



## Effects of recreational beaches on chironomid assemblages in a large, shallow lake

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### ABSTRACT

The recreational use of water bodies presents new challenges and pressures on lake ecosystems. We focused on how recreational beaches influence the shoreline biodiversity of Lake Balaton, Hungary. Taking into account the establishment of beaches, we examined natural reed vegetated shorelines (representing natural situation), open areas (representing areas, where reed has been removed), as well as beaches. We assessed the abiotic parameters as well as the chironomid assemblages of these habitats. We found that the transformation of reeds through open habitats to beaches is associated with multiple changes in environmental properties and with a decrease in habitat heterogeneity. We observed that the transformation of reeds to beaches caused an 18% reduction in chironomid taxa richness and a moderate drop in their abundance. This reduction can be explained by the removal of reeds, because this action transforms a productive system to an unproductive one, and by the assumed dependence of chironomid richness and abundance to the organic-matter content of the sediment. Our analyses showed that the composition of chironomids was sensitive to the transformation of the habitats, and to the natural differences in the northern and southern shorelines of the lake. These findings suggest that the establishment and use of recreational beaches had a negative effect on local biodiversity. Although beaches can promote diversified societal and economic benefits, our results show that they can also generate conservation issues related to biodiversity loss. Consequently, action plans focusing on the maintenance and the establishment of recreational beaches should carefully consider both economic and conservation aspects.

### 1. Introduction

Man-made alterations of the environment have caused major changes in the global distribution of organisms (Vitousek et al., 1997). Several species have been eliminated or replaced from areas dominated by humans as a consequence of climate change, pollution, over-harvesting, introduction of non-native species and habitat transformation (Chapin et al., 2000). Freshwaters are under pressure from anthropogenic impacts and suffering from declines in biodiversity far greater than terrestrial ecosystems, and thus their conservation requires special attention (Dudgeon et al., 2006; Strayer and Dudgeon, 2010).

Lakes and ponds have experienced decades of intensive use for agricultural and aquacultural purposes, have been polluted and are going through changes due to climate warming (Johnson et al., 2018). In recent decades, however, some of these pressures have been mitigated or

even eliminated thanks to different action plans such as the Clean Water Act (USA) or Water Framework Directive (Europe). At the same time, however, the recreational use of waterbodies has increased including various water sports, fishing, bird watching or bathing on beaches. These activities present new challenges and pressures for lake ecosystems. Although the importance of tourism for human well-being and local economies is well appreciated, less attention has been paid to the effects of tourism on lake ecosystems (Monz et al., 2013; Venohr et al., 2018). Unfortunately, only limited information is available on how recreational beaches influence the habitat and the biodiversity of a lake's shoreline (but see Brauns et al., 2007). To fill this knowledge gap, here we focus on how the establishment and the use of recreational beaches influence freshwater biodiversity.

Obviously, the shoreline of a lake is not necessarily adequate for recreational beaches, because - among other features - natural

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vegetation (including emergent, floating, and submerged vegetation) is a physical obstacle for many recreational activities (e.g. swimming). Consequently, the removal of shoreline vegetation is an essential step for establishing beaches. Shoreline vegetation such as submerged macrophytes or reed are unique systems with well-defined habitat structure and associated ecological communities (Cheruvilil et al., 2000; Varga, 2001). Therefore, the removal of this vegetation might cause changes in the habitat structure, and might eliminate or replace organisms which depend on habitat complexity.

Besides the establishment of beaches, visitors cause disturbance to bottom-dwelling communities by treading. Although trampling experiments performed in headwater stream systems report both negative (Escarpinati et al., 2014) and neutral effects (Bossley and Smiley, 2018), recreational beaches are assumed to have a negative effect on macroinvertebrate communities because some sensitive species cannot cope with the selective force of treading (see filtering hypothesis in Poff, 1997). In agreement with this assumption, a comparative study performed in German lowland lakes found that the diversity of macroinvertebrates in recreational beaches is significantly lower than that in natural shorelines (Brauns et al., 2007). Brauns et al. (2007) explained this pattern by the reduced habitat heterogeneity (missing roots, coarse woody debris, reed and stones) in recreational beaches compared to that in natural shorelines. Consequently, there is still no clear idea on how recreational beaches influence bottom-dwelling organisms.

Chironomids are an important member of the littoral, shore, and benthic macroinvertebrate communities. Their activity is important for nutrient cycling, they act as bioturbators by reworking the top-sediment layers – oxygenating and cycling nutrient and organic matter (Armitage et al., 1995). Chironomids provide food for fish species in their larval form, and for terrestrial species such as birds, bats and predatory insects as adults. Finally, chironomid larvae have diverse environmental optima and tolerance, which make them an ideal model group for freshwater biomonitoring studies (Rosenberg, 1992).

With its 593 km<sup>2</sup> surface area, Lake Balaton is the largest shallow lake in Central Europe, and one of the region's foremost touristic destinations. It has a long shoreline (240 km) due to its shape: it is 77.9 km long (approximately in an east–west direction) and on average 7.2 km wide. The lake bottom is covered by soft sediment (Tóth, 2016), which is dominated by chironomid communities (60 to 95% of the total biomass of macroinvertebrates, Specziár and Bíró, 1998). The natural shoreline of the lake is vegetated by reeds (Tóth, 2016). The dominant northern winds produce contrasting shoreline types: the northern shoreline is wind-protected and covered by silty substrate, while the southern shoreline is exposed to wind and intensive wave activity, and covered by sand. To fulfil the demand of increasing tourism, natural reed-vegetated shorelines have been cleared, which has resulted in open soft-bottom areas. Afterwards, these areas were filled with sand in the northern shoreline (this action was not required in the southern shoreline, where the dominant substrate is sand) and then used as recreational beaches. This means that - similar to other tourist lakes all over the world - natural reed-covered shorelines were transformed to recreational beaches, with some differences in the northern and southern shorelines of the lake.

The objective of the present study was to reveal the effects of recreational beaches on habitat structure and associated chironomid communities of Lake Balaton. Particularly, we are interested in answering the following questions: (1) How habitat transformation influences environmental properties? (2) Do these changes result in distinct habitat types considering environmental properties? (3) How recreation beaches influence the richness, abundance and composition of chironomid communities? (4) How environmental variables influence the richness, abundance and composition of chironomid communities? Considering the sensitivity of chironomids to the environment and the process of establishing beaches in Lake Balaton, we formulated the following hypotheses:

H1: The transformation of reed-covered shorelines to beaches has a significant impact on the richness, abundance and composition of

chironomid communities because chironomids are sensitive to changes in habitat properties.

H2: The transformation of reed-covered shorelines to soft bottom area has significant effect on chironomid communities because chironomids are sensitive to the habitat alteration associated with the removal of reed.

H3: In the southern shoreline, the transformation of soft bottom area to beaches has significant effect on chironomid communities due to the effect of trampling.

H4: In the northern shoreline, the transformation of soft bottom area to beaches has effect on chironomid communities because chironomids are sensitive to sand addition.

## 2. Methods

### 2.1. Study area and sampling design

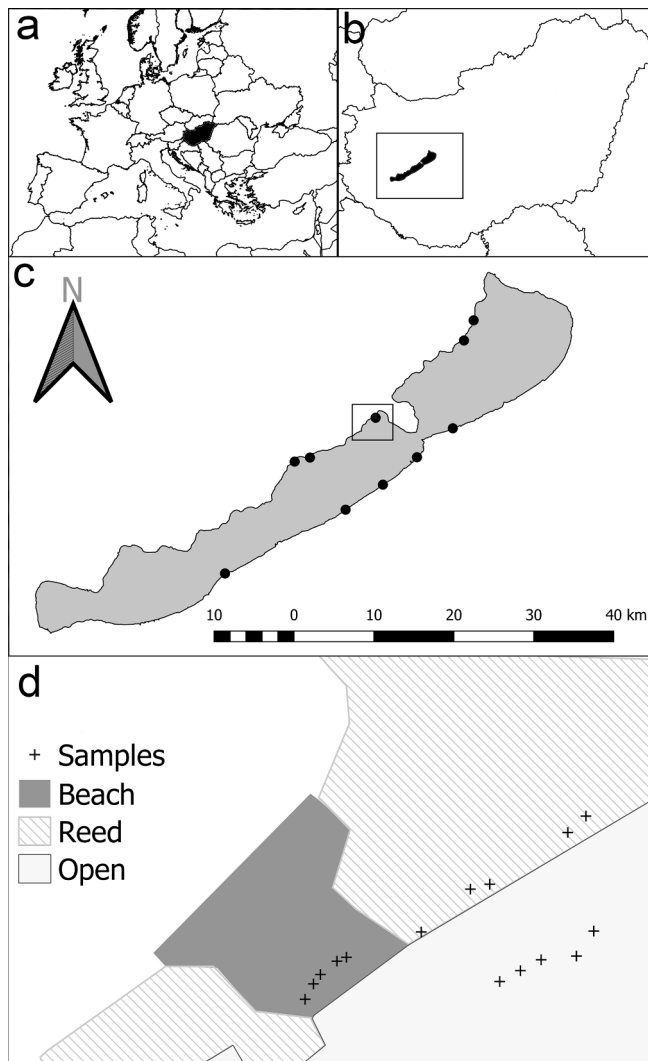
Lake Balaton is a multi-purpose freshwater lake used to source drinking water for the nearby settlements and for diverse recreational activities including bathing, sailing and sport fishing. To accommodate tourism, extended sections of the lake shoreline were turned into beaches, the natural vegetation was removed, and the shore was stabilized with concrete and riprap structures. In order to account for the differences between the northern and southern shorelines, 5–5 sampling sites were selected on each shoreline. Three habitats were sampled within each site: (1) natural reed-vegetated shoreline hereafter referred to as reed habitat, (2) open area, which is not used as a beach and (3) beach habitat that is used by beach goers/impacted by beach goers i.e. < 1.5 m depth (Fig. 1, Suppl. Fig. 1). Within each site and habitat, 5 sampling points (1 m<sup>2</sup> area) were randomly selected. Consequently, our sampling design consisted of 2 [shorelines] × 5 [sampling sites] × 3 [habitats] × 5 [sampling points] = 150 samples.

### 2.2. Sampling and identification of chironomids

Benthic chironomid larvae were sampled between 8 and 26 July 2019 using an Ekman grab sampler (sampling area: 0.022 m<sup>2</sup>). To increase the representativeness of samples and to support comparability with other studies (Árva et al., 2015a; Specziár et al., 2018), three sampling units were taken at each sampling point. These were then merged and considered as one sample (total area per sample: 0.065 m<sup>2</sup>). Samples were washed through a 0.25 mm mesh sieve and transported to a laboratory in a cooling box. Chironomids were separated from the sediment alive by the sugar flotation method (Anderson, 1959), euthanized and preserved in 70% ethanol. Chironomid larvae were slide-mounted and identified to species or to the lowest possible taxonomic level (further details in Árva et al., 2015b).

### 2.3. Environmental variables

The position of each sampling point was recorded using a Global Positioning System (GPS) receiver and the following parameters were recorded: shoreline position (north or south), habitat (reed, open or beach), water depth (m), water temperature (°C), pH and dissolved oxygen (DO, mgL<sup>-1</sup>) just above the bottom. Vegetation cover within a circle of 3-m diameter around the sampling point was estimated visually as the percentage of emergent (reed), submerged and floating-leaved macrophytes, and filamentous algae (mostly *Cladophora* sp., hereafter algae). The substrate composition of the samples was visually estimated as the percentage of silt (grain size < 0.06 mm), sand (0.06–2 mm) and mollusc shell (mainly *Dreissena polymorpha* (Pallas, 1771) and *D. bugensis* (Andrusov, 1897)). Organic matter content of the samples (Fine particulate organic matter [FPOM], Coarse particulate organic matter excluding reed leaves [CPOM] and reed leaves) was also visually assessed using a score varying between 0 (not present) to 5 (extremely abundant). Our visual habitat assessment methods are widely used in



**Fig. 1.** Map of the study area: (a) Hungary in Europe, (b) the position of Lake Balaton in Hungary, (c) Lake Balaton with study sites (full dots), and (d) the schematic representation of the study design in reed, open and beach habitats.

freshwater ecology (Hughes et al., 2010). Relative organic matter content was assessed in the upper 2 cm of the sediment layer according to loss-on-ignition method at 550 °C for 1 h (LOI550, Heiri et al., 2001). Organic matter content could not be quantified in six of the samples due to the low amount of collectable sediment in some reed habitat sampling points. We selected these environmental variables based on the known sensitivity of chironomids (Árvai et al., 2015b, 2017).

#### 2.4. Statistical analyses

Based on our visual assessment, the majority of the samples contained no or a limited amount of reed leaves, CPOM and FPOM (scores 0 or 1; Suppl. Fig. 2). A centred Principal Component Analysis (PCA) showed that the first principal component explained the majority (75%) of among-sample variation and, therefore, we used it only as an indicator of organic matter. Akaike Information Criterion corrected for the number of cases and parameters estimated (AICc) (Garamszegi and Mundry, 2014) was used to select the best-fit linear model explaining the effects of habitat, shoreline position and their interaction on environmental variables. In case of a significant habitat effect, a Tukey test was used for multiple comparisons.

Variance Inflation Factors (VIFs) were used to check for collinearity of environmental variables. Based on VIF, the percent cover of silt and

sand showed collinearity (Pearson  $r = -0.868$ ,  $P < 0.001$ ). This result showed that the substrate composition of a sample was dominated by sand or silt, but the two components rarely co-occurred in high proportions. To avoid collinearity, we disregarded the use of silt in the further analyses. Linear Discriminant Analysis (LDA) was used to examine the separation of the three habitats based on environmental variables.

Linear models (LMs) were used to check the individual and joint effects of habitat and shoreline position on the richness and abundance of chironomid communities. In these analyses, taxon richness and log-transformed abundance were used separately as response variables (both modelled by Gaussian distribution). LMs were used to examine which environmental variables influenced the taxon richness (number of taxa) and abundance of chironomids. Due to missing data, relative organic matter as a predictor was omitted from these analyses. The best-fit models were selected using AICc and Akaike weights (Garamszegi and Mundry, 2014). Delta AICc indicates the difference in the fit between a particular model considered and that of the best fit model. The AIC weight represents the probability of the model that was calculated among all possible pairs.

Analysis of variance using distance matrices (Anderson, 2001; hereafter ADONIS) was used to test how habitat type, shoreline position and their interaction influenced community composition measured with Bray-Curtis distance (Podani, 2000). Indicator species analysis (Dufrene and Legendre, 1997) was used to select indicator species for the different habitats in different shoreline positions. Because a detrended correspondence analysis (DCA) indicated a relatively long gradient length (4.254 in standard deviation units on the first axis) in our community data, we chose canonical correspondence analysis (CCA). CCA showed that the first eight canonical axes explained 35.2% of community variation. The *envfit* function of the vegan package was used to select environmental variables with significant effects. Analyses were run in the R statistical environment (R Core Team, 2020) using the *faraway* (Faraway, 2016), *multcomp* (Hothorn et al., 2008), *MuMIn* (Barton, 2020) and *vegan* (Oksanen et al., 2019) packages.

### 3. Results

#### 3.1. Environmental differences between habitats

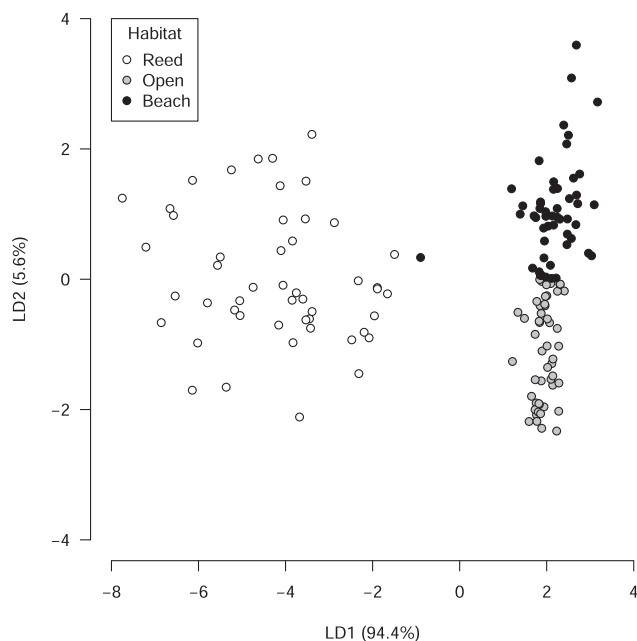
Environmental variables showed significant differences between habitats (Table 1). The open habitat was characterised by deep water and high pH. The reed habitat was characterised by low DO and a high proportion of mollusc shell content. Furthermore, the cover of reed, other macrophytes and algae were highest in reed habitat. The beach habitat differed from reed and open habitat as it had the highest proportion of sand substrate. The amount of organic matter and relative organic matter decreased from reed to open habitat, and then from open to beach habitat. Finally, water temperature and the amount of silt were highest in open habitat, followed by reed and beach habitats. The best-fit models showed that in most cases, not only habitat, but also shoreline position, as well as the interaction of habitat and shoreline position explained environmental parameters (Table 1). The inclusion of the interaction in the best-fit statistical model suggests that the differences in environmental variables between habitats depended on shoreline position. In the southern shoreline, the proportion of sand was high (about 80%) and more or less the same in different habitats, while in the northern shoreline we observed high values only in beach habitat (Suppl. Fig. 3).

LDA showed overall differences in environmental variables between the studied habitats (Fig. 2). The first axis explained 94.4% of the between-habitat variance and clearly separated reed habitat from open and beach habitats, while the second axis explained 5.6% of the between-habitat variance and separated open and beach habitats. In addition, LDA showed that the reed habitat was the most heterogeneous as the sampling points occupied a wide range of the first axis compared

**Table 1**

Comparison of environmental variables of reed, open and beach habitats. Variables are given as mean ( $\pm$ SE). Values not sharing an index letter proved to be different at  $P < 0.05$  in pairwise comparisons based on Tukey test. The best-fit model included the predictor variables habitat, shoreline position, and their interactions, selected based on AICc.

Environmental variable	Reed	Open	Beach	Predictors of the best-fit model based on AICc
Water depth (m)	0.86 ( $\pm$ 0.07) a	1.39 ( $\pm$ 0.07) b	0.95 ( $\pm$ 0.04) a	Habitat + Shoreline position + Interaction
Water temperature (C°)	22.80 ( $\pm$ 0.18) ab	23.26 ( $\pm$ 0.17) a	22.55 ( $\pm$ 0.19) b	Habitat
pH	8.47 ( $\pm$ 0.02) a	8.68 ( $\pm$ 0.01) b	8.54 ( $\pm$ 0.02) a	Habitat + Shoreline position
Dissolved oxygen (mg/L)	6.36 ( $\pm$ 0.02) a	7.20 ( $\pm$ 0.01) b	6.95 ( $\pm$ 0.02) b	Habitat + Shoreline position
Sand (%)	42.2 ( $\pm$ 6.93) a	45.7 ( $\pm$ 6.22) a	84.6 ( $\pm$ 3.88) b	Habitat + Shoreline position + Interaction
Silt (%)	34.2 ( $\pm$ 4.54) a	51.8 ( $\pm$ 6.05) b	13.3 ( $\pm$ 3.91) c	Habitat + Shoreline position + Interactions
Mollusc shells (%)	7.5 ( $\pm$ 4.47) a	2.5 ( $\pm$ 0.70) b	2.1 ( $\pm$ 0.94) b	Habitat + Shoreline position + Interactions
Organic matter (PCA axis value, $\log(x + 1)$ transformed)	0.13 ( $\pm$ 0.06) a	-0.08 ( $\pm$ 0.03) b	-0.24 ( $\pm$ 0.03) c	Habitat + Shoreline position + Interactions
Relative organic matter (%)	10.33 ( $\pm$ 0.06) a	6.19 ( $\pm$ 0.03) b	1.85 ( $\pm$ 0.03) c	Habitat + Shoreline position + Interactions
Cover of reed (%)	52.4 ( $\pm$ 2.26) a	0.0 ( $\pm$ 0.00) b	0.00 ( $\pm$ 0.00) b	Habitat
Cover of macrophytes (%)	20.2 ( $\pm$ 3.99) a	8.5 ( $\pm$ 2.07) b	5.8 ( $\pm$ 1.39) b	Habitat + Shoreline position + Interactions
Cover of algae (%)	3.6 ( $\pm$ 1.68) a	0.0 (0.00) b	0.6 ( $\pm$ 0.06) b	Habitat + Shoreline position



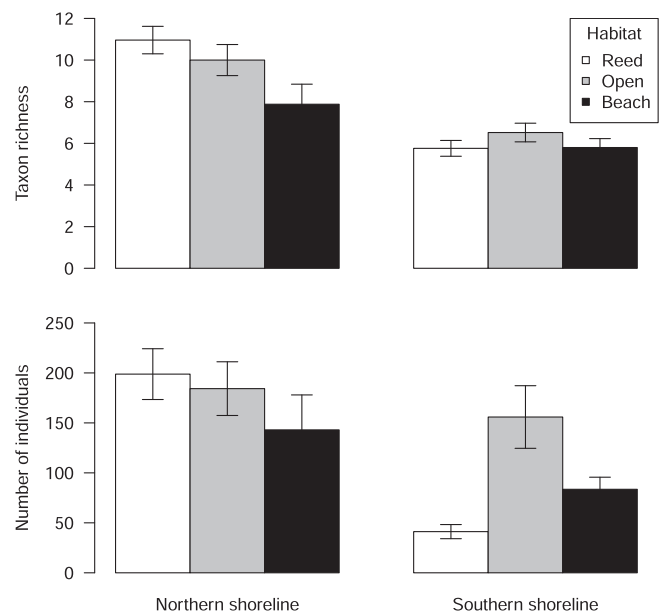
**Fig. 2.** Ordination plot of linear discriminant analysis (LDA) showing the separation of habitats based on environmental variables.

to open and beach habitats.

**3.2. Taxon richness and abundance of chironomids**

Altogether 37 taxa were found among the 20,168 identified individuals (Suppl. Appendix 1). The most dominant taxa were *Cladotanytarsus mancus* gr (Walker, 1856) (5967 individuals), *Polypedilum nubeculosum* (Meigen, 1804) (3915 individuals), *Cladopelma virescens* (Meigen, 1818) (1747 individuals) and *Procladius choreus* (Meigen, 1818) (1529 individuals).

**Hypothesis 1..** The transformation from natural reed shoreline to recreational beach had an overall negative impact on the richness and abundance of chironomids (Fig. 3, Table 2). In general, the transformation caused an 18% reduction in the taxon richness. The mean taxon richness of chironomids for reed and beach habitats were 8.36 and 6.81, respectively. The richness of chironomids depended on the shoreline position with the Northern shoreline having higher richness. Furthermore, the effect of habitat transformation on taxon richness was also shoreline specific, as indicated by the significant interaction term in our model (Table 2). Taxon richness significantly decreased on the Northern shoreline, while it did not change on the Southern shoreline (Fig. 3). Habitat transformation caused a 5.6% reduction



**Fig. 3.** Response of taxon richness (top) and number of individuals (bottom) on the transformation of the reed-covered shoreline (reed) to open habitat (open) and to recreational beaches (beach) in the northern (left) and southern (right) shorelines of Lake Balaton. Bars show mean values and whiskers are standard errors.

in the number of individuals from 120 in reed to 113 individuals in beach habitat. We observed less individuals in the Southern shoreline, and the effect of habitat transformation on the abundance of chironomids was shoreline specific (Table 2, Fig. 3).

**Hypothesis 2..** We found no evidence that the transformation of reed shoreline to open habitat caused a significant reduction in the taxon richness of chironomids (Table 2, Fig. 3), even though we observed a numerical reduction from 8.36 to 8.26 taxa per sample, and also a shoreline-dependent richness pattern (Table 2, Fig. 3). There was no significant difference in abundance between the reed and open-water habitats. (Table 2, Fig. 3). However, the abundance of chironomids seemed to be shoreline position-specific, and the significant interaction between shoreline position and habitat suggested that in the southern shoreline open habitats support a richer chironomid fauna than reed habitats (Fig. 3).

**Hypotheses 3. and 4.** We found no evidence that moving from open areas to beaches would decrease the richness and abundance of chironomids, neither in the northern nor in the southern shoreline of the lake (Table 2, Fig. 3).

**Table 2**  
Output of linear models (LMs) testing hypotheses regarding taxon richness and number of individuals.

Hypothesis number	Compared habitats	Response variable	Predictor	Estimate	Error	t value	P
1	Reed vs. Beach	Taxon richness	Beach	-3.080	0.918	-3.354	<b>0.001</b>
			South	-5.200	0.918	-5.662	<b>&lt;0.001</b>
			Interaction	3.120	1.299	2.402	<b>0.018</b>
		Number of individuals (log-transformed)	Beach	-0.907	0.291	-3.122	<b>0.002</b>
			South	-1.744	0.291	-6.002	<b>&lt;0.001</b>
			Interaction	1.631	0.411	3.971	<b>&lt;0.001</b>
2	Reed vs. Open	Taxon richness	Open	-0.960	0.817	-1.174	0.243
			South	-5.200	0.817	-6.362	<b>&lt;0.001</b>
			Interaction	1.720	1.156	1.488	0.140
		Number of individuals (log-transformed)	Open	-0.301	0.278	-1.083	0.282
			South	-1.744	0.277	-6.275	<b>&lt;0.001</b>
			Interaction	1.393	0.393	3.544	<b>&lt;0.001</b>
3	Open vs. Beach (southern shoreline)	Taxon richness	Beach	-0.720	0.619	-1.162	0.251
		Number of individuals (log-transformed)	Beach	-0.368	0.317	-1.159	0.252
4	Open vs. Beach (northern shoreline)	Taxon Richness	Beach	-0.368	0.317	-1.159	0.252
		Number of individuals (log-transformed)	Beach	-0.368	0.317	-1.159	0.252

**Table 3**  
The three best-fit linear models explaining the effects of environmental variables on the taxon richness (numbers of taxa) and abundance of chironomids.

Response variable	Predictors (slope)	df	AICc	Delta AICc	Weight
Taxon richness	algae (-0.06), water depth (-2.93), organic matter (2.47), pH (-5.27), reed (-0.04), sand (-0.04), macrophytes (0.04), temperature (0.51)	10	743.1	0.00	0.316
	water depth (-3.17), organic matter (2.55), pH (-5.25), reed (-0.05), sand (-0.04), macrophytes (0.04), temperature (0.46)	9	744.7	1.52	0.148
	algae (-0.06), water depth (-2.96), organic matter (2.46), pH (-5.26), reed (-0.04), sand (-0.05), macrophytes (0.04), shells (-0.01), temperature (0.52)	11	745.4	2.31	0.100
Number of individuals	water depth (-0.61), organic matter (0.48), oxygen (-0.39), reed (-0.02), sand (-0.01), temperature (0.21)	8	458.1	0.00	0.022
	organic matter (0.56), pH (-1.32), reed (-0.01), sand (-0.01), temperature (0.19)	7	458.5	0.42	0.018
	organic matter (0.68), oxygen (-0.41), reed (-0.01), temperature (0.23)	6	458.6	0.43	0.018

The best fit model with the lowest AICc and with the highest probability of fit revealed that the taxon richness of chironomids was influenced by several environmental variables (Table 3). This model indicated a strong positive effect (slope > 1) for organic matter, and a strong negative effect (slope < -1) for water depth and pH, as well as the effects of algae, reed cover, sand, macrophytes and temperature (Table 3). Alternative and still plausible statistical models included these strong positive and negative effects, as well as other effects (Table 3). The weights of the best models were extremely low (2.2, 1.8 and 1.8% for the first three) suggesting that the explanation of chironomid abundance is not straightforward and several alternative statistical models are plausible. The best fit model revealed the importance of several environmental variables with weak impact (Table 3). Alternative and still plausible statistical models suggested the importance of several environmental variables, mostly with weak effects (Table 3).

3.3. Community composition

Analysis of variance using distance matrices (ADONIS) revealed that the community composition of chironomids was different between the reed and beach habitats, and between the northern and southern shorelines (Table 4). We also found an interaction effect suggesting that the difference between the reed and beach habitats strongly depended on the shoreline position (Table 4). Considering our second hypothesis, we found that there was a compositional difference in the community between reed and open habitats, between the northern and southern shorelines, and there was an interaction effect (Table 4). Considering the compositional differences between open and beach habitats, we found marginally-significant differences in the southern shoreline (Table 4, hypothesis 3) and significant differences in the northern shoreline (Table 4, hypothesis 4). These findings suggested that the composition of

**Table 4**  
Output of ADONIS testing hypotheses regarding community composition using Bray-Curtis distance.

Hypothesis number	Compared habitats	Predictor	Df	SS	MS	F	R <sup>2</sup>	P
1	Reed vs. Beach	Habitat	1	2.709	2.709	12.349	0.091	<b>0.001</b>
		Shoreline	1	4.379	4.379	19.958	0.146	<b>0.001</b>
		Interaction	1	1.758	1.758	8.012	0.058	<b>0.001</b>
		Residuals	96	21.065	0.219		0.704	
		Total	96	29.913			1.000	
2	Reed vs. Open	Habitat	1	2.386	2.386	10.222	0.073	<b>0.001</b>
		Shoreline	1	5.455	5.455	23.368	0.166	<b>0.001</b>
		Interaction	1	2.639	2.639	11.306	0.080	<b>0.001</b>
		Residuals	96	22.409	0.233		0.681	
		Total	96	32.89			1.000	
3	Open vs. Beach (southern shoreline)	Habitat	1	0.487	0.487	2.293	0.045	0.054
		Residuals	48	10.200	0.213		0.954	
		Total	49	10.688			1.000	
4	Open vs. Beach (northern shoreline)	Habitat	1	1.668	1.668	6.079	0.112	<b>0.001</b>
		Residuals	48	13.170	0.275		0.888	
		Total	49	14.838			1.000	

chironomids was highly sensitive both to shoreline position and habitat differences.

Indicator value analysis showed that there were ten indicator taxa for natural reed habitat (*Polypedium nubeculosum*, *Cladopelma virescens*, *Chironomus balatonicus* Dévai, Wülker & Scholl 1983, *Microtendipes chloris* agg., *Cladopelma viridulum* [Linnaeus, 1767], *Ablabesmyia longistyla* Fittkau, 1962, *Paratanytarsus* sp., *Tanytarsus* sp., *Zavreliella marmorata* [van der Wulp, 1859], *Psectrocladius sordidellus* gr.), six for open (*Procladius choreus*, *Tanytus kraatzi* [Kieffer, 1912], *Tanytus punctipennis* Meigen, 1818, *Fleuria lacustris* Kieffer, 1924, *Microchironomus tener* [Kieffer, 1918] and *Parachironomus varus* [Goetghebuer, 1921]), and a single taxon for beach habitat (*Dicrotendipes nervosus* [Staege, 1839]) in the northern shoreline. Indicator value analyses revealed four indicator taxa for open habitat in the southern shoreline (*Lipiniella moderata* Kalugina, 1970, *Cladotanytarsus mancus* gr., *Cryptochironomus defectus* [Kieffer, 1913] and *Cricotopus sylvestris* gr.). CCA showed that the environmental variables had a significant impact on the community structure of chironomids (Fig. 4). The first CCA axis explained 17.1% of variance in the chironomid community, representing a gradient of decreasing proportion of sand and increasing amount of organic matter. The second CCA axis explained 9.6% variance and represented a habitat gradient with increasing reed, mollusc shells and decreasing oxygen and pH. We also found that northern reed habitat was present mostly (but not exclusively) at the top of the plot, northern open habitat at the bottom-right side of the plot, all southern habitats at the left side of the plot, while northern beach sites positioned mostly close to southern sites. Distribution of sites' scores indicated substantially higher

heterogeneity at northern than southern habitats.

#### 4. Discussion

Only limited information is available on how recreational beaches influence the biodiversity of lake shorelines. To fill this knowledge gap, we collected chironomid assemblages from natural reed-vegetated shorelines, from open areas as well as from beaches, and compared their diversity. We found that the transformation of reed habitats to beaches had a negative effect on the taxonomic richness and abundance of chironomids, and that this habitat transformation influenced the composition of chironomid assemblages. These findings suggest that the establishment and use of recreational beaches had a negative effect on local biodiversity.

Habitat alteration is among the greatest anthropogenic impacts influencing freshwater biodiversity (Chapin et al., 2000). We found that the removal of reed (i.e. the transformation of reed habitat to open one) resulted in increasing water depth and decreasing cover of reed (both can be linked to the transformation of the habitat), as well as associated with less obvious changes, such as the reduction of mollusc shells, macrophytes, algae and organic matter (Table 1). The reduction of organic matter (Table 1) can be explained by the fact that *Phragmites australis* is among the most productive plants, and only a small proportion of this production is consumed by herbivores (Newman, 1991). Consequently, reeds contribute not only to the scenic beauty of the landscape, but form the basis of a detritus-based ecosystem. In these systems, detritus accumulates at the bottom in the form of shed leaves and dead stems (Bedford and Powell, 2005), and provides both substrate and food for organisms (Karádi-Kovács et al., 2015). This food source together with the unique habitat structure (Fig. 2) provide suitable habitat for algae, macrophytes and molluscs. Moreover, the shells of molluscs can persist for a long time after the molluscs die, and thus can provide habitat for other organisms (Schmidlin et al., 2012). All of these findings suggest that the removal of reeds is associated with multiple changes in habitat structure (Fig. 2), and that these changes might provoke changes in resident assemblages.

The transformation of open habitats to beaches is also associated with some changes in the habitat parameters (Table 1). We found, for instance, decreasing water depth and increasing proportion of sand in beaches. These parameters, however, depended on the shoreline position as well as on the interaction of these two factors (Table 1). Significant interactions reflect differences in the construction of beaches at the northern and southern shorelines: our habitat assessment clearly identified the sand addition at the northern shoreline. We also found that while reed present a heterogeneous habitat, this habitat heterogeneity is clearly reduced in beaches (Fig. 2). In sum, we observed that the transformation of reed habitats to beaches resulted in altered habitat parameters, as well as in a reduction of habitat heterogeneity.

We found that the transformation of natural reed habitats to beaches caused a decrease in taxon richness and abundance (Table 2). This result is in agreement with a similar case study performed in German lowland lakes (Brauns et al., 2007) and fits to the overall effect of urbanization on freshwater macroinvertebrate diversity (Gál et al., 2019; de Vries et al., 2020), as well as to the known negative effect of human disturbances on macroinvertebrates in coastal sandy beaches (Costa et al., 2020). However, Brauns et al. (2007) distinguished 5 habitat types within natural shorelines (roots, coarse woody debris, reed, sand and stones) and explained biodiversity of natural sites by the existence of five habitat types. In the present study, we focused exclusively on reed habitat and explained biodiversity by changes in habitat parameters, as well as by the within-reed habitat heterogeneity. As the explanations of these case studies are non-exclusive and both are related to the assumed positive effect of habitat heterogeneity on biodiversity (Palmer et al., 2010), we conclude that our findings supplement the results of Brauns et al. (2007) and support the general view that human-induced habitat alteration has a negative effect on shoreline biodiversity.

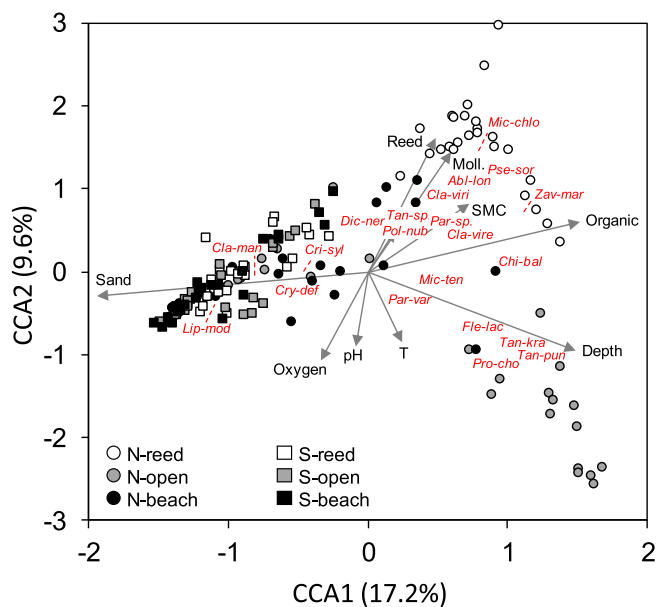


Fig. 4. Ordination plot of canonical correspondence analysis. White circles show reed, grey circles open, while black circles beach habitats, circles show sites at the northern shoreline, while squares sites at the southern shoreline. Red text displays indicator taxa (Abi-lon: *Ablabesmyia longistyla*, Chi-bal: *Chironomus balatonicus*, Cla-man: *Cladotanytarsus mancus* gr., Cla-vire: *Cladopelma virescens*, Cla-viri: *Cladopelma viridulum*, Cri-syl: *Cricotopus sylvestris* gr., Cry-def: *Cryptochironomus defectus*, Dic-ner: *Dicrotendipes nervosus*, Fle-lac: *Fleuria lacustris*, Lip-mod: *Lipiniella moderata*, Mic-chl: *Microtendipes chloris* agg., Mic-ten: *Microchironomus tener*, Par-sp.: *Paratanytarsus* sp., Par-var: *Parachironomus varus*, Pol-nub: *Polypedium nubeculosum*, Pro-cho: *Procladius choreus*, Pse-sor: *Psectrocladius sordidellus* gr., Tan-kra: *Tanytus kraatzi*, Tan-pun: *Tanytus punctipennis*, Tan-sp.: *Tanytarsus* sp., Zav-mar: *Zavreliella marmorata*), grey arrows and text show environmental variables (scale factor = 2 for plotting) proved to be significant by envfit test (Moll: Mollusc shells, T: Temperature, SCM: submersed macrophyte coverage). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We observed that the removal of reed (hypothesis 2), as well as the effect of trampling (hypothesis 3) and sand addition (hypothesis 4) had no significant effect on the local taxon richness of chironomids (Table 2). However, the estimate values of these hypotheses were always negative (Table 2) suggesting a non-significant reduction of richness. Considering the overall negative effect of habitat transformation from reed to beach on both richness and abundance (hypothesis 1 which involves each above mentioned hypothesis), we argue that at least some of these intermediate steps (hypotheses 2, 3 and 4) should influence diversity. However, we could not detect any significant effect for these intermediate steps probably due to our sample sizes combined with the variability of chironomid communities in Lake Balaton (Árvai et al., 2015b). Linear models explaining the potential effect of environmental variables indicated that the amount of organic matter in the sample could support, in agreement with the productivity-biodiversity relationship (Chase and Leibold, 2002), a higher level of chironomid richness (Table 3). Linear models also showed that water depth had a negative effect on the taxon richness and abundance of chironomids (Table 3). This finding is in agreement with our previous investigations on the chironomid assemblages of Lake Balaton: shoreline habitats are rich and abundant in chironomids, while offshore locations are poor in taxa and abundance (Árvai et al., 2015a, b). Moreover, recent studies give detailed support about the predominant importance of gradients in substratum composition (i.e. proportion of sand vs. silt), water depth and macrophyte coverage in chironomid beta, and correspondingly, gamma diversity in Lake Balaton (Árvai et al., 2015b; Specziár et al., 2018).

Chironomid taxa have diverse environmental optima and tolerance (Rosenberg, 1992). In support, we found that the composition of chironomids showed sensitivity to the transformation of reed to beach habitat (Hypothesis 1), to the transformation of reed to open habitat (Hypothesis 2), as well as to the addition of sand (Hypothesis 4). All of these effects were associated with remarkable changes in the habitat parameters provoked by human activity. Moreover, we found that chironomid assemblages differed in the northern and southern shorelines: this finding suggests that within-lake natural differences also had strong impacts on the composition of chironomids. Considering the response of chironomid assemblages to their environment, Árvai et al. (2015a) distinguished four major habitats in Lake Balaton: reed habitat, riprap habitat (not relevant in this study), macrophyte-free open water habitat with silt substrate and southern littoral habitat (both reed and open) with sand substrate. Highly-consistent indicator taxa support that reed habitat, open habitat and southern open water habitat in our study correspond to this habitat classification. Indicator taxa of reed habitat are generally associated with the presence of macrophytes and macroscopic algae (*Cladopelma virescens*, *C. viridulum*, *Microtendipes chloris* agg., *Paratanytarsus* sp., *Polypedilum nubeculosum*, *Psectrocladius sordidellus* gr., *Tanytarsus* sp., *Zavreliella marmorata*), prefer moderate to high amount of decomposing organic matter (*Chironomus balatonicus*, *Paratanytarsus* sp., *Tanytarsus* sp.) and tolerate low concentrations of dissolved oxygen (*Cladopelma virescens*, *C. viridulum*, *Paratanytarsus* sp., *Tanytarsus* sp.) (Cañedo-Argüelles and Rieradevall, 2011; Árvai et al., 2015a, 2017). Indicator taxa of open habitat generally associate with deeper water, silt sediment with low to moderate amount of decomposing organic matter (*Procladius choreus*, *Tanytarsus punctipennis*, *Fleurella lacustris*, *Microchironomus tener*), but also include elements that indicate the presence or proximity of macrophytes, high amount of decomposing organic matter and occasional oxygen deficit (*Tanytarsus kraatzi*, *Parachironomus varus*) (Wolfram, 1996; Árvai et al., 2015a, 2017); namely, that we sampled open habitat within the littoral zone. Indicator taxa of the southern littoral zone typically occurred on sandy substrate (*Lipiniella moderata*, *Cladotanytarsus mancus* gr., *Cryptochironomus defectus*) and on sandy or other hard substrates often with algal coating (*Cricotopus sylvestris* gr.) (Wolfram, 1996; Moller Pillot, 2009; Árvai et al., 2015a, 2017). In the southern shoreline, beach building seems to have altered chironomid assemblages within the natural range of southern littoral habitat described by Árvai et al. (2015a). In the northern

shoreline, however, beaches clearly represent a new artificial habitat type. The characteristic occurrence of *D. nervosus* on northern beaches along with the high abundance of *Cladotanytarsus mancus* gr. could be related to relatively well-oxygenated shallow water, a decreased amount of silt and a moderate amount of decomposing organic matter in the sediment, and to a moderate density of macrophytes and macroscopic algae, at least compared to the nearby reed and open habitats (Árvai et al., 2015a, 2017). Consequently, and in agreement with previous studies, our results support the importance of environmental controls in structuring littoral macroinvertebrate communities (Heino, 2013; Heino and Tolonen, 2018).

Increasing evidence has demonstrated that residential shoreline and catchment development by humans are the leading threats to biodiversity in lake ecosystems (Miler et al., 2013; Twardochleb and Olden, 2016). The development of shorelines and lake catchments is frequently associated with increasing recreational and tourist activity. Although the importance of tourism for human well-being and local economy is well appreciated, less attention has been paid to the effects of tourism on lake ecosystems (Monz et al., 2013; Venohr et al., 2018). Cao et al. (2016) found that a tourism-stress index of lakes was negatively correlated with the richness of lake littoral macroinvertebrate communities. This finding suggests that tourism, in general, has a negative effect on the biodiversity of lakes. Our results supplement this finding and emphasize that artificial beaches have negative effects on local biodiversity.

Our findings have several implications for decision making. To maintain biodiversity of natural reed habitats, it would be important to estimate their distribution and quality along the shoreline of the lake. Remote sensing provides an ideal toolkit for this purpose, because it can assess not only the size of reed vegetated areas, but also its quality as well as its temporal dynamics (Jing et al., 2020; Tóth, 2018). Moreover, different modelling and forecasting techniques allow predicting future changes (Tiyasha and Yaseen, 2020; Zhou, 2020). Based on these predictions, and considering touristic needs and protecting laws, the future of natural reed areas, as well as their diversity could be maintained.

From a conservation perspective, our findings suggest for decision making that natural reed habitats should not be transformed to beaches in the future, especially not along the northern shoreline. Formerly widely-distributed reed areas of Lake Balaton are now fragmented with a total area of only 11 km<sup>2</sup> (Tóth and Szabó, 2012) while the majority of the shoreline is transformed to rip-rap habitat. It follows that artificial rip-rap habitats should be the first candidates for creating recreational beaches instead of natural reeds. This means that decision making still has alternatives satisfying touristic and economic needs without eliminating habitats with high conservation importance.

Although the effect of these shoreline alterations seems now to be substantial just locally, our results could provide a proper base for the detection of human impacts affecting the biodiversity of the whole lake in the longer term. Moreover, our results could be extrapolated to other lakes as well as to other ecosystems. In sum, although beaches can promote diversified societal and economic benefits, our results show that they can also generate conservation issues related to biodiversity loss. Consequently, action plans focusing on the maintenance and the establishment of recreational beaches should carefully consider both economic and conservation aspects.

## 5. Conclusions

There is a common view among freshwater ecologists that minor alterations have negligible effects on aquatic ecosystems (Jennings et al., 1999; McGoff et al., 2013). Although the establishment and use of recreational beaches are associated with less conspicuous and only local changes in the environment, cumulatively, these changes have significant impacts on freshwater biodiversity. We found that recreational beaches caused habitat alteration and contributed to the decrease of richness and abundance of chironomids as well as to the replacement of

some taxa. In conclusion, our study provides evidence of the negative impact of artificial beaches on the shoreline biodiversity of lakes.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107469>.

### References

- Anderson, M.J., 2001. A new methodology for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.p.x>.
- Anderson, R.O., 1959. A modified flotation technique for sorting bottom fauna fauna samples. *Limnol. Oceanogr.* 4, 223–225. <https://doi.org/10.4319/lo.1959.4.2.0223>.
- Armitage, P., Cranston, P.S., Pinder, L.C.V., 1995. *The chironomidae. The biology and ecology of non-biting midges*. Springer.
- Árva, D., Specziár, A., Erős, T., Tóth, M., 2015a. Effects of habitat types and within lake environmental gradients on the diversity of chironomid assemblages. *Limnologica* 53, 26–34. <https://doi.org/10.1016/j.limno.2015.05.004>.
- Árva, D., Tóth, M., Horváth, H., Nagy, S.A., Specziár, A., 2015b. The relative importance of spatial and environmental processes in distribution of benthic chironomid larvae within a large and shallow lake. *Hydrobiologia* 742, 249–266. <https://doi.org/10.1007/s10750-014-1989-z>.
- Árva, D., Tóth, M., Mozsár, A., Specziár, A., 2017. The roles of environment, site position, and seasonality in taxonomic and functional organization of chironomid assemblages in a heterogeneous wetland, Kis-Balaton (Hungary). *Hydrobiologia* 787, 353–373. <https://doi.org/10.1007/s10750-016-2980-7>.
- Barton, K., 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>.
- Bedford, A.P., Powell, I., 2005. Long-term changes in invertebrates associated with the litter of *Phragmites australis* in a managed reedbed. *Hydrobiologia* 549, 267–285. <https://doi.org/10.1007/s10750-005-5439-9>.
- Bossley, J.P., Smiley, P.C., 2018. Effects of student-induced trampling on aquatic macroinvertebrates in agricultural headwater streams. *Water* 10, 77. <https://doi.org/10.3390/w10010077>.
- Brauns, M., Gracia, X.-F., Walz, N., Pusch, M.T., 2007. Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. *J. Appl. Ecol.* 44, 1138–1144. <https://doi.org/10.1111/j.1365-2664.2007.01376.x>.
- Cao, Y., Wang, B., Zhang, J., Wang, L., Pan, Y., Wang, Q., Jian, D., Deng, G., 2016. Lake macroinvertebrate assemblages and relationship with natural environment and tourism stress in Jiuzhaigou Nature Reserve, China. *Ecol. Ind.* 62, 182–190. <https://doi.org/10.1016/j.ecolind.2015.11.023>.
- Cañedo-Argüelles, M., Rieradevall, M., 2011. Early succession of the macroinvertebrate community in a shallow lake: response to changes in the habitat condition. *Limnologica* 41, 363–370. <https://doi.org/10.1016/j.limno.2011.04.001>.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242. <https://doi.org/10.1038/35012241>.
- Chase, J.M., Leibold, M.A., 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416, 427–430. <https://doi.org/10.1038/416427a>.
- Costa, L.L., Zalmon, I.R., Faini, L., Defeo, O., 2020. Macroinvertebrates as indicators of human disturbances on sandy beaches: a global review. *Ecol. Ind.* 118, 106764. <https://doi.org/10.1016/j.ecolind.2020.106764>.
- de Vries, J., Kraak, M.H.S., Verdonchot, P.F.M., 2020. A conceptual model for simulating responses of freshwater macroinvertebrate assemblages to multiple stressors. *Ecol. Ind.* 117, 106604. <https://doi.org/10.1016/j.ecolind.2020.106604>.
- Dudgeon, D., Arthington, A.H., Gessner, M.A., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stuaeny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182. <https://doi.org/10.1017/S1464793105006950>.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAIIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAIIST]2.0.CO;2).
- Cheruvilil, K.S., Sorano, P.A., Serbin, R., 2000. Macroinvertebrates associated with submerged macrophytes: sample size and power to detect effects. *Hydrobiologia* 441, 133–139. <https://doi.org/10.1023/A:1017514824711>.
- Escarpinati, S.C., Siqueira, T., Medina, P.B., Roque, F.d.O., 2014. Short-term effects of visitor trampling on macroinvertebrates in karst streams in an ecotourism region. *Environ. Monit. Assess.* 186, 1655–1663. <https://doi.org/10.1007/s10661-013-3483-x>.
- Faraway, J., 2016. faraway: Functions and Datasets for Books by Julian Faraway. R package version 1.0.7. <https://CRAN.R-project.org/package=faraway>.
- Garamszegi, L.Z., Mundry, R., 2014. Multimodel-inference in comparative analysis. In: Garamszegi, L.Z. (Ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology. Concepts and Practice*, Springer, Heidelberg, pp. 305–331.
- Gál, B., Szivák, I., Heino, J., Schmera, D., 2019. The effect of urbanization on freshwater macroinvertebrates - Knowledge gaps and future research directions. *Ecol. Ind.* 104, 357–364. <https://doi.org/10.1016/j.ecolind.2019.05.012>.
- Heino, J., 2013. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? *Oecologia* 171, 971–980. <https://doi.org/10.1007/s00442-012-2451-4>.
- Heino, J., Tolonen, K.T., 2018. Ecological niche features override biological traits and taxonomic relatedness as predictors of occupancy and abundance in lake littoral macroinvertebrates. *Ecography* 41, 2092–2103. <https://doi.org/10.1111/ecog.03968>.
- Heiri, O., Lotter, A.F., Lamcke, G., 2001. Loss of ignition as a method for estimating organic and carbon content in sediments: reproducibility and comparability of results. *J. Paleolimnol.* 25, 101–110. <https://doi.org/10.1023/A:1008119611481>.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biometrical J.* 50, 346–363. <https://doi.org/10.1002/bimj.100425>.
- Hughes, D.L., Brossett, M.P., Gore, J.A., Olson, J.R., 2010. *Rapid bioassessment of stream health*. CRC Press.
- Jennings, M.J., Bozek, M.A., Hatzenbeler, G.R., Emmons, E.E., Staggs, M.D., 1999. Cumulative effects of incremental shoreline habitat modification on fish assemblages in the North Temperature Lakes. *North Am. J. Fish. Manag.* 19, 18–27. [https://doi.org/10.1577/1548-8675\(1999\)019%3C0018:CEOISH%3E2.0.CO;2](https://doi.org/10.1577/1548-8675(1999)019%3C0018:CEOISH%3E2.0.CO;2).
- Jing, Y., Zhang, F., He, Y., Kung, H., Johnson, V.C., Arikena, M., 2020. Assessment of spatial and temporal variation of ecological environmental quality in Ebinur Lake Wetland National Nature Reserve, Xinjiang, China. *Ecol. Indicators* 110, 105874. <https://doi.org/10.1016/j.ecolind.2019.105874>.
- Johnson, R.K., Hallstan, S., Zhao, Y., 2018. Disentangling the response of lake littoral invertebrate assemblages to multiple pressures. *Ecol. Ind.* 85, 1148–1157. <https://doi.org/10.1016/j.ecolind.2017.10.075>.
- Karádi-Kovács, K., Selmeczy, G.B., Padisák, J., Schmera, D., 2015. Food, substrate or both? Decomposition of reed leaves (*Phragmites australis*) by aquatic macroinvertebrates in a large shallow lake (Lake Balaton, Hungary). *Annales de Limnologie - Int. J. Limnol.* 51, 79–88. <https://doi.org/10.1051/limn/2015002>.
- McGoff, E., Solimini, A.G., Pusch, M.T., Jurca, T., Sandin, L., 2013. Does lake habitat alteration and land-use pressure homogenize European littoral macroinvertebrate communities? *J. Appl. Ecol.* 50, 1010–1018. <https://doi.org/10.1111/1365-2664.12106>.
- Miler, O., Porst, G., McGoff, E., Pilotto, F., Donohue, L., Jurca, T., Solimini, A., Sandin, L., Irvine, K., Aroviita, J., Clarke, R., Pusch, M.T., 2013. Morphological alteration of lake shores in Europe: a multimetric ecological assessment approach using benthic macroinvertebrates. *Ecol. Ind.* 34, 398–410. <https://doi.org/10.1016/j.ecolind.2013.06.002>.
- Moller Pillot, H.K.M., 2009. *Chironomidae larvae. Biology and ecology of the Chironomina*. KNNV Publishing, Zeist.
- Monz, C.A., Pickering, C.M., Hadwen, W.L., 2013. Recent advances in recreation ecology and implications of different relationships between recreation use and ecological impact. *Front. Ecol. Environ.* 11, 441–446. <https://doi.org/10.1890/120358>.
- Newman, R., 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *J. North Am. Benthol. Soc.* 10, 89–114. <https://doi.org/10.2307/1467571>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>.
- Palmer, M.A., Menninger, H.L., Bernhardt, E., 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshw. Biol.* 55, 205–222. <https://doi.org/10.1111/j.1365-2427.2009.02372.x>.
- Podani, J., 2000. *Introduction into the exploration of multivariate biological data*. Backhuys, Leiden.
- Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction of stream ecology. *J. N. Am. Benthol. Soc.* 16, 391–409. <https://doi.org/10.2307/1468026>.
- R Core Team, 2020. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rosenberg, D.M., 1992. Freshwater biomonitoring and chironomidae. *Netherlands J. Aquatic Ecol.* 26, 101–122. <https://doi.org/10.1007/BF02255231>.
- Schmidlin, S., Schmera, D., Baur, B., 2012. Alien molluscs affect the composition and diversity of native macroinvertebrates in a sandy flat of Lake Neuchâtel, Switzerland. *Hydrobiologia* 679, 233–249. <https://doi.org/10.1007/s10750-011-0889-8>.
- Specziár, A., Bíró, P., 1998. Spatial distribution and short-term changes of benthic macrofauna in Lake Balaton (Hungary). *Hydrobiologia* 389, 203–216. <https://doi.org/10.1023/A:1003563228162>.
- Specziár, A., Árva, D., Tóth, M., Móra, A., Schmera, D., Várbró, G., Erős, T., 2018. Environmental and spatial drivers of beta diversity components of chironomid



- metacommunities in contrasting freshwater systems. *Hydrobiologia* 819, 123–143. <https://doi.org/10.1007/s10750-018-3632-x>.
- Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. *J. N. Am. Benthol. Soc.* 29, 344–359. <https://doi.org/10.1899/08-171.1>.
- Tiyasha, T.M.T., Yaseen, Z.M., 2020. A survey on river water quality modelling using artificial intelligence models: 2000–2020. *J. Hydrol.* 585, 124670 <https://doi.org/10.1016/j.jhydrol.2020.124670>.
- Tóth, R.V., 2016. Reed stands during different water level periods: physico-chemical properties of the sediment and growth of *Phragmites australis* of Lake Balaton. *Hydrobiologia* 778, 193–207. <https://doi.org/10.1007/s10750-016-2684-z>.
- Tóth, R.V., 2018. Monitoring spatial variability and temporal dynamics of *Phragmites* using unmanned aerial vehicles. *Front. Plant Sci.* 9, 728. <https://doi.org/10.3389/fpls.2018.00728>.
- Tóth, V., Szabó, K., 2012. Morphometric structural analysis of *Phragmites australis* stands in Lake Balaton. *Annales de Limnologie - International Journal of Limnology* 48, 541–251. <https://doi.org/10.1051/limn/2012015>.
- Twardochleb, L.A., Olden, J.D., 2016. Human development modifies the functional composition of lake littoral invertebrate communities. *Hydrobiologia* 775, 167–184. <https://doi.org/10.1007/s10750-016-2727-5>.
- Varga, I., 2001. Macroinvertebrates in reed litter. *Int. Rev. Hydrobiol.* 86, 573–585. [https://doi.org/10.1002/1522-2632\(200107\)86:4/5%3C573::AID-IROH573%3E3.0.CO;2-9](https://doi.org/10.1002/1522-2632(200107)86:4/5%3C573::AID-IROH573%3E3.0.CO;2-9).
- Venohr, M., Langhans, S.D., Peters, O., Hölker, F., Arlinghaus, R., Mitchell, L., Wolter, C., 2018. The underestimated dynamics and impacts of water-based recreational activities on freshwater ecosystems. *Environ. Rev.* 26, 199–213. <https://doi.org/10.1139/er-2017-0024>.
- Vitousek, P.M., Mooney, H.A., Lubchenko, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499. <https://doi.org/10.1126/science.277.5325.494>.
- Wolfram, G., 1996. Distribution and production of chironomids (Diptera, Chironomidae) in a shallow, alkaline lake (Neusiedler See, Austria). *Hydrobiologia* 318, 103–115. <https://doi.org/10.1007/BF00014136>.
- Zhou, Y., 2020. Real-time probabilistic forecasting of river water quality under data missing situation: deep learning plus post-processing techniques. *J. Hydrol.* 589, 125164 <https://doi.org/10.1016/j.jhydrol.2020.125164>.