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# Effects of habitat types and within lake environmental gradients on the diversity of chironomid assemblages

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ABSTRACT

Understanding the distribution of biotic diversity across various spatial scales and environmental gradients is important from fundamental, practical and conservation biological aspects. We applied a hierarchical diversity partitioning framework to quantify the variability of sample level $\alpha$- and $\beta_1$-diversity, and environment related $\beta_2$-diversity of benthic chironomid assemblages within and among a priori defined habitat types, and along the gradients of individual environmental factors in a large and shallow lake (Lake Balaton, Hungary). Taxon richness (both additive and multiplicative) and Shannon index based diversity approaches yielded highly concordant results. The $\alpha$-diversity was much lower and $\beta_1$-diversity higher than predicted by null model and both measures varied substantially among habitat types and along most individual environmental gradients. The $\beta_2$-diversity indicated a marked variability of taxon (identified at species to genus level) pool among habitat types and higher than predicted taxon turnover along all examined environmental gradients. Moreover, the observed $\beta_2$-diversity varied greatly among individual environmental gradients. The difference between the expected and observed $\beta_2$-diversity values suggests that taxon turnover was most influential (in decreasing order) along the algae coverage gradient, the lake bed substratum gradient and the macrophyte coverage gradient among others. We argue that within-lake environmental heterogeneity and its effect on the taxon richness should receive more attention in biodiversity assessment and conservation. Management could benefit from the identification of within lake gradients along which taxonomic turnover maximizes.



## 1. Introduction

Exploring patterns of biodiversity is fundamental to understand many ecological processes (Ricklefs, 2004). For instance, the framework of diversity partitioning which quantifies local ($\alpha$), regional ($\gamma$) and turnover (beta) components of diversity has greatly contributed to our understanding of assembly processes in metacommunities at a variety of spatial and temporal scales (Gering et al., 2003; Crist and Veech, 2006; Anderson et al., 2011; Kraft et al., 2011). Diversity components (i.e. $\alpha$, $\beta_1$, ..., $\beta_n$) have important conservational biological implications as well as they provide fundamental information on how to allocate areas and habitats to be involved in an effective environmental management program (Gering et al., 2003; Thrush et al., 2010).

Conceptual models and empirical studies concerning biodiversity distributions of lakes focused primarily on broad scale, geographical and temporal processes (Stendera and Johnson, 2005; Ptacnik et al., 2010; Suurkuukka et al., 2012; Angeler and Drakare, 2013; Hamerlík et al., 2014). Although fine scale, microhabitat level distribution of species is widely studied in lentic organisms (e.g. Brodersen, 1995; Čerba et al., 2010; Luoto, 2012; Specziár et al., 2013; Árva et al., 2015), the role of within lake habitats in shaping diversity patterns and their contribution to total (lake level or regional) diversity is less known (but see Flach et al., 2012; Tóth et al., 2013). Suurkuukka et al. (2012) revealed that unspecified within lake patterns included about 50% of the overall regional littoral macroinvertebrate diversity in boreal lakes. Likewise, it is largely unknown how biodiversity is distributed across specific within lake environmental gradients and/or habitat types. Partitioning within lake $\beta$-diversity for stochastic or unspecified among sample variability (i.e. $\beta_1$) and structured environment related species turnover (i.e. $\beta_2$ or higher $\beta$ levels) components would yield basic information about the influence of within lake environmental heterogeneity on species diversity. By identifying environmental gradients along which the species turnover rate is the highest would facilitate focusing of conservation actions to the most important pieces of environmental heterogeneity.

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In this study, we examine the response of local α-diversity and hierarchical β-diversity components expressed as taxon richness (i.e. number of taxa at species or genus level) and Shannon diversity index of benthic chironomid (Diptera, Chironomidae) assemblages to within lake environmental heterogeneity in a large and shallow lake (Lake Balaton, Hungary). Benthic chironomids is a popular model group for freshwater biomonitoring studies (Rosenberg, 1992; Wilson and Ruse, 2005; Miloševič et al., 2013). Chironomid larvae have diverse environmental optima and tolerances and relatively good dispersal ability in their winged terrestrial adult phase (Armitage, 1995). Thus according to metacommunity theory (Leibold et al., 2004; Cottenie, 2005; Beisner et al., 2006) environmental filtering (i.e. species sorting) shapes their fine scale species distribution patterns, while the role of spatial processes (i.e. dispersal limitation) become influential in their assemblage organization only at broad geographical scales (Mykrä et al., 2007; Landeiro et al., 2012; Heino, 2013a, 2013b; but see Árva et al., 2015). Accordingly, in lakes with high environmental heterogeneity a substantial part in their species turnover could be related directly to habitat types and environmental gradients due to inter-specific separation of species optima and tolerance ranges (Rae, 2004; Puntí et al., 2009; Árva et al., 2015). Thus not just relative abundance patterns but also species turnover rates can predictably differ among various within lake environmental gradients. To our knowledge, however, there are no studies comparing the role of species turnover along various within lake environmental gradients. Specific aims of the study are to analyse: (1) how sample level α-diversity (i.e. local taxon richness and Shannon diversity index) and among sample $\beta_1$-diversity vary among a priori defined characteristic habitat types of the lake; (2) how sample level α-diversity and among sample $\beta_1$-diversity change along the gradient of individual environmental factors (e.g. water depth, substratum type); and (3) to what extent $\beta_2$-diversity among the habitat types and along particular environmental gradients contribute to total chironomid diversity of the lake.

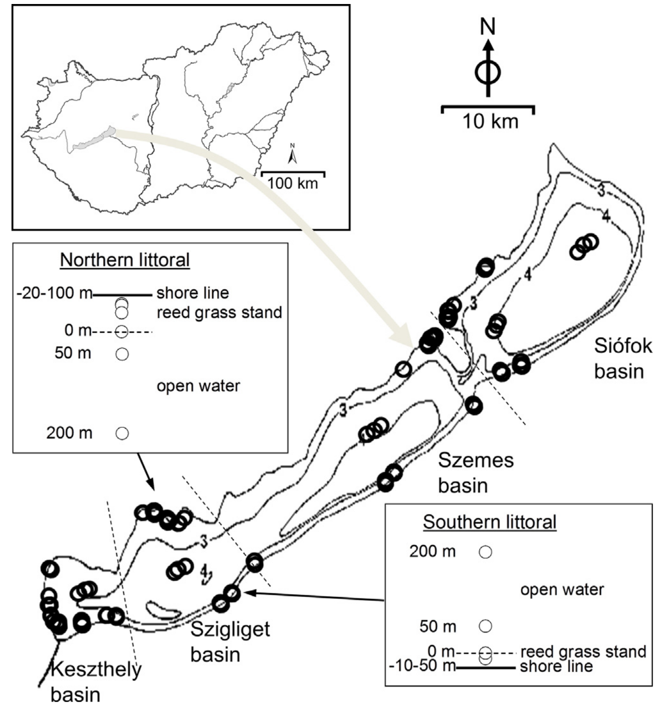


**Fig. 1.** Distribution of sampling sites in Lake Balaton, Hungary. Examined habitats included offshore area, natural-like littoral habitat transects from the riparian edge of the reed grass stand towards the macrophyte-free inshore area (typically one to three sites within the reed grass stand, one in the edge of the reed grass stand and the open water, and at 50 and 200 m distances from the reed grass stand; examples of typical northern littoral and southern littoral transects are presented), small boat harbours situated within the reed grass stand, stands of the most characteristic submerged and floating leaved macrophytes, and modified littoral areas, large sailing-vessel and ship harbours, ripraps and nearby littoral areas. The small map of Hungary in the upper left corner indicates the location of Lake Balaton.

## 2. Materials and methods

### 2.1. Study area

Balaton is the largest shallow lake (surface area: 596 km$^2$; mean depth: 3.2 m) in Central Europe, situated at 46°42′–47°04′N, 17°15′–18°10′E and 104.8 m above sea level (Fig. 1). The lake is slightly alkaline (400 mg l$^{-1}$ of $Ca^{2+}$ and $Mg^{2+}(HCO_3^-)_2$) with a decreasing trophic gradient (i.e. chlorophyll-a concentration from 26.6 to 9.7 μg l$^{-1}$, mean data of 2008–2012; Ministry of Environmental Protection and Water Management of Hungary, http://www.ktm.hu/balaton/lang_en/index.htm) from SW to NE along its longitudinal axis (see also Istvánovics et al., 2007). Based on habitat characteristics, Lake Balaton can be divided into a little variable open water area spreading to >85% of the lake with silt substrate, largely homogeneous physico-chemical features and with no macrovegetation, and to a much heterogeneous littoral zone exhibiting marked environmental gradients along the distance from shore, water depth, macrophyte coverage, swash exposition (i.e. the northern littoral is much less affected by wind induced waves than the southern littoral) and human impact including the establishment of artificial habitat types as well (measured ranges of environmental gradients are shown in Appendix A). Today only about 47% of the lake shore is covered by emergent macrovegetation (dominant species is reed grass *Phragmites australis*), whereas submerged macrohytes form loose and sporadic stands in the littoral zone. Significant sections (>50%) of the shore have been protected with concrete or rocks (artificial habitat covered by rocks hereafter referred to as riprap) which are generally covered by filamentous algae (mainly *Cladophora* sp.) up to 0.5 m water depth. Several large, and many small boat harbours were built along the lake for commercial and recreational purposes.

### 2.2. Chironomid sampling and identification

Benthic chironomid assemblages were sampled at 128 sites between 26 June and 13 July 2012 (Fig. 1). The sites were distributed across the whole lake and covered all ranges of habitat and environmental gradients (see below). Three merged Ekman grab sediment samples were taken per site (total sampled area per site: 0.036 m$^2$), washed through a 0.25 mm mesh sieve and transported to the laboratory in a cooling box. Riprap habitats were sampled by cleaning and washing algal coating and sediment from a measured rock surface corresponding to area of Ekman grab samples into plastic containers. Chironomids were separated from sediment samples alive by sugar flotation method (Anderson, 1959), and euthanized and preserved in 70% ethanol for later identification. Chironomids were digested in KOH (potassium hydroxide) to eliminate non-chitinous tissues and slide-mounted in Euparal®. Identification was performed to species or the lowest possible taxonomic level (species group to genus; for more details see Árva et al., 2015).

### 2.3. Habitat assessment and environmental factors

Parallel to chironomid sampling, we measured a series of environmental factors (Appendix A) that have been found influential