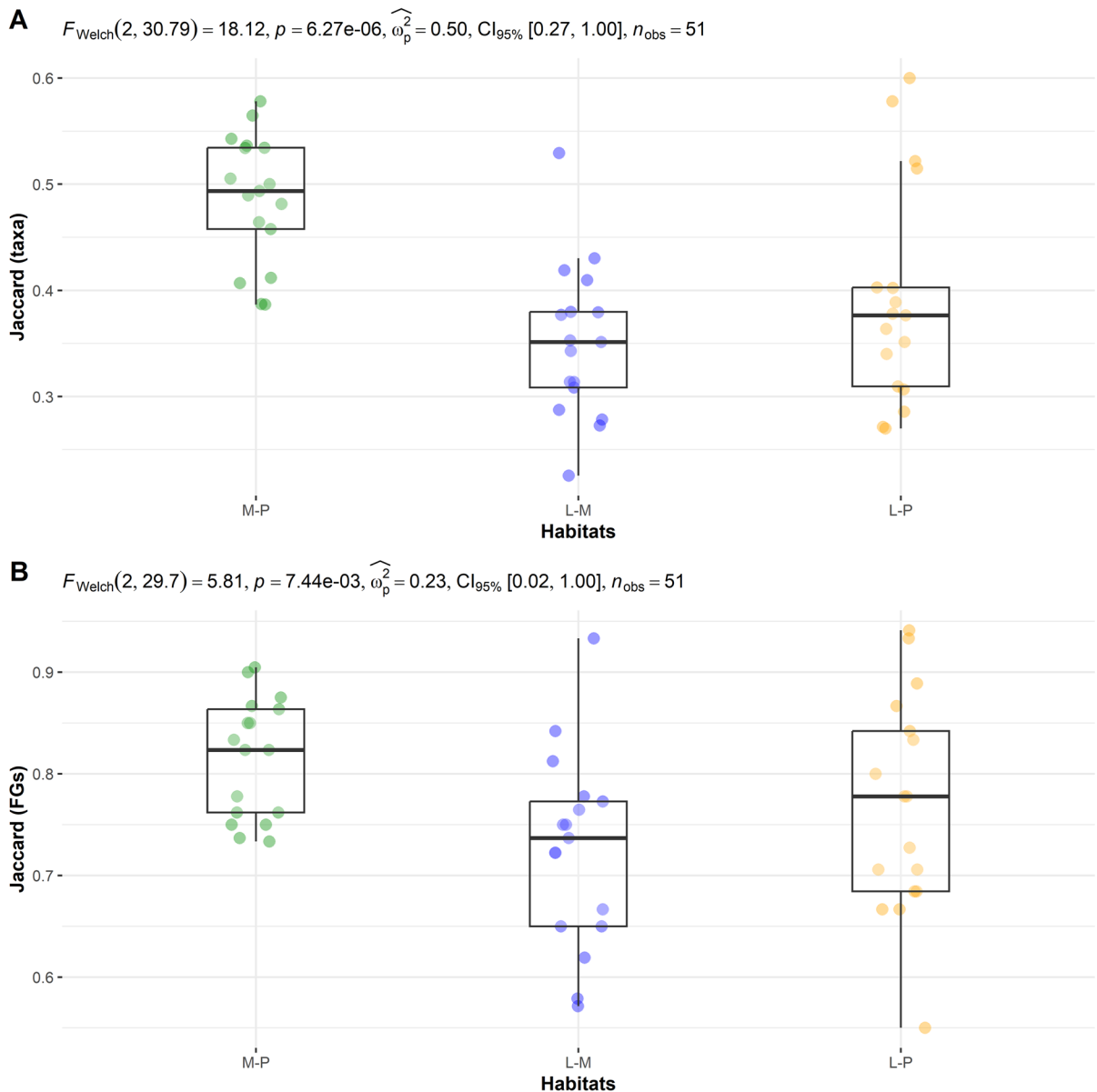
Fig. 5 Jaccard similarity index values between habitat pairs **A** for taxa and **B** for FGs. *M* metaphyton, *P* non-isolated phytoplankton, *L* limnocorral (isolated phytoplankton)

Discussion

In this study, we investigated how metaphytic assemblages of the littoral vegetation affected the composition and diversity of pelagic phytoplankton in a small eutrophic pond. The relevance of this question is more pronounced in the case of small shallow lakes, where because of their high littoral-pelagial ratio the extended macrovegetation has a strong impact on the metabolism of the whole lake (Wetzel et al., 1972; Carpenter & Lodge, 1986). Macrophytes besides shaping the physical properties of the ecosystems

and enable microgradients of resources to develop (Declerck et al., 2007; Wijewardene et al., 2022), have an array of complex interactions (competition, mutualism, commensalism) with their epi- and metaphytic microalgal assemblages (Koleszár et al., 2022; Mutinová et al., 2016; Roijackers et al., 2004). In the

Table 3 Results of the ANOVA and Kruskal–Wallis tests of diversity metrics

Diversity measures	ANOVA	Tukey-test	
	P	Pairs	*P* adjusted
Number of taxa	0.0003	L–M	0.0003
		L–P	0.0048
		M–P	0.6524
Number of FGs	0.0219	L–M	0.0206
		L–P	0.1173
		M–P	0.7297
Shannon diversity of taxa	0.1340	L–M	–
		L–P	–
		M–P	–
Shannon diversity of FGs	0.0406	L–M	0.0664
		L–P	0.9984
		M–P	0.0746
Evenness of taxa	0.2990	L–M	–
		L–P	–
		M–P	–
Evenness of FGs	0.0863	L–M	–
		L–P	–
		M–P	–
B–P diversity of taxa	0.1330	L–M	–
		L–P	–
		M–P	–
CCR of taxa (B–C)	0.3910	L–M	–
		L–P	–
		M–P	–
CCR of FGs (B–C)	0.414	L–M	–
		L–P	–
		M–P	–
CCR of taxa (Jaccard)	0.0049	L–M	0.0248
		L–P	0.8687
		M–P	0.0065
CCR of FGs (Jaccard)	0.0377	L–M	0.5134
		L–P	0.2839
		M–P	0.0296
Jaccard similarity of taxa	0.00004	(L–M)–(M–P)	0.00003
		(L–P)–(M–P)	0.0036
		(L–P)–(L–M)	0.3166
Jaccard similarity of FGs	0.0178	(L–M)–(M–P)	0.0130
		(L–P)–(M–P)	0.2744
		(L–P)–(L–M)	0.3467

Table 3 (continued)

	K–W	Pairwise Wilcoxon test	
	P	Pairs	P adjusted
B–P diversity of FGs	0.2937	L–M	–
		L–P	–
		M–P	–

In the case of a significant ANOVA or Kruskal–Wallis, pairwise post-hoc tests (Tukey-test or pairwise Wilcoxon test respectively) were carried out

K–W Kruskal–Wallis test, *B–P diversity* Berger–Parker diversity, *CCR* Community change rate, *B–C* Bray–Curtis dissimilarity
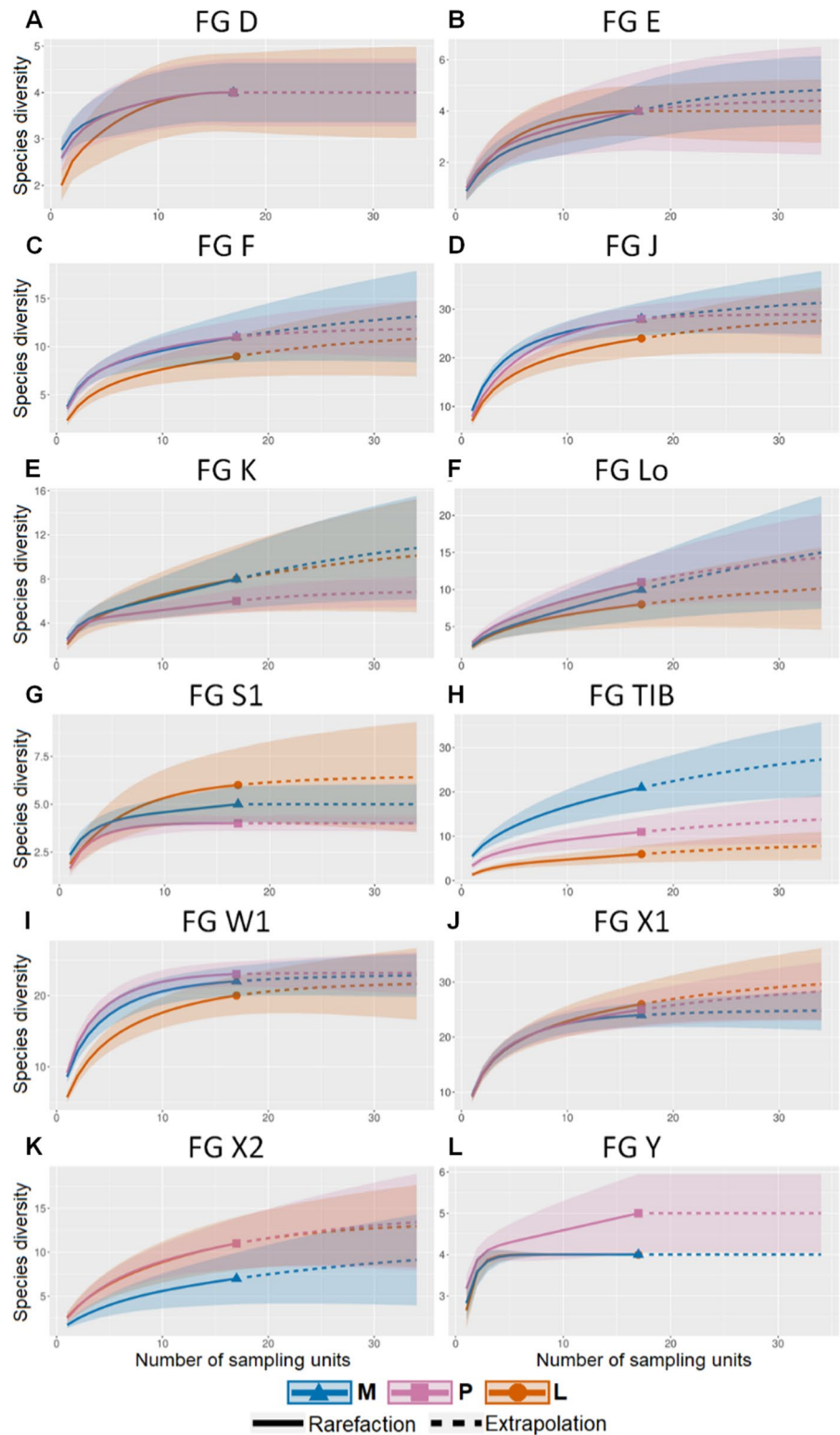
experimental pond, the littoral vegetation consisted primarily of *N. alba* and *C. demersum*. These species are quite widely distributed, *C. demersum* is an invasive cosmopolitan species (GBIF Secretariat, 2022; GISD, 2023) while *N. alba* is widespread in Europe and can be found in several other locations (GBIF Secretariat, 2022). Both species are associated with waters on a wide scale of trophic states (Brock, 1985; GISD, 2023) and can be dominant in oxbow lakes (Krasznai et al., 2010). Because of the shading effect of *Nymphaea* and the well-known allelopathic effect of *Ceratophyllum* on cyanobacteria and microalgae (Amorim et al., 2019; Dong et al., 2019), this vegetation is less favourable for the development of species rich metaphytic assemblages in comparison to *Utricularia* and *Salvinia* stands where more diverse metaphytic assemblages can develop (Fehér, 2003; Krasznai et al., 2008). Nevertheless, some studies have contradictory results concerning the relationship between macrophytes and phytoplankton diversity. For example Muylaert et al. (2010) found negative relationship between phytoplankton generic diversity and macrophyte cover in shallow lakes. The authors highlighted the importance of growing time, that is influenced by latitude (more diverse assemblages can develop at lower latitudes due to longer growing seasons). Furthermore, the paper stressed the importance of grazing by zooplankton and its changing importance along latitudinal gradient. In contrast Diniz et al. (2023) found that the presence of floating and submerged macrophytes increased species diversity under eutrophic conditions in tropical ponds. Van den Berg et al. (1998) highlighted that biomass changes and composition of algal assemblages are impacted by the density of macrophytes. They con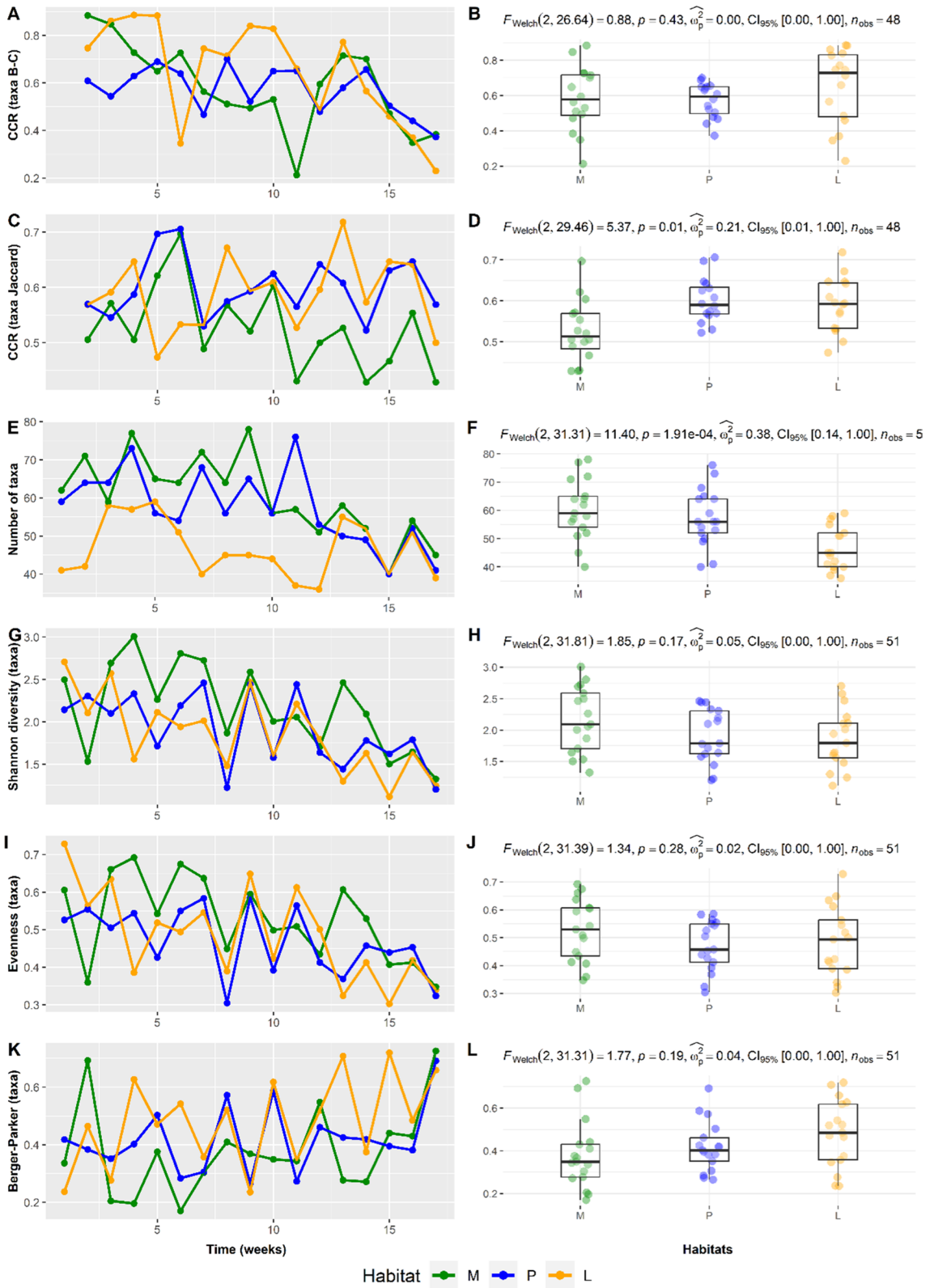cluded that increased density of macrophytes promotes sedimentation loss of algae. Therefore, flagellated taxa that are able to reduce their sedimentation might be able to stay in the water column (e.g. *Cryptomonas* sp. and *Rhodomonas* sp.), while others may sink. Pełechata & Pełechaty (2010) showed that an emerged macrophyte [*Phragmites australis* (Cav.) Trin. ex Steud.] overgrown by *C. demersum* had quite similar phytoplankton community composition as a *C. demersum* and *N. alba* dominated part of the water and the open water surface as well.

In our experimental setup the NMDS ordination clearly distinguished the three habitats, and both the ANOSIM and PERMANOVA indicated that the habitats show significant differences in terms of their microflora. These results supported our main hypothesis that metaphytic assemblages have an effect on the composition of the pelagial phytoplankton.

Not surprisingly some tychoplanktic elements, mostly diatoms from the TIB group [*Achnanthidium minutissimum* (Kützing) Czarnecki, *Amphora pediculus* (Kützing) Grunow ex Schmidt, *Navicula veneta* Kützing, *Nitzschia dissipata* (Kützing) Rabenhorst, etc. see Supplementary Table 2] were unique for the metaphyton. Differences, however, did not restrict exclusively to this group. We found larger functional redundancy of planktic FGs (J, W1, F, Lo,) in the metaphyton, than in the isolated part of the pond. These results are in accordance with previous findings (Borics et al., 2003). Investigating microflora of bog-lakes Borics et al. (2003) also experienced that planktic algae, especially those that lack capability of active locomotion were not present in the open water, but were abundant among the macrovegetation, where they settled on the surface of submerged plants, and avoided sinking to the bottom.

Fig. 6 Saturation curves of taxa in the functional groups (which had at least 4 taxa). *FG* for functional group, *L* for limnocorral (isolated phytoplankton), *M* for metaphyton, *P* for non-isolated phytoplankton

A

B $F_{\text{Welch}}(2, 26.64) = 0.88, p = 0.43, \widehat{\omega_p^2} = 0.00, \text{CI}_{95\%}[0.00, 1.00], n_{\text{obs}} = 48$

C

D $F_{\text{Welch}}(2, 29.46) = 5.37, p = 0.01, \widehat{\omega_p^2} = 0.21, \text{CI}_{95\%}[0.01, 1.00], n_{\text{obs}} = 48$

E

F $F_{\text{Welch}}(2, 31.31) = 11.40, p = 1.91\text{e-}04, \widehat{\omega_p^2} = 0.38, \text{CI}_{95\%}[0.14, 1.00], n_{\text{obs}} = 5$

G

H $F_{\text{Welch}}(2, 31.81) = 1.85, p = 0.17, \widehat{\omega_p^2} = 0.05, \text{CI}_{95\%}[0.00, 1.00], n_{\text{obs}} = 51$

I

J $F_{\text{Welch}}(2, 31.39) = 1.34, p = 0.28, \widehat{\omega_p^2} = 0.02, \text{CI}_{95\%}[0.00, 1.00], n_{\text{obs}} = 51$

K

L $F_{\text{Welch}}(2, 31.31) = 1.77, p = 0.19, \widehat{\omega_p^2} = 0.04, \text{CI}_{95\%}[0.00, 1.00], n_{\text{obs}} = 51$

Habitat ● M ● P ● L

◀**Fig. 7** Line graphs: changes of taxa based community change rates and diversity metrics during the study period. Boxplots: differences in metric values among the habitats. The three colours indicate the three habitats. Bray–Curtis distances between consecutive samplings as community change rate in time (**A**) and between habitats (**B**). 1-Jaccard index values between consecutive samplings as community change rate in time (**C**) and between habitats (**D**). Number of taxa in time (**E**) and between habitats (**F**). Changes of Shannon diversity values in time (**G**) and between habitats (**H**). Pielou's evenness values in time (**I**) and between habitats (**J**). Berger–Parker diversity in time (**K**) and between habitats (**L**). Abbreviations and colours: *M* metaphyton, green, *P* non-isolated phytoplankton, blue, *L* limnocorral (isolated phytoplankton), yellow

Among the FGs that showed high redundancy in the metaphyton, the W1 group deserves more attention. Small-celled dinoflagellates and euglenophytes constitute this group (Reynolds et al., 2002). We recorded 29 euglenophyte species in the studied pond of which 24 belonged to W1, and 5 (*Trachelomonas* spp.) to W2 group. Euglenophytes have long been considered as pond dwellers preferring eutrophic environments (Pringsheim, 1953, 1956; Wetzel, 1983). Recent studies highlighted their importance in epipelic environments (Round & Eaton, 1966; Hašler et al., 2008; Şahín et al., 2010; Poulíčková et al., 2014). Other authors (Marshall & Orr, 1948; Smayda et al., 2020) found that *E. proxima* Dangeard blooms were associated to oxic/anoxic boundary layer developed in meromictic lakes. Several recent findings (Burchardt et al., 2006; Padisák et al., 2003; Scheffer et al., 2006; Poniewozik & Juráň, 2018) revealed the importance of high macrophyte coverage for the development of rich euglenophyte assemblages. The above results suggest that there is still not enough knowledge on the autecology of euglenophytes to fully understand their occurrence and role in the metaphytic environments.
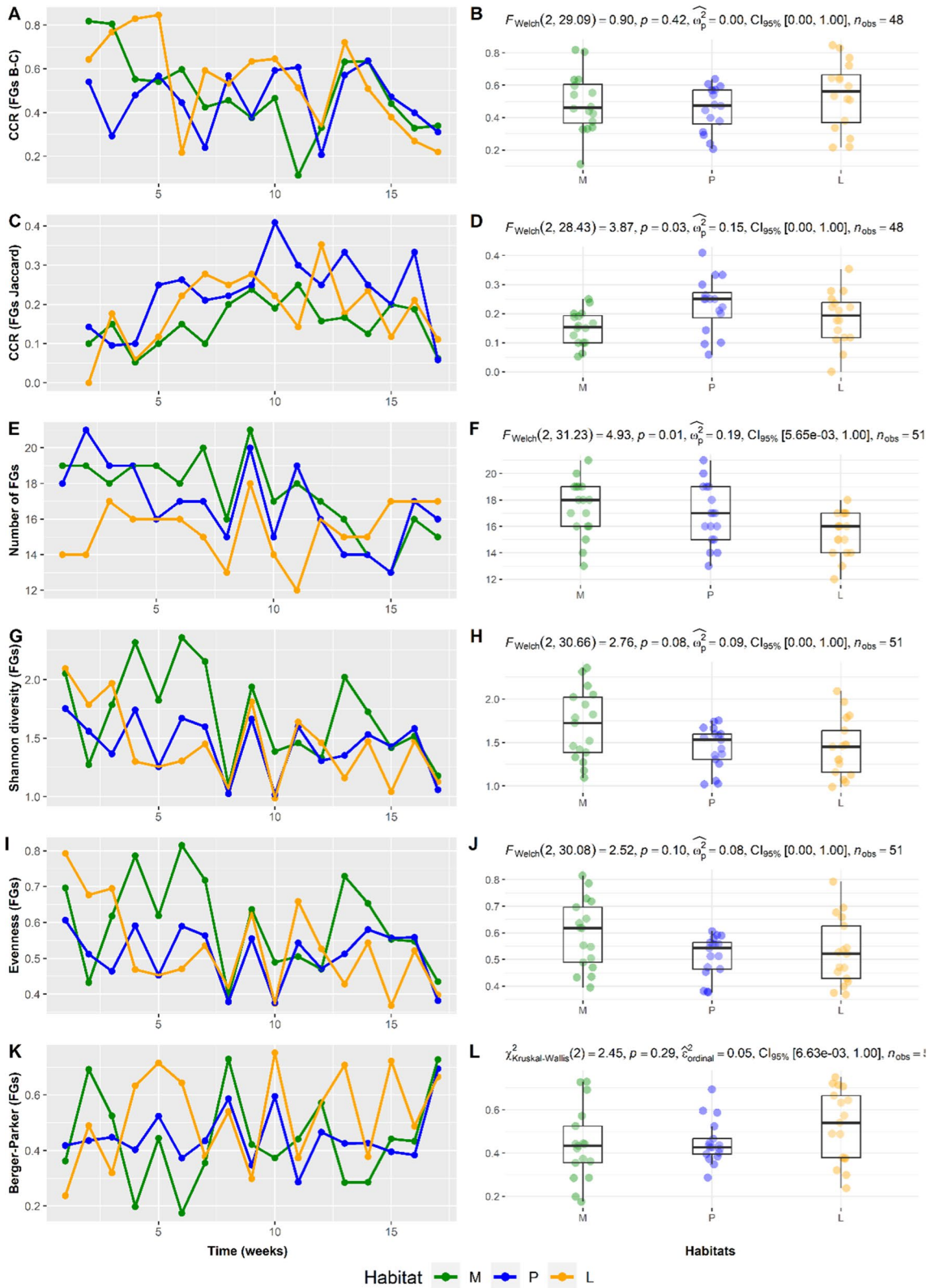
While richness values showed considerable differences among the habitats, there were no differences in the Shannon diversity values. The similar values in Pielou's evenness referred to similarities in the abundance of dominant taxa. However, we note here that the use of Shannon diversity is controversial in the literature, because it combines evenness and richness into a univariate vector that is difficult to interpret (Borics et al., 2021). In addition to this, diversity metrics are not sensitive to species replacements and thus, they cannot display well smaller compositional differences (T-Krasznai et al., 2023 submitted to this volume).

In contrast to Shannon diversity, the Jaccard similarity index values indicated well the differences between the microflora of limnocorral (L) and the other two habitats (M, P), both for the species and FGs. These results support our suggestion that the metaphyton is a source of several species that occur in the open water and considerably contributes to its species and functional richness.

Several research highlights that phytoplankton in the temperate lakes show considerable compositional changes throughout a year (Reynolds, 1989; Padisák et al., 1998; Deng et al., 2020). These compositional alterations could be observed in all three habitats. Although we hypothesised that macrophytes mitigate stochastic environmental effects throughout the study period, therefore lower community change rate values were expected in the metaphyton, the results only partially supported this assumption. While Bray–Curtis dissimilarity based community change rate did not show significant differences, the incidence-based community change rate values (1-Jaccard index) supported the hypothesis in the case of taxa, indicating less changes in the metaphytic habitat (M) than in the isolated (L) and non-isolated phytoplankton (P). However, in the case of FGs, there were only significant difference between the metaphyton (M) and the non-isolated phytoplankton (P), which showed the largest community change during the study period. We think that these findings can be explained by the fact that the mass effect between the metaphyton and the open water phytoplankton is not a continuous process, but is affected by occasional water movements. The mass effect means a temporarily unpredictable and stochastic species input.

We should emphasise here that the strengths of the source-sink dynamics between the metaphyton and plankton is a size specific process. In small lentic standing waters, the nutrient uptake and the physical structure of macrophytes create microgradients in nutrient and light availability (Declerck et al., 2007). These differences allow the creation of several microhabitats, which enable high taxa- and functional diversity to develop. In contrast, in the case of large lakes, the wind-induced waves homogenise the microflora of the lake, including that of the littoral vegetation. In these systems, because the continuously mixed littoral cannot enrich the open water with

A CCR (FGs B-C) vs Time (weeks)

B $F_{\text{Welch}}(2, 29.09) = 0.90$, $p = 0.42$, $\widehat{\omega_p^2} = 0.00$, $\text{CI}_{95\%}$ [0.00, 1.00], $n_{\text{obs}} = 48$

C CCR (FGs Jaccard) vs Time (weeks)

D $F_{\text{Welch}}(2, 28.43) = 3.87$, $p = 0.03$, $\widehat{\omega_p^2} = 0.15$, $\text{CI}_{95\%}$ [0.00, 1.00], $n_{\text{obs}} = 48$

E Number of FGs vs Time (weeks)

F $F_{\text{Welch}}(2, 31.23) = 4.93$, $p = 0.01$, $\widehat{\omega_p^2} = 0.19$, $\text{CI}_{95\%}$ [5.65e-03, 1.00], $n_{\text{obs}} = 51$

G Shannon diversity (FGs) vs Time (weeks)

H $F_{\text{Welch}}(2, 30.66) = 2.76$, $p = 0.08$, $\widehat{\omega_p^2} = 0.09$, $\text{CI}_{95\%}$ [0.00, 1.00], $n_{\text{obs}} = 51$

I Evenness (FGs) vs Time (weeks)

J $F_{\text{Welch}}(2, 30.08) = 2.52$, $p = 0.10$, $\widehat{\omega_p^2} = 0.08$, $\text{CI}_{95\%}$ [0.00, 1.00], $n_{\text{obs}} = 51$

K Berger-Parker (FGs) vs Time (weeks)

L $\chi^2_{\text{Kruskal-Wallis}}(2) = 2.45$, $p = 0.29$, $\widehat{\epsilon^2_{\text{ordinal}}} = 0.05$, $\text{CI}_{95\%}$ [6.63e-03, 1.00], $n_{\text{obs}} = $

Habitat ● M ● P ● L

◄**Fig. 8** Line graphs: changes of FG based community change rates and diversity metrics during the study period. Boxplots: differences in metric values among the habitats. The three colours indicate the three habitats. Bray–Curtis distances between consecutive samplings as community change rate in time (**A**) and between habitats (**B**). 1-Jaccard index values between consecutive samplings as community change rate in time (**C**) and between habitats (**D**). Number of FGs in time (**E**) and between habitats (**F**). Changes of Shannon diversity values in time (**G**) and between habitats (**H**). Pielou's evenness values in time (**I**) and between habitats (**J**). Berger–Parker diversity in time (**K**) and between habitats (**L**). Abbreviations and colours: *M* metaphyton, green, *P* non-isolated phytoplankton, blue, *L* limnocorral (isolated phytoplankton), yellow

metaphytic elements (Várbíró et al., 2017), the impact of the source-sink dynamic must be negligible.

Conclusion

Here we demonstrated that the microalgal flora of the littoral vegetation is neither a shaded, low biomass assemblage of euplanktic elements, nor an assemblage in which simply tichoplanktic elements prevail. Rather it consists of functionally and taxonomically diverse assemblages that enrich the phytoplankton of the open water with new elements. Understanding the main drivers of diversity of the metaphyton requires recognising the small environmental gradients that potentially develop among the macrophytes and reveal the autecology of species and FGs that exploit of these unique habitats.

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

Declarations

Conflict of interest The authors declare no conflict of interest.

Research involving human and animal participants No human participants and animals were involved in the research.

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