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Benthic diatom metacommunities at different spatial scales

Cover photo: Illustration of Lake Stechlin by Anna Tomka

“Eventually everything connects - people, ideas, objects. The quality of the connections is the key to quality per se.”

Charles Eames

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Ph.D. Dissertation

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BENTHIC DIATOM METACOMMUNITIES AT DIFFERENT SPATIAL SCALES

Készült a Pannon Egyetem **Kémiai és Környezettudományi Doktori Iskolája** keretében

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Elfogadásra javaslom (igen / nem) ……………………….

(aláírás)

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Elfogadásra javaslom (igen / nem) ……………………….

(aláírás)

A jelölt a doktori szigorlaton ....%-ot ért el,

Az értekezést bírálóként elfogadásra javaslom:

Bíráló neve: …...................... …................. igen /nem

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(aláírás)

Bíráló neve: …...................... …................. igen /nem

……………………….

(aláírás)

A jelölt az értekezés nyilvános vitáján …..........%-ot ért el.

Veszprém, ………………………. ………………………….

a Bíráló Bizottság elnöke

A doktori (PhD) oklevél minősítése…...............................

…………………………

Az EDHT elnöke

Abbreviations

NT	Neutral theory
PD	Patch dynamics
ME	Mass-effect
SS	Species-sorting
TP	Total phosphorus
TN	Total nitrogen
VIF	Variance inflation factor
$\boldsymbol{\beta}_{\mathbf{BC}}$	Multiple-site Bray-Curtis dissimilarity
$\boldsymbol{\beta}_{\mathbf{BC.BAL}}$	Abundance balanced variation component of multiple-site Bray-Curtis dissimilarity
$\boldsymbol{\beta}_{\mathbf{BC.GRA}}$	Abundance gradient component of multiple-site Bray-Curtis dissimilarity
$\boldsymbol{\beta}_{\mathbf{SOR}}$	Multiple-site Sørensen dissimilarity
$\boldsymbol{\beta}_{\mathbf{SIM}}$	Turnover component of multiple-site Sørensen dissimilarity
$\boldsymbol{\beta}_{\mathbf{NES}}$	Nestedness component of multiple-site Sørensen dissimilarity
dbMEM	Distance-based Moran’s eigenvector
PCoA	Principal coordinate analysis
ANOVA	Analysis of variance
RDA	Redundancy analysis
NMDS	Non-metric multidimensional scaling
ANOSIM	Analysis of similarities
DI-PROF	Diatom index for planktonic taxa
DI-BENT	Diatom index for benthic taxa
DI-LIT	Diatom index for littoral samples
DO%	Dissolved oxygen saturation
SRSi	Soluble reactive silica
SRP	Soluble reactive phosphorus
COD	Chemical oxygen demand
Pt	Intensity of the brown colour in platinum units
LI	Light irradiance
$\boldsymbol{\beta}_{\mathbf{bray}}$	Pairwise Bray-Curtis dissimilarity

$\beta_{bray.bal}$	Abundance balanced variation component of pairwise Bray-Curtis dissimilarity
$\beta_{bray.gra}$	Abundance gradient component of pairwise Bray-Curtis dissimilarity
β_{sor}	Pairwise Sørensen dissimilarity
β_{sim}	Turnover component of pairwise Sørensen dissimilarity
β_{nes}	Nestedness component of pairwise Sørensen dissimilarity
$\beta_{bray-null}$	Pairwise Bray-Curtis dissimilarity under null models
$\beta_{sor-null}$	Pairwise Sørensen dissimilarity under null models
$\beta_{bray-diff}$	Pairwise Bray-Curtis dissimilarity beyond null models
$\beta_{sor-diff}$	Pairwise Sørensen dissimilarity beyond null models
MRM	Multiple regression on distance matrices
PCA	Principal component analysis
$D_{\%diff}$	Percentage difference dissimilarity
D_S	Sørensen dissimilarity
$LCBD_{D\%diff}$	Local contribution to β-diversity computed from percentage difference dissimilarity matrix
$LCBD_{ReplB\%diff}$	Local contribution to β-diversity for replacement by decomposing $LCBD_{D\%diff}$
$LCBD_{NesB\%diff}$	Local contribution to β-diversity for nestedness by decomposing $LCBD_{D\%diff}$
$LCBD_{DS}$	Local contribution to β-diversity computed from Sørensen dissimilarity matrix
$LCBD_{ReplBS}$	Local contribution to β-diversity for replacement by decomposing $LCBD_{DS}$
$LCBD_{NesBS}$	Local contribution to β-diversity for nestedness by decomposing $LCBD_{DS}$
$SCBD_{ab}$	Species contribution to β-diversity computed from Hellinger-transformed species abundance data
$SCBD_{pa}$	Species contribution to β-diversity computed from species incidence data

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Content

Abstract

To understand the establishment of local communities, the comprehensive investigation of their underlying processes at regional level is required. However, the several available diversity indices and statistical methods might reveal distinct results and led to disparate conclusions depending on whether they are based on species abundance (or relative abundance, biomass etc.) or incidence data. The aim of the research in this dissertation was to study benthic diatom metacommunities at different spatial extents – within a lake; across lakes covering two small regions; across lakes at intermediate spatial scale – applying both abundance- and incidence-based analyses and to compare whether they provide different results. Accordingly, the main objectives were the following:

(i) to investigate the temporal and spatial patterns of benthic diatom communities in the oligo-mesotrophic Lake Stechlin;

(ii) to explore the diversity and structuring mechanisms of two benthic diatom metacommunities across natural and reconstructed soda pans encompassing two small areas of the Carpathian Basin;

(iii) to examine the diversity and driving forces of a benthic diatom metacommunity across small freshwater lakes at intermediate spatial scale of the Carpathian Basin, and to assess the ecological uniqueness of the individual lakes and species.

The major conclusions of the thesis were as follows:

(i) In the littoral region of Lake Stechlin, species richness of the spring communities was lower and the proportion of Mediophyceae species settled from the phytoplankton, predominantly *Stephanodiscus neoastraea* and *Stephanodiscus rugosus*, was more prominent compared to autumn communities. Consequently, sampling for ecological status assessment in spring is not recommended due to the high relative abundance of centric taxa at the beginning of summer stratification. Metrics of α-diversity (species richness and Shannon diversity) and community composition were not segregated based on the three basins, however, the variation of nutrient forms within a narrow scale might have caused relatively high β-diversity enhanced by species replacement. In turn, species' autecological preferences did not differ remarkably and, in accordance with the nutrients, indicated the change of the lake from the originally oligotrophic to mesotrophic status.

(ii) In diatom metacommunities of ecosystems affected by multiple environmental stressors such as soda pans, environmental filtering overrode the impact of spatial variables within the small regions, indicating the importance of the deterministic processes. Fairly high β-diversity primarily due to species replacement was observed both across the natural soda pans in the Danube-Tisza Interfluve and across the reconstructed soda pans in the Fertő-Hanság region, however, species richness was higher in the reconstructed pans compared to that of natural ones. Furthermore, interfering with the environmental filtering, pure temporal distances also induced the changes of diatom communities in the reconstructed soda pans regarding the one-year period and one of its possible reasons might be the periodical or permanent water supply. Nevertheless, it can not be excluded that the significant temporal effect might have been resulted from the overrepresentation of temporal scale as well.

(iii) Across small freshwater lakes at intermediate spatial scale, β-diversity of the benthic diatom metacommunity was high mainly due to the species replacement and α-diversity (species richness) of the individual lakes was also high. The structure of diatom communities was affected by both the local environmental characteristics inherent to species-sorting and the dispersal limitation due to spatial variables complying with the neutral theory and patch dynamics. With the elimination of the spatially more “isolated” lakes, the effect of spatial distance became negligible and the role of environmental filtering increased. Local contribution to β-diversity (LCBD) was influenced by local environmental variables and a strong positive correlation was found between LCBD and LCBD in terms of species replacement. The ecologically most unique sites hosted relatively low species richness, and common species with medium-sized or broad niches contributed mostly to the regional β-diversity.

At all investigated spatial scales, abundance- and incidence-based analyses led to the similar conclusions regarding β-diversity and metacommunity mechanisms, however, they revealed different results in some issues: in null model analyses, the importance of underlying deterministic and stochastic processes was indicated differently; moreover, they highlighted distinct patterns of species’ ecological uniqueness across small freshwater lakes. Furthermore, high proportion of unexplained variances was observed at all spatial scales, which can be resulted from unmeasured environmental variables, demographic- and colonization-extinction stochasticity and from correlations among species.

Zusammenfassung

Um die Bildung lokaler Gemeinschaften von Lebewesen zuverstehen, muss man die grundlegenden Prozesse auf regionaler Stufe umfassend untersuchen. Die unterschiedlichen Diversitätsindizes und statistischen Methoden könnten jedoch zu unterschiedlichen Ergebnissen und Schlussfolgerungen führen, abhängig davon, ob sie auf den Häufigkeits(Abundanz)daten (relative Häufigkeit, Biomasse usw.) oder nur auf den Vorkommens(Inzidenz)daten beruhen. Das Ziel der Dissertation war es, die Metagemeinschaften von benthischen Kieselalgen in unterschiedlichen räumlichen Bereichen – innerhalb eines kleinen Sees; zwischen Seen in zwei kleinen Regionen; zwischen Seen in einer mittelgroßen Region– mit der Anwendung von Analysen, beruhend auf Abundanz- und Inzidenzdaten, zu vergleichen. Dementsprechend waren die Hauptziele der Dissertation die folgenden:

(i) die zeitlichen und räumlichen Strukturen der benthischen Kieselalgengemeinschaften innerhalb des kleinen, oligo-mesotrophen Stechlinsees zu erforschen;

(ii) die Diversität und Strukturierungsmechanismen zweier benthischer Kieselalgen-Metagemeinschaften in natürlichen und restaurierten Salzseen in zwei kleinen Regionen des Karpatenbeckens zu untersuchen;

(iii) die Diversitäts und Strukturierungsmechanismen einer benthischen Kieselalgen-Metagemeinschaft kleiner Süßwasserseen in einer mittelgroßen Region des Karpatenbeckens zu erforschen und die ökologische Einzigartigkeit der einzelnen Seen und Arten zu bewerten.

Die wichtigste Schlussfolgerungen aus der Doktorarbeit:

(i) Im Uferbereich des Stechlinsees war der Artenreichtum der Kieselalgengemeinschaften im Frühjahr niedriger, und der Anteil der aus dem Phytoplankton sedimentierten Arten der Klasse Mediophyceae, insbesondere *Stephanodiscus neoastraea* und *Stephanodiscus rugosus*, war stärker ausgeprägt als im Herbst. Folglich wird die Probenahme für die Bewertung des ökologischen Zustandes im Frühjahr wegen der hohen relativen Häufigkeit von zentrischen Taxa zu Beginn der Sommerstratifizierung nicht empfohlen. Die α-Diversität (Artenreichtum und Shannon Diversität) und die Artenzusammensetzung der Gemeinschaft unterschieden sich nicht zwischen den drei Seebecken. Die

Veränderung der Nährstoffgehalte innerhalb eines engen Bereichs könnte jedoch zu relativ hoher β-Diversität aufgrund des Austausches der Arten geführt haben. Andererseits waren die autökologischen Präferenzen der Arten nicht bedeutend unterschieden und, in Übereinstimmung mit den Nährstoffen, indizierten sie die Veränderung des Sees vom ursprünglich oligotrophen zum mesotrophen Zustand.

(ii) In Kieselalgen-Metagemeinschaften von Ökosystemen wie Salzseen, die durch mehrere Umweltstressoren beeinflusst sind, hat der Filtereffekt der Umwelt den Einfluss von räumlichen Variablen innerhalb der kleinen Regionen überdeckt, was die Wichtigkeit der deterministischen Prozesse zeigt. Relativ hohe β-Diversität wurde in den natürlichen Salzseen der Donau-Theiß-Platte als auch in den restaurierten Salzseen des Nationalparks Fertő-Hanság beobachtet, die größtenteils durch den Austausch von den Arten ausgelöst wurde. Der Artenreichtum war jedoch in den restaurierten Salzseen höher, als in den natürlichen Gewässern. Zeitliche Abstände haben jedoch die Filterfunktion durch die Umwelt beeinflusst, was Veränderungen der Kieselalgengemeinschaften in den Salzseen des Nationalparks Fertő-Hanság bezüglich des einjährigen Zeitraums veranlasst hat. Einer der möglichen Gründe könnte die periodische oder permanente Wasserzufuhr sein. Es kann jedoch nicht ausgeschlossen werden, dass der zeitliche Effekt überbewertet wird.

(iii) Zwischen kleinen Süßwasserseen in einer mittelgroßen Region war die β-Diversität der Kieselalgen-Metagemeinschaft hoch, hauptsächlich aufgrund des Austausches von den Arten. Auch die α-Diversität (Artenreichtum) der einzelnen Seen war hoch. Die Strukture der Kieselalgengemeinschaften wurde durch locale Umweltmerkmale bezüglich der Artenvergemeinschaftung als auch durch beschränkte Ausbreitung aufgrund der räumlichen Variablen entsprechend der neutralen Theorie und der Patch-Dynamik beeinflusst. Mit der Beiseitigung der räumlich mehr "isolierten" Seen wurde der Effekt des räumlichen Abstandes vernachlässigbar und die Filterfunktion der Umwelt hat zugenommen. Der locale Beitrag zur β-Diversität (LCBD) wurde durch locale Umweltmerkmale beeinflusst, und es wurde eine starke positive Korrelation zwischen LCBD und LCBD bezüglich des Artenaustausches gefunden. Die ökologisch einzigartigsten Seen sind relative artenarm, und die häufigen Arten mit mittelgroßen oder breiten Nischen haben größtenteils zu der regionalen β-Diversität beigetragen.

Bezüglich der Mechanismen und β-Diversität der Metagemeinschaften haben die Analysen beruhend auf Häufigkeits- und Vorkommensdaten in jeder untersuchten räumlichen Ausdehnung zu den ähnlichen Schlussfolgerungen geführt. In einigen Fragen haben sie jedoch unterschiedliche Ergebnisse aufgedeckt: in Nullmodellanalysen wurde die Wichtigkeit der grundlegenden deterministischen und stochastischen Prozessen abweichend indiziert; überdies haben sie verschiedene Muster der ökologischen Einzigartigkeit von Arten in kleinen Süßwasserseen hervorgehoben. Außerdem wurde ein hoher Anteil ungeklärter Varianz in jeder der untersuchten räumlichen Skalen beobachtet, der sich aus nicht bestimmten Umweltvariablen, demographischer und Kolonisation-Austerben-Stochastizität und aus Korrelationen zwischen den Arten ergeben kann.

Kivonat

A lokális élőlény közösségek kialakulásának megértéséhez a mögöttes folyamatok regionális léptékű, átfogó vizsgálata szükséges. Azonban a rendelkezésre álló számos diverzitás index és statisztikai módszer eltérő eredményekre világíthat rá és különböző következtetésekhez vezethet attól függően, hogy a fajok gyakorisági (vagy relatív gyakoriság, biomassza stb.) vagy csupán elterjedési adatain alapszik. A disszertációban tárgyalt kutatás célja volt a bentikus kovaalga metaközösségek vizsgálata különböző térbeli kiterjedés esetén – egy kis tavon belül; kis tavak között két kis régión belül; kis tavak között közepes térbeli skálán – alkalmazva gyakorisági és elterjedési adatokon alapuló elemzéseket, illetve ezek összehasonlítása az esetleges eltérő eredmények feltárása céljából. Ennek megfelelően a fő célkitűzések a következők voltak:

(i) tanulmányozni a bentikus kovaalga közösségek időbeli és térbeli mintázatát az oligo-mezotróf Stechlin-tóban;

(ii) a Kárpát-medence két kis területén található természetes, valamint élőhely-rekonstrukció alatt álló szikes tavaiban feltárni két bentikus kovaalga metaközösség diverzitását és strukturáló folyamatait;

(iii) a Kárpát-medence közepes térbeli skáláján édesvízi kis tavak esetén megvizsgálni egy bentikus kovaalga metaközösség diverzitását és alakító tényezőit, illetve megbecsülni az egyes tavak és kovaalga fajok ökológiai egyediségét.

Az értekezés fő konklúziói a következők voltak:

(i) A Stechlin-tó litorális régiójában a tavaszi kovaalga közösségek fajgazdagsága alacsonyabb volt és a fitoplanktonból kiülepedett Mediophyceae osztályhoz tartozó fajok, elsősorban a *Stephanodiscus neoastraea* és a *Stephanodiscus rugosus*, aránya kiemelkedőbb volt az őszi közösségekhez képest. Következésképpen a nyári rétegződés kezdetén a centrikus taxonok magas relatív gyakorisága miatt tavasszal az ökológiai állapotbecslés céljából történő mintavétel nem javasolt. Az α-diverzitás (fajgazdagság és Shannon diverzitás) metrikák és a közösség fajösszetétele nem különültek el a tó három medencéje alapján, azonban a tápanyagformák szűk tartományon belüli változása eredményezhette a fajok kicserélődéséből adódó, viszonylag magas β-diverzitást. Ugyanakkor a fajok autökológiai preferenciái nem különböztek jelentős mértékben, és a

tápanyagokhoz hasonlóan az eredetileg oligotróf tó mezotróf állapotúvá való változását indikálták.

(ii) Az olyan, több stressztényező hatásának kitett ökoszisztémákban, mint a szikes tavak, a kovaalga metaközösségek esetében a lokális környezet szelektáló hatása felülírta a térbeli változók szerepét kis térbeli skálán, amely utalt a determinisztikus folyamatok fontosságára. A fajok kicserélődésének köszönhetően meglehetősen magas β-diverzitás volt megfigyelhető a Duna-Tisza közi természetes szikes tavaknál és a Fertő-Hanság Nemzeti Park élőhely-rekonstrukció alatt álló tavainál is, azonban a fajgazdagság magasabb volt a rekonstruált szikes tavakban. A rekonstruált tavak egy éves mintavételi periódusára vonatkozóan az időbeli távolság is szerepet játszott a kovaalga közösségek változásában, megzavarva ezáltal a környezet szelektáló hatását, amelynek egyik lehetséges oka az időszakos vagy állandó vízutánpótlás. Mindazonáltal azt sem lehet kizárni, hogy a szignifikáns időbeli hatást az időbeli skála felülreprezentáltsága eredményezte.

(iii) Édesvízi kis tavak esetében közepes térbeli skálán, a bentikus kovaalga metaközösség β-diverzitása magasnak bizonyult a nagymértékű fajkicserélődés következtében, illetve az egyes tavak α-diverzitása (fajgazdagság) szintén magas volt. A kovaalga közösségek kialakulásában egyaránt szerepet játszottak a lokális környezeti változók a faj-szortírozó koncepciónak megfelelően, illetve a térbeli változók okozta diszperzió limitáció amely a neutrális és folt dinamika modellre jellemző. A térben „izoláltabb" néhány tó kizárása a vizsgálatból azt eredményezte, hogy a kisebb területen „jobban csoportosuló" mintavételi helyek esetében a faj-szortírozó mechanizmusok váltak dominánssá. A tavak β-diverzitáshoz való hozzájárulására (LCBD) befolyással voltak a víz fizikai és kémiai változói, valamint az LCBD és a fajcserére vonatkozó LCBD indexek között erős pozitív korreláció állt fenn. A legnagyobb ökológiai egyediséggel jellemezhető tavak fajgazdagsága viszonylag alacsony volt és közepes vagy széles niche-sel rendelkező, gyakori fajok járultak hozzá leginkább a regionális β-diverzitáshoz.

Mindegyik vizsgált térbeli skála esetében a faj gyakoriság- illetve faj elterjedés-alapú elemzések hasonló következtetésekhez vezettek a β-diverzitást és metaközösség folyamatokat illetően, azonban néhány vizsgálati pontban különböző eredményekre mutattak rá: eltérően jelezték a determinisztikus és sztochasztikus folyamatok fontosságát a null modell analízisek során; továbbá édesvízi kis tavaknál a fajok ökológiai egyediségének eltérő mintázataira világítottak rá. Továbbá mindegyik térbeli skála esetében nagy mértékű nem magyarázott variancia volt megfigyelhető, amely adódhat a nem vizsgált környezeti változókból, demográfiai és kolonizáció-kihalás sztochasztikusságból, illetve a fajok közötti korrelációkból.

1. General introduction

1.1. Concept, levels and measures of biodiversity

From the 1930s, species-specific approaches, such as investigating the natural history of species and their habitat preferences, were characteristic in applied sciences (e.g. forestry, wildlife management, fishery, range management). At dawn of conservation biology, the main goal of conservationists was to protect and save threatened and endangered species and the global decline in biodiversity received increasing attention (Soulé, 1986; Gibbons, 1992). Later, it has been recognized that the loss of species implies the loss of genetical diversity, community and ecosystem features, and this "extinction crisis" was considered as a result of disturbance and interruption of ecosystem processes. Consequently, studying ecological processes as possible causes of the rapid extinction has come to the fore: the concept "biodiversity" has arisen (Van Dyke, 2008) and it has been recognized that ecosystem attributes are required to be protected not only studied (Solow et al., 1993; Patten, 1994; Jordan et al., 1996). The term "biodiversity" originates from merging "biological" and "diversity" (Wilson & Peter, 1989). Although it has been defined in many ways (see definitions summarized by Van Dyke, 2008) and commonly used in fields of science and politics, it needs to be perceived that biodiversity definitions are largely dependent on thinking attitudes and philosophical engagements (Mayer, 2006). Based on the Convention on Biological Diversity, signed at the Earth Summit in Rio de Janeiro in 1992, biodiversity is "…the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." However, according to Van Dyke (2008), the most suitable and helpful definition for applied conservation biology was phrased by Sandlund et al. (1992) that is, biodiversity is "the structural and functional variety of life forms at genetic, population, community, and ecosystem levels."

Related to these, biodiversity is often classified according to the following three levels: genetic diversity (within-species or intraspecific diversity), species diversity (interspecific diversity) and ecosystem diversity (community diversity). Genetic diversity refers to the variability of genes within individuals or populations of species, species diversity means the variety of species, whereas ecosystem diversity relates to the different species assemblages, habitats and ecological processes (Pullin, 2002; Rawat & Agarwal, 2015).

The terms alpha-, beta- and gamma-diversity, as the three aspects (or levels) of biodiversity was introduced by Whittaker (1956, 1960).

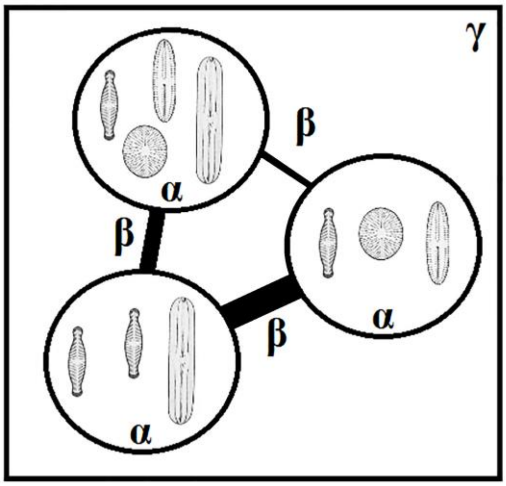

Figure 1 *Illustration of α-, β- and γ-diversity. Redrawn and modified from Jurasinski et al. (2009).*

Alpha (α)-diversity refers to the diversity within an ecological community (or in other words within a sample, site, sampling unit, plot etc.) (Fig. 1). The simplest method for measuring α-diversity is the compilation of a species list which consists of the species' names identified. By comparison, a more informative and standardized approach is the measure of species richness, i.e., recording the number of species for a given site or estimate species richness using species accumulation curves (Gotelli & Colwell, 2001; Chao, 2005). Despite its several benefits, such as easy "creation", presentation, interpretation and comparability of data, applying species richness as a diversity index has a major disadvantage: it provides no information about how individuals are distributed among the species (Van Dyke, 2008). To remedy this issue, many diversity indices have been introduced which take into account the number of individuals per sample and measure the evenness of species abundance distribution (e.g., Shannon, 1948; Simpson, 1949; Margalef, 1968; Pielou, 1969, 1975; Hill, 1973). Among them, the most widespread and most commonly used are for instance, Margalef's diversity index (Margalef, 1968) recommended for large sample sizes, Shannon index (Shannon, 1948) both for large and small sample size, and Pielou's evenness index (Pielou, 1969) related to Shannon index. Another approach to determine diversity within a community is the measure of taxonomic distinctness, which quantifies the relatedness between two species (or individuals) in the community (Clarke & Warwick, 1998). Taxonomic distinctness index is suggested to be applied in environmental monitoring and ecological status assessment and less affected by sample size than the former mentioned traditional indices (Warwick & Clarke, 1995, 1998).

Gamma (γ)-diversity is used to describe the diversity of communities at a higher aggregation level (within a landscape, Whittaker, 1960) evolved as a result of α-diversity of sampling sites within the landscape and the community differentiation among those sampling sites (Vane-Wright et al., 1991) (Fig. 1). However, in general, only a part instead of the whole landscape is sampled, that is, species richness does not represent the richness of the total landscape. Moreover, it is also necessary to pinpoint the spatial extent where the samples (and thus the species as well) are derived from (Jurasinski et al., 2009). Both α- and γ-diversity originates from count data thus, they can be considered as quantitative diversity (Beierkuhnlein, 2001) in turn, they are often criticized because the only difference between them is the extent of the area which they refer to (Jurasinski et al., 2009). Consequently, Jurasinski et al. (2009) proposed the use of a joint term “inventory diversity” instead of α- and γ-diversity separately.

Beta (β)-diversity, in simple terms, can be interpreted as the species diversity among communities of an area (Whittaker, 1960; Van Dyke, 2008) (Fig. 1). Furthermore, it represents the change of community composition between sampling units along a spatial, temporal or environmental gradient (Whittaker, 1975) and on the other hand it refers to the variation of species richness across different investigated scales (Jurasinski et al., 2009; Anderson et al., 2011). β-diversity as variation in species richness can be derived from multiplicative ($\beta = \gamma/\alpha$, Whittaker, 1960) or additive ($\beta = \gamma - \alpha$, Lande, 1996) partitioning of γ-diversity but none of the methods is appropriate for investigating compositional changes and their causes (Loreau, 2000; Crist et al., 2003). Investigation of β-diversity as changes in species composition can be conducted through several different methods: calculating similarity (or dissimilarity) indices, investigating the distance decay of similarity, applying ordination techniques or the sum of squares of a species matrix.

For estimating β-diversity by similarity/dissimilarity indices, two distinct approaches are available depending on the research question and the number of sampling sites involved. If the goal is to quantify how similar (or dissimilar) two communities are in their species composition (i.e., the biotic heterogeneity between them), either in space or in time, pairwise dissimilarity index should be calculated. However, the information about co-occurrence patterns is neglected by pairwise measures in three or more communities (sites, sampling units etc.). Therefore, if biotic heterogeneity across more than two assemblages is the question of interest, the use of multiple-site dissimilarity index is suggested instead of simply averaging of pairwise indices (Diserud & Ødegaard, 2007; Baselga, 2013a). Both in case of the pairwise and the multiple-site framework, an appropriate index (or indices) should be chosen depending on whether the community data set is qualitative (only species occurrences are documented – presence-absence/incidence data) or quantitative (abundance of species is also recorded – abundance data). It has long been emphasized that β-diversity is enhanced by the combination of two distinct processes: (i) turnover when environmental, spatial or historical constraints (Qian et al., 2005) result in the replacement of species by other species (Baselga, 2010), and (ii) nestedness (Baselga, 2010) when a non-random species loss (or gain) occurs and thus, species of the species poor community form the subset of (i.e., nested within) the richer community (Wright & Reeves, 1992; Ulrich & Gotelli, 2007). The most commonly used incidence-based dissimilarity index whose both pairwise and multiple-site approach provides the additive partitioning of total dissimilarity (β-diversity) into its turnover and nestedness-resultant components and helps to understand the underlying processes, is Sørensen index (Sørensen, 1948; Koleff et al., 2003; Baselga, 2010, 2012). It has been known for a long time now that pairwise Bray-Curtis index of dissimilarity is the abundance-based extension of Sørensen dissimilarity (Legendre & Legendre, 1998), however, its partition into components (Baselga, 2013b) and elaboration of its multiple-site framework are relatively new (Baselga, 2017). Similarly to the separation of Sørensen dissimilarity into turnover and nestedness (Baselga, 2010, 2012), total Bray-Curtis dissimilarity (variation in species abundances) can be divided additively into two antithetic parts: (i) balanced variation in abundance when some species' individuals in a community are replaced by the same number of individuals of distinct species from another community, and (ii) abundance gradients when some individuals are lost (or gained) from community to community (Baselga, 2013b, 2017). Formulation of pairwise and multiple-site Sørensen and Bray-Curtis dissimilarity is summarized in Appendix 1. Another approach related to indices based on resemblance is the taxonomic similarity index computed from species presence-absence data (Izsak & Price, 2001). Taxonomic similarity is derived from the average taxonomic distance and measures the average minimum path length between two species (or individuals) of two different communities. Thereby, its advantage is, compared to the conventional similarity/dissimilarity indices, that not only species level but higher levels of the taxonomic tree are also taken into consideration during the comparisons (Izsak & Price, 2001).

A potential approach to study whether species composition is related to geographical or environmental distance, is the investigation of the slope of the distance decay relationship (Whittaker, 1960). The phenomenon of distance decay assumes that similarity of communities decreases with the increase of spatial or in some cases, environmental distance (e.g. Beals, 1984; Nekola & White, 1999; Tuomisto et al., 2003, Astorga et al., 2012; Anderson et al., 2013) and by steeper slope of distance decay relationship, replacement of species is more intensive. Although this method is widespread, it has some drawbacks, such as dependence on the applied similarity coefficient, regression model and the scale of the study (Jurasinski et al., 2009).

A similar scale-dependent approach, but more comparable due to the independence from regression model, is the determination of halving distance, that is the distance at which the initial similarity is reduced by half (Soininen et al., 2007).

Ordination techniques targeting the reduction of inherent complexity in data sets are also suitable for estimating β-diversity by the length of ordination gradient. Since they represent distances/dissimilarities or similarities depending on their type and the chosen coefficient (Legendre & Legendre, 1998), β-diversity can be calculated as the average distance of a given sample from the group centroid (Anderson et al., 2006).

A related, popular method for determining driving forces of community variation (and thus β-diversity, as well), is the variation partitioning which is based on explaining variation in community data by spatial, temporal or environmental variables. Variation can be partitioned, for instance, applying PERMANOVA (permutational multivariate analysis of variance, Anderson, 2001, 2017; Anderson et al., 2008) in case of factorial predictors and based on RDA (redundancy analysis), CCA (canonical correspondence analysis) or dbRDA (distance-based redundancy analysis) for continuous variables (Borcard et al., 1992; Legendre & Anderson, 1999; McArdle & Anderson, 2001; Anderson et al., 2008).

A relatively novel approach of assessing β-diversity has been introduced recently by Legendre et al. (2005). They proposed applying the sum of squares of the raw community data for measuring the variation of species composition. Then, quantification of local contribution to β-diversity and that of species contribution to β-diversity is also provided (Legendre & De Cáceres, 2013) and extended for species replacement and richness difference components (Legendre, 2014).

1.2. Metacommunity theories

In community ecology of the early 1900s, local communities were typically considered as closed and isolated systems where populations regulate each other's birth and death rates as described, for instance, by the Lotka-Volterra population dynamic model (Lotka, 1910; Volterra, 1926) or its extended version, the Rosenzweig-McArthur model (Rosenzweig & MacArthur, 1963). In 1934, Gause (Gause, 1934) stated, based on his experiments, that two species possessing similar ecological parameters (i.e., do not differ in their resource utilizations) can never occupy the same niche, the stronger competitor displaces the other. Consequently, two or more species can only coexist if they are limited by different factors (known as "competitive exclusion principle" Hardin, 1960). The principle implied that organization of communities occurs due to competitive interactions, and served as the basis of niche assembly theory.

The niche assembly perspective assumes that species are ecologically different resulting in niche separation and that the increasing number of available niches induces the increase of the number of functional groups (species having similar skills to exploit similar resources) thereby biodiversity as well (Van Dyke, 2008). Contradicting Hardin's (1960) competitive exclusion principle, in fact, coexistence of many more species can be observed than would be allowed by the limiting factors (Hutchinson, 1961). Several ecologists have been inspired by this issue and they recognized that the solution lies in the spatial and temporal heterogeneity (Levins, 1969; Heerkloss & Klinkenberg, 1998; Descamps-Julien & Gonzalez, 2005).

In 2001, Hubbell formulated the unified neutral theory of biodiversity and biogeography, which contradicts the niche assembly theory (Hubbell, 2001). It presumes that there is no or only weak competitive interaction between species that are assembled by random processes and form open, non-equilibrium communities.

This idea served as a gateway to considering local communities as members of a metacommunity associated by the dispersal of species at different spatial and temporal scales (Leibold et al., 2004). Within the metacommunity framework (Leibold et al., 2004) four different concepts can be distinguished in explaining the importance of local- (species' competitive abilities, demographic processes) and regional-scale (degree of environmental heterogeneity, dispersal) processes.

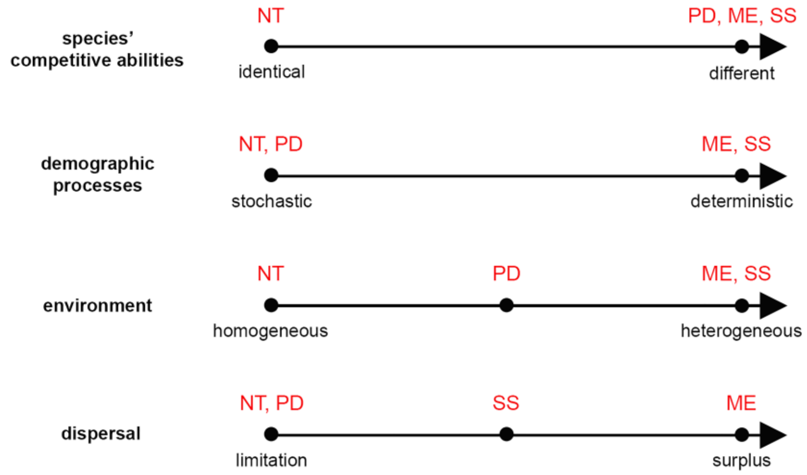

Figure 2 *Summary of assumptions about the main processes in the four metacommunity concepts (NT = neutral theory, PD = patch dynamics, ME = mass-effect, SS = species-sorting).*

In the neutral theory (NT), species are assumed to be identical concerning their interspecific interactions and response to any limiting factor; demographic processes (birth-death rates) are stochastic; the environment is homogeneous in the region; and dispersal of species is limited. The patch dynamics (PD) archetype assumes that the species' relative competitive abilities depend on the local environmental conditions; the population-level extinctions are stochastic due to the individual-level stochasticity; in previous simple PD models (e.g. Leibold et al., 2004; Holyoak et al., 2005) the environment is completely homogeneous or slightly heterogeneous however, complex "interface" models allow habitat heterogeneity in PD; dispersal is limited but interspecific differences in colonization abilities are allowed. In the mass-effect (ME) concept, competitive abilities and birth-death rates are assumed to be largely dependent on the local environment, which displays heterogeneous patterns; species are able to persist in suboptimal localities if there is a sufficient immigration from adjacent sites with high population density. The species-sorting (SS) concept, similarly to the ME, expects that the environment is heterogeneous, local conditions regulate the competitive abilities of species and the demographic processes; dispersal is sufficient thus, each species can persist in any habitat where it can achieve positive population growth (Leibold & Chase, 2018). Processes assumed to be acting in the four metacommunity archetypes are summarized in Fig. 2. Nevertheless, the role of these local- and regional-scale processes, and thus the interpretation of metacommunity concepts may change with spatial scale (Langenheder & Ragnarsson, 2007; Mykrä et al., 2007; Heino et al., 2010; Vilmi et al.,

2016) and the connectivity among sites (Göthe et al., 2013; Dong et al., 2016; Vilmi et al., 2016).

Although, the four major metacommunity perspectives serve as an apparently useful base for discussing metacommunity scenarios, they have been widely misconstrued and as a consequence, the fundamental aim of many researchers is erroneously to define which of these four paradigms might be responsible for the structure of a given metacommunity (Brown et al., 2017). However, in most cases, natural metacommunities are not structured corresponding exclusively to one of the four theories therefore, they should not be treated as alternative hypotheses but each of the community structuring processes should be integrated into an embracing metacommunity concept which recognizes the inference space as continuous (Brown et al., 2017, Leibold & Chase, 2018).

2. Main objectives

Dissimilarity between two (or more) communities can arise from the differences in species composition or abundances. The literature provides a number of indices for assessing β-diversity and exploring metacommunity processes, however, they might reveal distinct results leading to disparate conclusions depending on whether they are calculated from species abundance (or relative abundance, biomass etc.) or incidence data. Anderson et al. (2011) proposed that abundance should be included in analyses since it provides important and valuable information about community structure but species identities can be also informative, for instance, in conservational investigations. Legendre (2014) emphasized that abundance-based indices can be applied only if quantitative sampling was conducted at each site in accordance with the standard protocol ensuring the comparability of results. In turn, in case of compiling data from disparate sources (e.g. from different researchers, governmental reports, museum collections), the use of presence-absence data is preferable. Furthermore, spatial distance among sampling sites is also suggested to be taken into account before opting for the quantitative or the binary forms of dissimilarity indices (Legendre, 2014). Abundance-based calculations are presumed appropriate at small spatial scales since species are more likely to differ in their abundances rather than in their incidences. In contrast, incidence-based calculations are more preferable within large spatial extents where sampling sites probably host different species.

The aim of the research in this dissertation was to study benthic diatom metacommunities at three different spatial extents – within a lake; across lakes covering two small regions; across lakes at intermediate spatial scale – applying both abundance- and incidence-based analyses and to compare whether they provide different results. Accordingly, the main objectives were the following:

(i) to investigate the temporal and spatial patterns of benthic diatom communities in the oligo-mesotrophic Lake Stechlin;

(ii) to explore the diversity and structuring mechanisms of two benthic diatom metacommunities across natural and reconstructed soda pans encompassing two small areas in the Carpathian Basin;

(iii) to examine the diversity and drivers of a benthic diatom metacommunity across small freshwater lakes at intermediate spatial scale of the Carpathian Basin, and to assess the ecological uniqueness of the individual lakes and species.

3. Community patterns of benthic diatom flora in Lake Stechlin[1]

3.1. Introduction

The Baltic Lake District in northeastern Germany is composed of a multitude of lakes formed during the last glacial period (~12,000 years before). Some of the lakes are pristine and considered to represent high status in terms of the European Water Framework Directive. Lake Stechlin represents a highly valuable ecosystem. It belongs to the type of stratified lowland lakes with small catchment area and high content of calcite (Mathes et al., 2002). It is one of the most extensively studied lakes in northern Germany. Regular monitoring of its main limnological variables and biota was set in the 1950s in the context of the operation of a nuclear power plant (NPP) between 1966 and 1989. Through an external circulation system, the NPP's cooling water was taken from the mesotrophic Lake Nehmitz, the heated water was pumped into Lake Stechlin, and diverted back to Lake Nehmitz (Casper, 1985; Koschel et al., 2002).

Phytoplankton of Lake Stechlin has been studied since 1959 (Casper, 1985), and water chemistry and primary production measurements using the ^{14}C-technique started in 1970 (Koschel, 1974). Since 1994, a sampling program has been carried out to investigate the species composition and succession of phytoplankton (Padisák et al., 1998, 2010) and the occurrence of deep chlorophyll maxima (DCM) formed by cyanobacteria (Padisák et al., 1997, 2010; Selmeczy et al., 2016). In the last decade, an increasing abundance of cyanobacterial blooms indicated a change in water quality (Padisák et al., 2010; Üveges et al., 2012).

Diatom research in Lake Stechlin focused mainly on planktonic Centrales taxa. The population dynamics of two phycogeographically restricted unicellular diatom species were described (*Cyclotella tripartita* and *Stephanocostis chantaicus* - Scheffler & Padisák, 1997, 2000). In 1999, spatial and temporal changes in spring planktonic diatom populations were studied (Padisák et al., 2003). Scheffler et al. (2003, 2005) investigated the relationship between *Cyclotella comensis* and *Cyclotella pseudocomensis* with morphological, ecological, and molecular methods. Contrary to extensive and detailed phytoplankton studies, attached

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[1] A part of this chapter was published in the following papers:
Szabó, B., Padisák, J. & Stenger-Kovács, C. (2014). A Stechlin-tó (Németország) kovaalga összetétele. Hidrológiai Közlöny, 94: 79–81.
Szabó, B., Padisák, J., Selmeczy, G. B., Krienitz, L., Casper, P. & Stenger-Kovács, C. (2017). Spatial and temporal patterns of benthic diatom flora in Lake Stechlin, Germany. Turkish Journal of Botany, 41: 211–222.

diatoms of the lake received much less scientific interest. In 1974 and 1975 (thermal load period), biomass and primary production of periphyton in the littoral zone were determined. Thereafter, a list of diatom taxa found in the probes was compiled and published in Casper's (1985) synthesis. Scheffler & Schönfelder (2004) reported on the microflora of Lake Stechlin and their list contains the species number of benthic diatoms. Schönfelder et al. (2002) estimated the relationship between littoral diatom composition and environmental factors in northeastern German lakes including Lake Stechlin. In addition, Stechlin is included in the Water Framework Directive monitoring program of Brandenburg and related reports define reference conditions by means of analysis of diatoms (Schönfelder, 2002; Schönfelder et al., 2005). Although spatial and temporal patterns of epiphyton growth in Lake Stechlin have been studied extensively (Périllon et al., 2017; Périllon, 2017), international publications concerning such patterns of diversity and species composition of benthic diatom communities are lacking.

3.2. Aims

In the current research, it was investigated whether there is any difference in species composition and diversity of benthic diatom communities along the shoreline of Lake Stechlin at two different sampling dates (2013 spring and 2014 autumn). In 2013, the lake was covered by ice until the middle of April and the thermal stratification started in early May, when the first sampling was conducted. Since the lake's phytoplankton can be characterized by an intense diatom bloom before the summer stratification (Scheffler & Padisák, 1997; Padisák et al., 1998), it was assumed that, due to the planktonic taxa sinking from the phytoplankton, a remarkable difference will be found compared to the autumn communities.

In addition, the spatial patterns of community composition and diversity were examined. King et al. (2002, 2006) observed that assemblages in small lakes are quite homogeneous therefore, since Lake Stechlin has a relatively small surface area (< 5 km^2) and no difference was found between the horizontal distribution of phytoplankton in two basins (Fuchs et al., 2016), it was hypothesized that benthic diatom communities in the littoral zone should also be relatively homogeneous.

3.3. Material and Methods

3.3.1. Study area

Lake Stechlin is located in northeastern Germany on the southern border of the Mecklenburg Lake District (53°10′/13°02′) (Fig. 3).

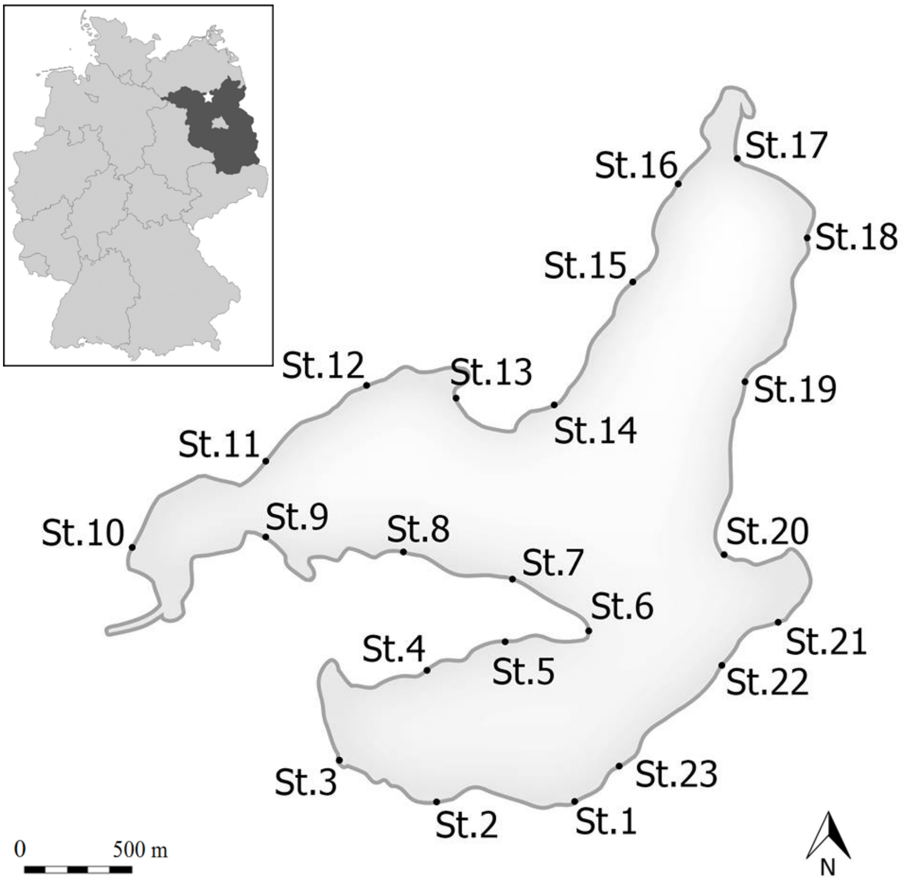

Figure 3 *Location of Lake Stechlin in Germany and the sampling sites.*

The lake is deep, dimictic (in some years warm monomictic) and only slightly affected by anthropogenic impacts. Its trophic status is originally oligotrophic, but in the early 2000s a change towards mesotrophic conditions was observed. Based on a long-term investigation, Selmeczy et al. (2019) assumed that the symptoms of eutrophication are probably caused by internal changes rather than by external anthropogenic pressure. The rising dominance of Cyanobacteria were probably induced by an extreme weather event, namely the long-lasting winter in 1995-1996, and are related to the increase of relative water column stability (RWCS). Additionally, increase of the TP content might be likely due to the deliberation of phosphorus from the sediment that was accumulated when the mesotrophic cooling water of the nuclear power plant was pumped back into Lake Stechlin. The lake has a surface area of 4.25 km^2, a calculated volume of 96.9 × 10^6 m^3, a maximum depth of 69.5 m located in the north basin, and the mean depth is 22.8 m. It is divided into four basins: north, west, south, and central. The basins have relatively small surface areas (1.3, 1.1, 0.9, and 1.0 km^2) and belong to the category of deep lakes based on their relative depths (5.3%, 3.5%, 3.3% and 5.2%). The lake has a temporary surface inflow from Lake Dagow and a surface runoff through the Polzow canal from the south basin of Lake Stechlin to the north basin of Lake Nehmitz. The shore of Lake Stechlin is vegetated by mixed forests consisting mainly of deciduous trees and almost 50% of their crowns hang over the water; the shoreline development factor is 2.1 (Casper, 1985). TP and TN concentrations and trophic level based on TP concentrations (OECD, 1982) of samples taken from the deepest point monthly between February 2013 and December 2014 are summarized in Table 1. Data represent the average of samples taken at 0-, 5-, and 10-m depths.

Table 1 *Concentration of TP and TN (euphotic zone, 0–10 m; mean ± SD) and trophic status at the deepest point of Lake Stechlin. TL = trophic level based on TP concentration (OECD, 1982), O = oligotrophic, M = mesotrophic.*

sampling date	TP [µg L^{-1}]	TN [µg L^{-1}]	TL
05.02.2013	27.0 ± 0	424.0 ± 0	M
16.04.2013	17.0 ± 0	81.0 ± 0	M
07.05.2013	15.7 ± 1.5	82.0 ± 7.0	M
04.06.2013	15.7 ± 2.1	436.7 ± 8.4	M
09.07.2013	13.3 ± 1.2	476.0 ± 66.9	M
08.08.2013	12.7 ± 2.5	432.0 ± 15.0	M
18.09.2013	11.3 ± 0.6	526.7 ± 84.9	M
08.10.2013	9.3 ± 2.3	577.0 ± 70.1	O
14.11.2013	12.0 ± 1.0	469.3 ± 15.9	M
04.12.2013	10.3 ± 0.6	328.3 ± 50.8	M
15.01.2014	23.0 ± 0	392.0 ± 0	M
25.02.2014	22.0 ± 0	499.0 ± 0	M
18.03.2014	22.0 ± 0	478.0 ± 0	M
10.04.2014	16.0 ± 0	374.0 ± 0	M
13.05.2014	15.3 ± 1.5	432.7 ± 77.0	M
11.06.2014	16.3 ± 0.6	422.3 ± 86.4	M
09.07.2014	10.0 ± 0	469.7 ± 45.5	M
14.08.2014	12.0 ± 0	376.0 ± 0	M
08.09.2014	9.0 ± 0	397.0 ± 0	O
08.10.2014	12.0 ± 0	420.0 ± 0	M
06.11.2014	17.0 ± 0	575.0 ± 0	M
04.12.2014	12.0 ± 0	653.0 ± 0	M

3.3.2. *Sampling and processing of samples*

Phytobenthos samples were taken from natural stone substrates in the littoral zone at 23 different sites of Lake Stechlin (Fig. 3) on 3 May 2013 and 26 September 2014. Epilithic diatom sampling followed the standard method (King et al., 2006). Diatom valves were cleaned by hot hydrogen-peroxide method (CEN, 2003) in order to remove the organic material and were embedded in Pleurax© resin. A minimum of 400 valves was counted in each sample using a Zeiss Axio Imager A1 with a Planapochromat DIC lens at 1000× magnification. Accurate identification of centric species was conducted using a Hitachi S-4500 field emission scanning electron microscope (Hitachi Corporation, Tokyo, Japan). Species were identified according to the relevant taxonomic guides (Lange-Bertalot, 2001; Krammer, 2002; Levkov et al., 2010; Hofmann et al., 2011; Bey & Ector, 2013; Houk et al., 2014). The species were classified into two groups following Medlin & Kaczmarska (2004): Mediophyceae (polar centrics and radial Thalassiosirales) and Bacillariophyceae (pennates). The most frequent and abundant taxa were identified according to either of the following two criteria: (1) occurred in at least four samples and (2) reached a relative abundance of at least 5% in any of the samples.

In 2014, water temperature (°C), conductivity (µS cm^{-1}), and pH were measured *in situ* with an HI 9828 multiparameter probe (Hanna Instruments, Limena, Italy). Water samples for analysis of total nitrogen and total phosphorus were also collected at all sampling points (Fig. 3) and analyzed by flow injection analysis (FIA-System, FOSS, Hillerød, Denmark) (APHA, 1998). Preferences of the individual taxa with respect to pH and trophic status were determined according to Van Dam et al. (1994). The German Red List was used to assess the conservational status of the species (Lange-Bertalot, 1996).

3.3.3. *Statistical analyses*

To estimate α-diversity of diatom communities, species richness and Shannon diversity index (Shannon, 1948) were calculated for each sampling point. It was investigated whether these diversity metrics differ in the basins at the two sampling dates using repeated measures ANOVA (Type III). The t-test for unequal variances (Welch's t-test) was used to examine the differences in the relative abundance of Mediophyceae and Bacillariophyceae diatom species between spring and autumn.

Non-metric multidimensional scaling (NMDS) was applied to study whether there is a difference between the epilithic diatom communities at the two sampling dates and in the three basins. Differences were tested statistically using analysis of similarities (ANOSIM). Since Mediophyceae species tend to be rather planktonic than members of the benthos, NMDS and ANOSIM were repeated to investigate the same differences retaining only diatoms belonging to the class Bacillariophyceae. Before performing NMDS, species abundance data were square root transformed and then submitted to Wisconsin double standardization (Bray & Curtis, 1957; Cottam et al., 1973).

Using the autumn samples when planktonic diatom species do not dominate the benthic communities, the overall β-diversity was assessed within the lake applying abundance-based multiple-site Bray-Curtis dissimilarity (β_{BC}), which was partitioned into its two components: abundance balanced variation ($\beta_{BC.BAL}$) and abundance gradients ($\beta_{BC.GRA}$) (Baselga, 2017). Then, diatom abundance data was transformed into presence-absence data and the same estimation was performed using incidence-based multiple-site Sørensen dissimilarity index (Baselga, 2010). Sørensen index (β_{SOR}) was also divided into its components: turnover (β_{SIM}) and nestedness (β_{NES}) component (Baselga et al., 2007; Baselga, 2010). In addition, a mean Euclidean distance was calculated for the standardized environmental variables measured in 2014 autumn which intended to quantify the environmental heterogeneity.

Furthermore, the relative contribution of pure and shared effect of environmental heterogeneity and spatial distance to variability of the autumn diatom communities was investigated with variation partitioning method (Peres-Neto et al., 2006). In this analysis, two data matrices were used to define the two explanatory variable groups. One of that was the group ‘environmental’, which consisted of the water physical and chemical parameters measured in the littoral region. Prior to this, collinearity of the variables was tested by computing variance inflation factor (VIF) and none of the variables were removed from the model because they did not exhibit a value above 10 (James et al., 2014). In the group ‘spatial distance’, distance-based Moran’s eigenvectors (dbMEMs) were included as explanatory variables computed by principal coordinate analysis (PCoA) of a truncated geographic distance matrix among sampling locations (Borcard & Legendre, 2002; Borcard et al., 2004). Variation partitioning was performed both for Hellinger transformed (Legendre & Gallagher, 2001; Borcard et al., 2011) species abundance and species incidence data. ANOVA (permutations = 999) of RDA models were run to assess the significance of adjusted R^2 values for testable fractions (pure environmental and spatial distance).

Statistical analyses were carried out in R statistical computing environment (R Development Core Team, 2017). Betapart package (Baselga et al., 2017) was used for the calculation of β-diversity indices, codep (Guenard et al., 2017) and ape (Paradis et al., 2004) for dbMEM analysis and PCoA and vegan package (Oksanen et al., 2017) for variation partitioning.

3.4. Results

The environmental, especially physical, parameters did not show considerable variation along the littoral region in 2014 autumn. The mean Euclidean distance of the standardized environmental variables was 2.97. Conductivity was low, all sampling sites were alkaline and water temperature did not change remarkably on the day of sampling. Only TP and TN varied along a relatively wide range, however, they did not exhibit high values typical of eutrophic or hypereutrophic conditions (Table 2).

Table 2 *Physical and chemical parameters measured in the littoral region of Lake Stechlin in September 2014.*

variable	unit	mean±SD	min	max
conductivity	µS cm^{-1}	259±2	251	265
pH		8.4±0.1	8.2	8.6
temperature	°C	16.8±0.2	16.4	17.1
TP	µg L^{-1}	14.5±4.7	11.0	29.0
TN	µg L^{-1}	429.1±54.3	281.0	542.0

A total of 118 diatom taxa were identified, of which 41 species were reported in the species list published by Casper (1985) (Appendix 2). Preferences in pH of the water were available for 71% of the species (Appendix 2): 24% of these taxa were circumneutral, 59% alkaliphilous, and 17% alkalibiontic. With respect to trophic preferences, information was available for 79 taxa (Appendix 2). Most of the species (39%) belonged to the category eutraphentic and 29% were meso-eutraphentic. A considerable proportion (14%) of taxa was tolerant to oligo- to eutrophic environment. Altogether 13% of species belonged to categories 2 (oligomesotraphentic) and 3 (mesotraphentic) and 4% mainly occur in oligotrophic waters. Only one individual of a species was found in the category hypereutraphentic.

During this study, 15 species were found that belong to some of the categories of the Red List for Central Europe (Appendix 2, 3). Five of them belong to category 3 (“endangered”): *Achnanthidium rosenstockii*, *Aneumastus stroesei*, and *Diploneis parma* were represented by only one individuum; *Planothidium joursacense* appeared with a small number of individuals; and *Karayevia laterostrata* was characteristic in the 2014 samples. Two taxa were “extremely rare”: *Cocconeis neodiminuta* and *Navicula hofmanniae*, which appeared only occasionally in some samples. Some species were found that are not endangered but are in regression (listed by decreasing number of occurrences): *Cocconeis neothumensis*, *Navicula subalpina*, *Brebissonia lanceolata*, *Psammothidium bioretii*, *Cymbellafalsa diluviana*, *Cavinula scutelloides*, *Encyonema lacustre*, and *Stauroneis gracilis*.

The species richness of the individual samples ranged from 23 to 41 and the Shannon diversity varied between 1.98 and 2.78. The species richness (Fig. 4a) differed significantly between 2013 and 2014, while Shannon diversity (Fig. 4b) did not show a significant difference at the two sampling dates (Table 3).

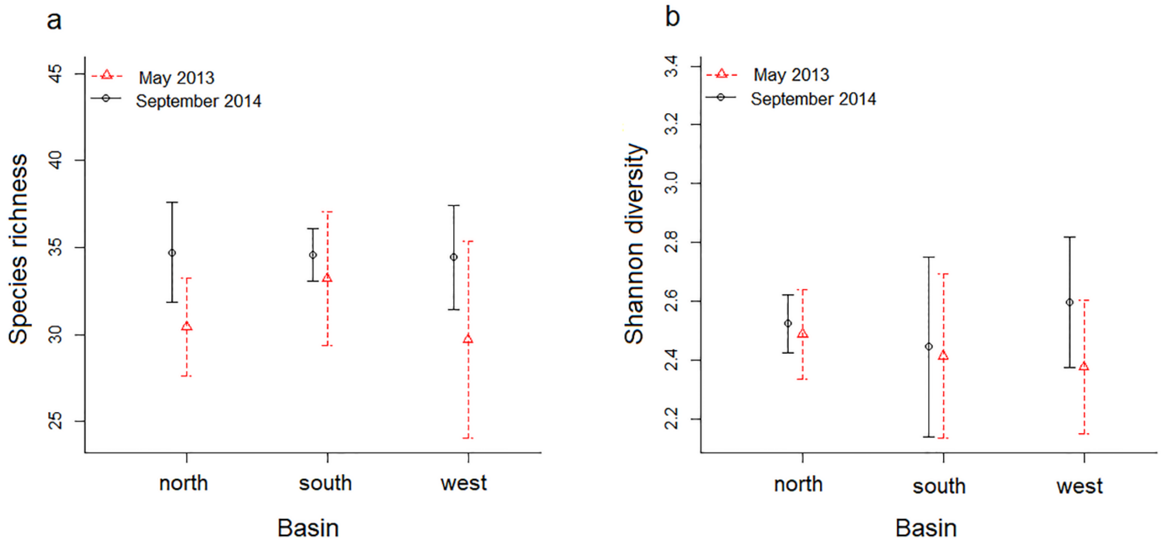

Figure 4 *Mean and standard deviation (SD) of species richness (a) and Shannon diversity (b) in the three basins of Lake Stechlin in May 2013 and September 2014.*

Mean of species richness was lower in May 2013 (31 ± 4) than in September 2014 (35 ± 2). The average diversity was 2.42 ± 0.22 in spring 2013, while that of the samples from autumn 2014 was 2.52 ± 0.23. No significant differences were found between the three basins based on species richness and Shannon diversity (Figs. 4a, b; Table 3).

Table 3 *Spatial and temporal effect on diversity metrics based on results of repeated measures ANOVA (Type III) (numDf = degrees of freedom in the numerator, denDf = degrees of freedom in the denominator, F = F value, P = P value).*

		numDf	**denDf**	**F**	**P**
Species richness	Basin	2	40	0.024	0.977
	Sampling date	1	40	5.379	0.026
	Basin*Sampling date	2	40	1.163	0.323
Shannon diversity	Basin	2	40	0.829	0.783
	Sampling date	1	40	0.089	0.767
	Basin*Sampling date	2	40	0.783	0.464

Statistically significant differences were found between 2013 and 2014 samples based on the relative abundance of species belonging to class Mediophyceae (Df=22.393, P<0.001) and Bacillariophyceae (Df=22.438, P<0.001) (Fig. 5).

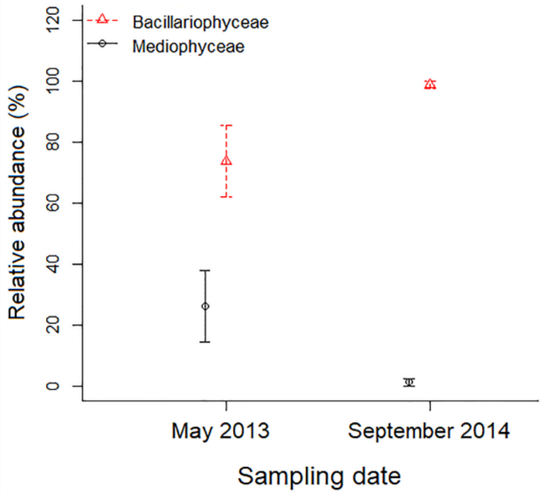

Figure 5 *Mean and standard deviation (SD) of the relative abundance of Mediophyceae and Bacillariophyceae diatom species in Lake Stechlin in May 2013 and September 2014.*

In spring 2013, the mean contribution of Mediophyceae taxa to the total number of individuals reached 26.2%, due to dominance of *Stephanodiscus rugosus* and *Stephanodiscus neoastraea* (Appendix 4). In the 2014 samples, the average proportion of Mediophyceae species was only 1.2%.

NMDS projection displayed a clear separation according to the two sampling dates (ANOSIM R = 0.933, P = 0.001), however, the communities from the three basins (ANOSIM R = –0.023, P = 0.701) were not separated (Fig. 6a). For only Bacillariophyceae taxa (Fig. 6b) a similar result was found: structure of the diatom communities was different in the two years

(ANOSIM R = 0.819, P = 0.001) and there was no separation according to the basins (ANOSIM R = –0.019, P = 0.678).

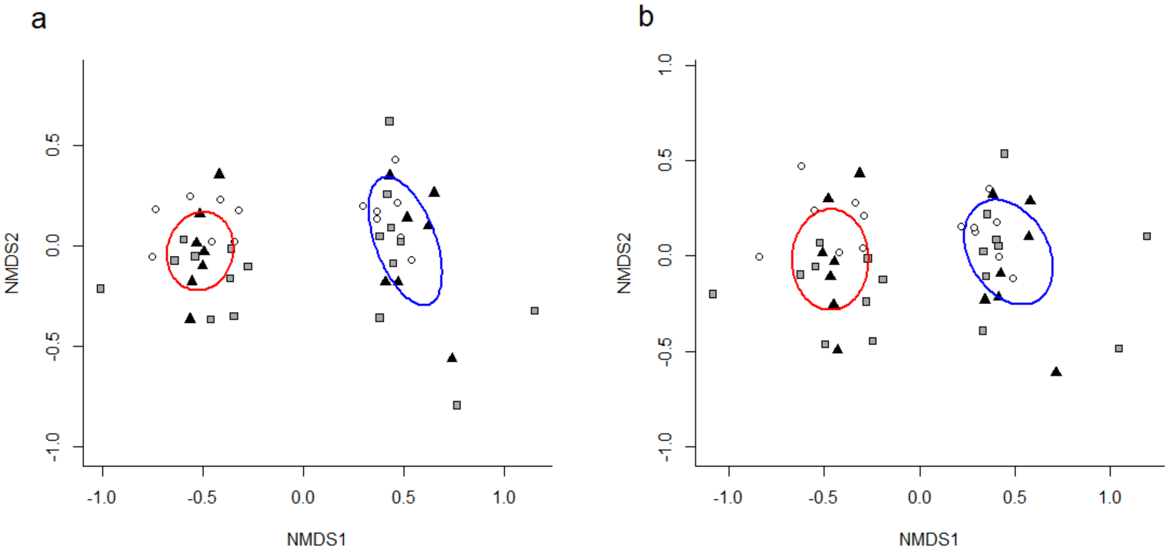

Figure 6 *NMDS projection of phytobenthos samples from Lake Stechlin based on transformed and standardized relative abundance data of total diatom species (Bray–Curtis distance, stress 0.134) (a) and that of Bacillariophyceae diatom species (Bray–Curtis distance, stress 0.150) (b) (open circle = north basin, grey square = south basin, black triangle = west basin). Red and blue ellipses are drawn around centroid of 2013 and 2014 classes.*

The most frequent (counted in ≥4 samples) and abundant (maximum relative abundance ≥5%) species in both years were *Achnanthidium minutissimum*, *Amphora pediculus*, *Cocconeis placentula* var. *euglypta*, *Fragilaria capucina* var. *perminuta*, and *Gomphonema pumilum* var. *rigidum*. The most important Bacillariophyceae taxa with the same criteria in the 2013 samples were *Cymbella compacta*, *Diatoma ehrenbergii*, *D. moniliformis*, *Fragilaria capucina* var. *vaucheriae*, *Gomphonema olivaceum*, *G. olivaceum* var. *olivaceoides*, *Nitzschia dissipata*, and *Rhoicosphenia tenuis*. In 2014, they were *Cocconeis neothumensis*, *Encyonopsis subminuta*, *Epithemia sorex*, *Fragilaria brevistriata*, *Karayevia clevei*, *K. laterostrata*, *Navicula cryptotenelloides*, *N. reichardtiana*, *N. tripunctata*, *Nitzschia dissipata* var. *media*, *N. lacuum*, *N. sociabilis*, and *Planothidium frequentissimum*. The most frequent and abundant taxa belonging to the class Bacillariophyceae are presented in Appendix 5.

The overall β-diversity of the autumn communities (n=23) within the lake was relatively high according to the abundance-based (β_{BC}=0.851) as well as the incidence-based (β_{SOR}=0.816) multiple-site framework. In both cases, β-diversity patterns were enhanced mainly by the component accounting for species replacement (abundance balanced variation: $\beta_{BC.BAL}$=0.841 and turnover: β_{SIM}=0.798), whereas the component accounting for subsets (abundance gradients: $\beta_{BC.GRA}$=0.010 and nestedness β_{NES}=0.018) was very low.

The variation partitioning results, based on diatom abundance and presence-absence data as well, revealed that neither the environmental variables (P_{ab}=0.257, P_{p-a}=0.457) nor the spatial distance (P_{ab}=0.862, P_{p-a}=0.532) alone affected significantly the benthic diatom assemblages. However, their shared fraction explained 7.3% of the community variation in case of abundance data and 3.8% in case of incidence data (Fig. 7).

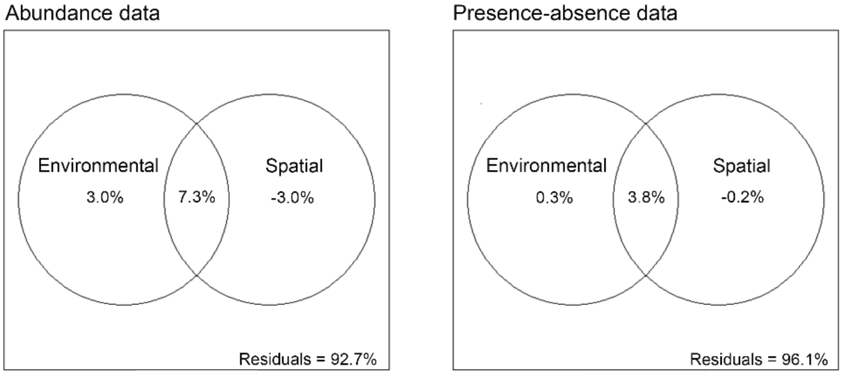

Figure 7 *Results of variation partitioning for Hellinger transformed species abundance and presence-absence data from Lake Stechlin. Fractions are shown as percentages of total variation based on adjusted R^2 values (Environmental = environmental variables, Spatial = spatial distance). Residuals indicate the unexplained variances.*

3.5. Discussion

3.5.1. Diatom species of the littoral zone

In accordance with the slightly alkaline environment determined in the littoral region of the lake, most of the species found in the phytobenthos were alkaliphilous or alkalibiontic, while others preferred circumneutral waters. Except two sampling dates, the trophic status of the pelagic zone judged by the OECD criteria for TP (1982, Table 1) was mesotrophic both in 2013 and 2014, which is in accordance with the results found in the littoral region (Table 2). Schönfelder et al. (2002) determined a low nutrient content and low trophic state based on benthic diatom community of Lake Stechlin between 1992 and 1999. Using the same samples, Schönfelder et al. (2005) calculated three diatom indices and they gave distinct results: diatom index for planktonic (DI-PROF) and benthic (DI-BENT) taxa in the profundal zone indicated oligotrophic and weakly mesotrophic while index for littoral samples (DI-LIT) showed a strongly mesotrophic state. Their mean indicated slightly mesotrophic state. The results of the present study support the previous conclusions (Koschel et al., 2002; Padisák et al., 2010, Selmeczy et al., 2019) that the trophic status of the lake changed from oligotrophic to mesotrophic in the last several years, as most of the taxa identified in the epilithon were meso-eutraphentic, eutraphentic, or tolerate a wide range of trophic levels.

Many of the most frequent and abundant species earlier not listed by Casper (1985) are common in lakes of the Baltic Lake District (e.g., *Navicula cryptotenelloides*, *Planothidium frequentissimum*) or in water bodies of the alpine regions (e.g., *Diatoma ehrenbergii*), or in both areas (e.g., *Encyonopsis subminuta*, *Gomphonema olivaceum* var. *olivaceoides*, *G. pumilum* var. *rigidum*). Others are rather characteristic for large rivers (e.g., *Cymbella compacta*, *Nitzschia sociabilis*) (Hofmann et al., 2011). Among the identified Red List species absent from Casper's synthesis, there were some indicators of excellent ecological quality. These species can be found mainly in the alpine regions but rarely in the North German lakes (e.g., *Achnanthidium rosenstockii*, *Navicula subalpina*) and some are common in the latter area (e.g., *Cocconeis neothumensis*, *Cymbellafalsa diluviana*, *Planothidium joursacense*) (Hofmann et al., 2011).

3.5.2. Temporal and spatial patterns

In species richness and composition of diatom communities, significant temporal differences were found, which is probably due to the distinct sampling season (spring and autumn). Seasonal succession of phytoplankton in freshwater ecosystems (e.g., Padisák et al., 2006) is typically characterized by a spring diatom bloom and a less intense autumn bloom (e.g., Hinder et al., 1999; Simona et al., 1999). In Lake Stechlin, an explicit spring maximum and a moderate summer maximum of phytoplankton biomass can be observed. In addition to the autotrophic picoplankton, centric diatoms are prominent in the spring phytoplankton maximum, which starts to develop in early March and reaches a peak early in May. When water column stratification begins, biomass rapidly declines because diatoms sink to the hypolimnion (Scheffler & Padisák, 1997; Padisák et al., 1998). At the beginning of May 2013, a considerable proportion of Mediophyceae taxa were observed in the epilithic diatom samples due to the dominance of *Stephanodiscus rugosus* and *Stephanodiscus neoastraea*. *Stephanodiscus* species are considered to be among the most frequent diatoms in the spring phytoplankton bloom in Lake Stechlin (Padisák et al., 1998, 2003, 2010; Selmeczy et al., 2016). *Stephanodiscus minutulus* was commonly observed in the phytoplankton of Lake

Stechlin (Padisák et al., 1998, 2003). Its variable outline of areolae (often slit-like) and in many cases flat valve face surface was described in previous studies (e.g., Scheffler & Morabito, 2003; Cruces et al., 2010), whose features correspond to the morphological characteristics of *Stephanodiscus rugosus* described in Siemińska & Chudybowa (1979). Even nowadays, the differentiation between *S. minutulus* and *S. rugosus* is disputed. However, according to some taxonomists (e.g., Casper et al., 1988) *S. minutulus* and *S. rugosus* are considered identical, while Houk et al. (2014) regarded them as two different species. Moreover, molecular evidence does not prove the difference, thus not solving the confusion in the literature concerning these species.

Seasonal dynamics of littoral benthic diatoms are poorly described (Cantonati & Lowe, 2014); the results have quite dissimilar patterns. Several studies proved clear seasonal patterns of diatom communities (Barbiero, 2000; Rimet et al., 2015), while others did not find any explicit seasonal succession (Jones & Flower, 1986; Nygaard, 1994). In turn, biomass of benthic diatoms in Lake Erken varied seasonally and variation in species composition was strongly related to nutrient conditions and wind (Kahlert et al., 2002). In temperate lakes where temporal changes in littoral benthic diatoms are typical, the appropriate sampling frequency representative for the whole lake must be carefully chosen. In Germany, the Water Framework Directive guideline for monitoring phytobenthos calls attention to a potentially high percentage of planktonic diatoms and suggests excluding these species from counting (Schaumburg et al., 2014). Since the samples taken in spring 2013 contained a considerable amount of planktonic diatoms, sampling from Lake Stechlin for ecological quality assessment in this season is not suggested.

Rimet et al. (2015) supposed that the homogeneous or heterogeneous manner of benthic diatom communities can be affected by the size of the lake. In large lakes like Lake Balaton and Lake Geneva (Crossetti et al., 2013; Rimet et al., 2016) heterogeneity of littoral benthic communities was reported, which can be attributed to human impact, shore morphology (Snell & Irvine, 2015), or river inlets (i.e., point source of contaminants) (King et al., 2006; Rimet et al., 2016). On the other hand, waves can play an important role in the development of benthic communities in the wind-exposed littoral zone and makes them much more heterogeneous (Cantonati & Lowe, 2014). In contrast, as Lake Stechlin has a relatively small surface area and the anthropogenic impact is negligible, diatom communities of the epilithon were assumed to be homogeneous along the shoreline. The results of this study partly confirmed this expectation and the observations by King et al. (2002, 2006), since α-diversity (species richness and Shannon diversity) and community composition did not show any differences between the basins. However, β-diversity enhanced by species replacement among sampling sites was relatively high within the lake, no matter that the species' abundance was considered or their incidence only. Environmental heterogeneity assessed by the mean Euclidean distance of standardized environmental variables was small, the measured physical parameters (conductivity, pH, temperature) showed negligible variation among the 23 sampling sites, and change of TP and TN covered only a relatively small range of these nutrient forms' gradient. According to variation partitioning, the explained variation in communities was mostly related to spatially structured environmental differences. Nevertheless, a huge proportion of variances remained unexplained which might be the result of several processes. For instance, there might be unmeasured environmental variables that are important in terms of community development or rare species that were not collected during the sampling (Leibold & Chase, 2018). Stochasticity can also play an important role in metacommunities and it can appear at two scales. On the one hand, at the scale of individuals (demographic stochasticity) when change of birth and death rates might result in the spatial and temporal drift in relative abundances of individuals. This can occur when community size decreases below a certain threshold (Yu et al., 2001). On the other hand, stochasticity can appear at patch scale (patch stochasticity or colonization-extinction stochasticity) when a species has a finite probability of going extinct and colonizing an unoccupied patch in any time period (Leibold & Chase, 2018). In addition, residual variance might comprise latent variance due to correlations among species which can explain even 50% of the entire variance (Leibold & Chase, 2018).

Consequently, environmental variables showed moderate spatial change in the littoral region, which might have caused dissimilarities of diatom species composition. However, species represented similar autecological preferences, and neither α-diversity nor composition of the communities was unique in the three basins. Hence, for national monitoring surveys concerning benthic diatoms of Lake Stechlin, King et al.'s (2006) suggestion can be supported that for financial and practical reasons, sampling of benthic diatoms from the littoral region in a single site per lake is recommended.

4. Benthic diatom metacommunities across natural and reconstructed soda pans in the Carpathian Basin[2]

4.1. Introduction

Inland saline lakes develop typically in endorheic basins (closed drainage basins that retain water) of arid or semi-arid areas, where precipitation and evaporation are unbalanced (Williams, 2002). Limnological characteristics of small (< 50 ha), shallow (< 1 m) saline lakes are determined by the degree of precipitation and evaporation (Langbein, 1961), geomorphology (Dargám, 1995) and geochemistry (Simon et al., 2011). Soda lakes (or soda pans) can be distinguished as a specific group of saline lakes with high alkalinity and a dominance of sodium, carbonate and hydrogen carbonate ions (Boros et al., 2013). Soda pans respond sensitively even to relatively small fluctuations of weather and climate, which may result in irreversible changes in their natural properties (Hammer, 1990). Since they are hydrologically sensitive, soda lakes are especially vulnerable and there is an urgent need for conservation management, which focuses on the maintenance or restoration of their natural hydrological cycles (Boros et al., 2013; Stenger-Kovács et al., 2014; Lengyel et al., 2016).

Diatoms have short generation times (Rott, 1991) and respond rapidly to environmental changes. In alkaline, saline lakes diatoms have a competitive advantage over other algal groups as many diatom species can tolerate the extreme conditions due to, for example, their ability to osmoregulation, phenotypic plasticity and secondary photoprotective pigments (Krumbein et al., 1977; Bauld, 1981; Kirk, 1994), hence they may become dominant. The strong relationship between diatom communities and the main environmental variables supports the use of diatoms for tracking changes in the limnological features of soda pans (Stenger-Kovács et al., 2014).

Additionally, soda pans are considered as early warning indicators of both anthropogenic pollution and habitat restoration management (Smol & Stoermer, 2010). To improve ecological status assessment and efficiency of conservation management of these unique water bodies, a continuous monitoring of diatoms, and their application as bioindicators is highly recommended (Stenger-Kovács et al., 2014).

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[2] A part of this chapter was published in the following paper:
Szabó, B., Lengyel, E., Padisák, J., Vass, M. & Stenger-Kovács, C. (2018). Structuring forces and β-diversity of benthic diatom metacommunities in soda pans of the Carpathian Basin. European Journal of Phycology, 53: 219–229.

Studies of diatoms in soda pans of Central Europe have focused mostly on revealing the relationship between the water chemistry and the community composition (Stenger-Kovács et al., 2014, 2016; Lengyel et al., 2016). However, structuring forces of diatom communities in space and time have not been investigated in such ecosystems so far, probably because this is a new and rapidly developing area in ecology.

In general, different processes can influence community structure, for instance environmental filtering, dispersal-related processes, species interactions and ecological drift which can be resulted from demographic stochasticity and colonization-extinction stochasticity. The metacommunity framework (Leibold et al., 2004) provides an approach to investigate the dynamics of local communities that are linked by the dispersal of species within a region, forming a metacommunity. The framework involves four different perspectives concerning the relative importance of local and regional processes (Fig. 2), which help understanding of the mechanisms supporting β-diversity. β-diversity refers to the variation in community composition among sampling units within a region due to the species replacement and/or the richness differences along environmental, spatial or temporal gradients.

Areas with high β-diversity might have high conservation value and their preservation is essential even if the single sites have low species richness, since they can host a variety of species assemblages and their high community variation is strongly related to habitat heterogeneity (Whittaker, 1960, Manthey & Fridley, 2009). Thus, β-diversity studies provide valuable information for developing conservation strategies and also contribute to preserving the high conservation value of heterogeneous habitats (Condit et al., 2002).

4.2. Aims

In this study, the goals were (i) to assess the overall β-diversity of two spatially separated benthic diatom metacommunities in soda pans located in different parts of the Carpathian Basin (Fertő-Hanság region and Danube-Tisza Interfluve), and (ii) to determine the driving forces of β-diversity in regions with distinct physical and chemical features and diatom communities, at both spatial and temporal scales. More specifically, it was examined whether dissimilarities are attributable mainly to species replacement or to emergence of species subsets, and on the role of deterministic/stochastic processes in establishment of β-diversity and its components (thus in establishment of communities as well). Furthermore, the results in the context of conservation/restoration management will be discussed.

4.3. Material and Methods

4.3.1. Study areas

There are two regions in the Carpathian Basin where *ex lege* protected (Magyar Közlöny, 1996) soda pans can be found: one is in the Kiskunság National Park in the Danube-Tisza Interfluve and the other area is located around Lake Fertő/Neusiedlersee in the Fertő-Hanság National Park. These water bodies are endorheic, shallow waters with Secchi transparency of only a few centimetres (Horváth et al., 2013), pH of 9–10 (Stenger-Kovács et al., 2014), very high conductivity (may exceed 70,000 µS cm^{-1}, Boros et al., 2014) and daily temperature fluctuation (nearly 20°C, Vörös & Boros, 2010). Despite these similarities, the two main hydrological basins (Danube-Tisza Interfluve and Fertő-Hanság) differ substantially in regard to some physical and chemical parameters and in the biota of the pans (Stenger-Kovács et al., 2014). The water supply of soda pans in the Danube-Tisza Interfluve is provided by saline water from deep-layer aquifers (Mádl-Szőnyi & Tóth, 2009) and precipitation, therefore their hydrological sensitivity is very high (Hammer, 1990). In the Danube-Tisza Interfluve, soda pans have either natural or degraded status. In this study, only natural soda pans were sampled in this region. In contrast, all soda pans sampled in the Fertő-Hanság region (at the Hungarian side of Lake Fertő) are under habitat reconstruction (Boros et al., 2013) with the aim to ensure sufficient aquatic areas for migratory and nesting waterfowl. However, recent studies conducted on different organisms (Tóth et al., 2014; Lengyel et al., 2016) emphasized that the current condition of these reconstructed soda pans is far from the natural: they have worse ecological status than the reference pans which are located at the Austrian side of Lake Fertő.

4.3.2. Sampling and processing of samples

Benthic diatom samples were collected from soda pans in two different parts of the 'Hungarian lowlands' ecoregion: Fertő-Hanság (FH) and Danube-Tisza Interfluve (DT) (Fig. 8). Sampling was conducted monthly in the Fertő-Hanság region from three reconstructed pans between July 2013 and August 2014, and in the Danube-Tisza Interfluve from six pans in natural status between August 2014 and July 2015. In case when a pan was inaccessible for sampling or was completely dried out, samples could not be collected. Sampling sites, their GPS coordinates and the sample numbers are summarized in Appendix 6. Since both regions' data set included soda pans from one type of ecological status (i.e., only reconstructed pans were sampled in the FH region and only natural pans in the DT region), the two variables (region and the ecological status in the given region) were treated as associated with each other.

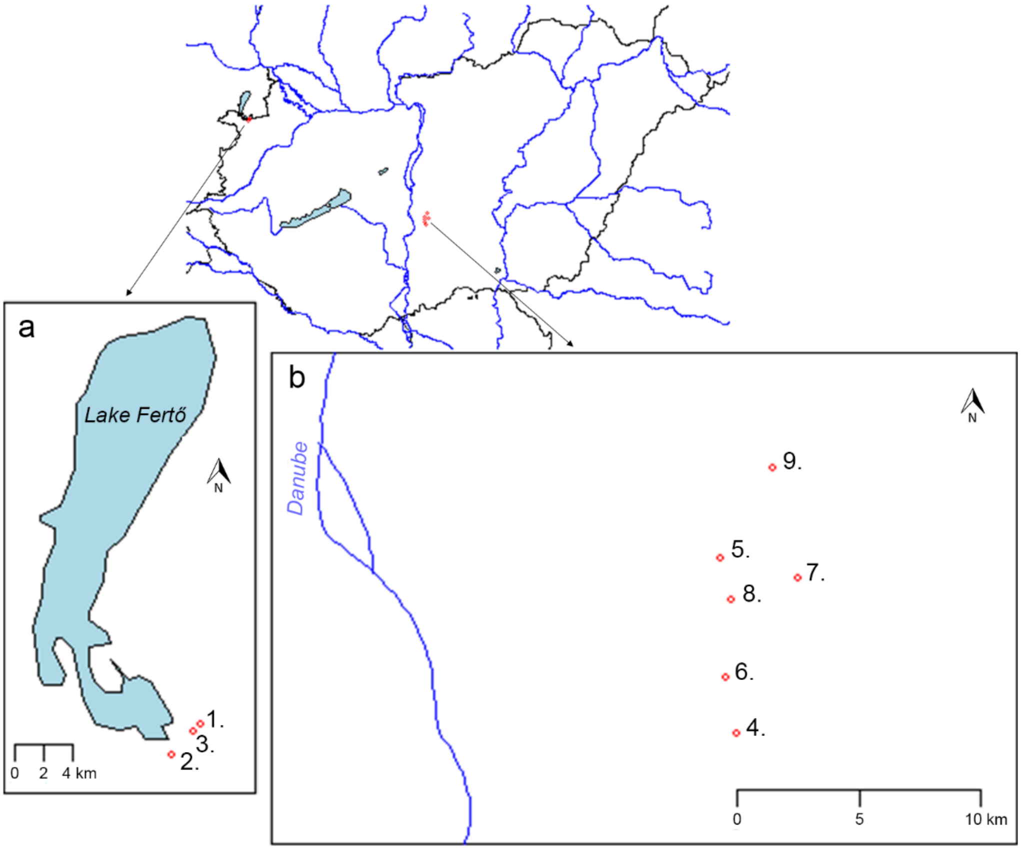

Figure 8 *Sampling sites in the Fertő-Hanság region (a) and in the Danube-Tisza Interfluve (b). Soda pan numbers are listed in Appendix 6.*

Epipelic samples were collected from mud (King et al., 2006) in the littoral region where the water depth varied between 5–10 cm. Preparation of diatom samples and light microscopic analysis followed the method detailed in Chapter 3.3.2. Small taxa were investigated with a Hitachi S-2600 N scanning electron microscope. Standard and specific taxonomic guides (Krammer & Lange-Bertalot, 1991, 1999a, 1999b, 2000; Witkowski et al., 2000; Krammer, 2000, 2002, 2003; Lange-Bertalot, 2001; Taylor et al., 2007; Levkov, 2009; Hofmann et al., 2011; Lange-Bertalot et al., 2011; Bey & Ector, 2013; Levkov et al., 2013; Stenger-Kovács & Lengyel, 2015) were used to identify diatoms at species level.

4.3.3. Analysis of physical and chemical parameters

During the sampling, conductivity, oxygen saturation (DO%), pH and water temperature were measured *in situ* with an HQ40d Hach Lange multimeter. Light irradiance (LI) was measured by a LI 1400 (LI-COR) apparatus equipped with a 143 spherical (4π) quantum micro sensor (US-SQS/L, Heinz Walz GmbH) directly above the epipelon in the shoreline. Water samples for laboratory analyses were also collected. Concentration of SRSi (Wetzel & Likens, 2000), SO_4^{2-}, nitrogen forms (NO_2^-, NO_3^-, NH_4^+), soluble reactive (SRP) and total phosphorus (TP) were measured with spectrophotometry (APHA, 1998) using a Metertech UV/VIS Spectrophotometer, SP8001. CO_3^{2-}, HCO_3^-, Cl^-, and COD were measured with titrimetric methods (APHA, 1998). To assess the amount of humic substances, intensity of the brown colour in platinum (Pt) units was determined according to Cuthbert & del Giorgio (1992).

4.3.4. Statistical analyses

Abundance- and incidence-based β-diversity were assessed by multiple-site Bray-Curtis dissimilarity (β_{BC}) and multiple-site Sørensen dissimilarity index, respectively. The former was partitioned into its abundance balanced variation ($\beta_{BC.BAL}$) and abundance gradients ($\beta_{BC.GRA}$) component (Baselga, 2017), and the latter into its turnover (β_{SIM}) and nestedness (β_{NES}) component (Baselga et al., 2007; Baselga, 2010).

Relationship of abundance balanced variation ($\beta_{bray.bal}$) and abundance gradient ($\beta_{bray.gra}$) as well as turnover (β_{sim}) and nestedness (β_{nes}) components to overall β-diversity values expected ‘under’ and ‘beyond’ random community assemblage given an Equiprobable-Fixed (EF) null model was investigated (Ulrich & Gotelli, 2007). At first, for the observed data sets, overall β-diversity was computed using pairwise dissimilarity indices: Bray-Curtis (β_{bray}) index for abundance and Sørensen (β_{sor}) index for incidence data. These were partitioned into $\beta_{bray.bal}$ and $\beta_{bray.gra}$, and into β_{sim} and β_{nes} following Baselga’s frameworks (Baselga, 2010, 2013b) in both regions. Then, EF null models were implemented to randomize the observation data matrix to generate ‘null’ communities (permutations = 1000) using the permatfull function in the vegan R package (Oksanen et al., 2017). At the EF null models, observed species richness of sites were maintained (r0 algorithm) during the randomization and sample species from the regional species pool equiprobably. Then, pairwise Bray-Curtis and Sørensen dissimilarity indices were calculated for each of the 1000 null matrices and their mean was computed ($\beta_{bray\text{-}null}$ and $\beta_{sor\text{-}null}$). The differences between the observed β-diversity (β_{bray} and β_{sor}) and β-diversity derived from null communities ($\beta_{bray\text{-}null}$ and $\beta_{sor\text{-}null}$) were quantified ($\beta_{bray\text{-}diff} = \beta_{bray} - \beta_{bray\text{-}null}$ and $\beta_{sor\text{-}diff} = \beta_{sor} - \beta_{sor\text{-}null}$), thereby the β-diversities independent of and beyond random chance were determined. To explore the relationship of the overall β-diversities (β_{bray}, β_{sor}) and their components ($\beta_{bray.bal}$, β_{sim} and

$\beta_{bray.gra}$, β_{nes}) with the expected β-diversities under ($\beta_{bray\text{-}null}$, $\beta_{sor\text{-}null}$) and beyond ($\beta_{bray\text{-}diff}$, $\beta_{sor\text{-}diff}$) null models, significances of the Pearson correlations were computed using Mantel permutation tests (permutations = 999). The applied null model analyses quantify the extent to which the dissimilarities among the observed communities differ from the random expectations, that is, from the dissimilarities obtained by randomizing the observed data. Thereby, they can provide an insight into whether the observed diatom communities are assembled by deterministic or stochastic processes or by both. The significant correlation between observed β-diversity values (as well as its components) and β-diversity values of randomized communities ($\beta_{bray\text{-}null}$, $\beta_{sor\text{-}null}$) indicates that communities are driven predominantly by stochastic processes (ecological drifts resulted from demographic and colonization-extinction stochasticity). However, in case of significant correlation between observed β-diversity and β-diversity deviates from the random expectations ($\beta_{bray\text{-}diff}$, $\beta_{sor\text{-}diff}$), the primary role of non-random (deterministic) processes is suspected (Azeria et al., 2011).

Environmental heterogeneity of both regions was assessed by computing a mean Euclidean distance for all standardized environmental variables.

The effect of environmental variables and the spatial and temporal variation on establishment of diatom communities was quantified for both regions. Estimates were carried out for Hellinger-transformed relative abundance (Legendre & Gallagher, 2001; Borcard et al., 2011) and presence-absence data. Prior to the final statistical analyses, a model selection procedure of redundancy analysis (RDA) (each term analyzed sequentially from first to last) was conducted using analysis of variance (ANOVA) to determine which physical and chemical parameters affect significantly the variance of diatom communities. During the subsequent analyses, these factors were included in the group ‘environmental variables’. All other physical and chemical parameters were eliminated. Before conducting RDA, all environmental factors were standardized). In the group ‘spatial distance’, distance-based Moran’s eigenvectors (dbMEMs) were involved computed by principal coordinate analysis (PCoA) of a truncated geographic distance matrix (Borcard & Legendre, 2002; Borcard et al., 2004). For dbMEM analysis and PCoA, codep (Guenard et al., 2017) and ape (Paradis et al., 2004) packages were used. For ‘temporal variation’, date of each sampling was converted to Julian day (i.e., to continuous count of days since the beginning of the Julian Period which makes easy the calculation of elapsed days between two events) and used as explanatory variables. Variation partitioning was conducted to reveal the importance of pure and shared effects of the three explanatory variable groups (environmental, spatial, temporal) on the variance of diatom communities, resulting in a total of seven fractions and residuals indicating the unexplained variance (Anderson & Gribble, 1998). Significance of adjusted R^2 values provided by variation partitioning for testable fractions (pure environmental, spatial and temporal effect) was determined with ANOVA (permutations = 999) of RDA models (Peres-Neto et al., 2006). Variation partitioning was performed with the varpart function in the vegan R package (Oksanen et al., 2017).

Since the representation of the spatial and temporal scales (and thereby the representation of the spatial and temporal β-diversity as well) was different in the two regions' data set, β-diversity and the drivers of metacommunities were investigated on two data subsets where the representation of the spatial and temporal scales is similar. The subset of the FH region's data included the samples collected monthly between 28 February 2014 and 28 July 2014 from Legény-tó, Borsodi-dűlő and Nyéki-szállás (n=18). To create the DT region's subset of data, four soda pans located at a similar distance from each other were selected (Bogárzó-szék, Böddi-szék, Kelemen-szék, Zab-szék) and samples collected monthly between 25 February 2015 and 29 July 2015 were considered (n=20). Bogárzó-szék in February and in March, Zab-szék in February and Kelemen-szék in July could not be sampled due to inaccessibility or to drying out of the pan.

For partitioning the variation in community dissimilarities of the data subsets, permutation-based (permutations = 1000) multiple regressions on distance matrices (MRM) (Legendre et al., 1994; Lichstein, 2007) were used. The following seven models were built: where (i) environmental distances (E), (ii) spatial distances (S), and (iii) temporal distances served as explanatory matrices separately; where (iv) environmental and spatial distances (E+S), (v) environmental and temporal distances (E+T), and (vi) spatial and temporal distances (S+T) were applied; and where (vii) all three groups of matrices were combined (E+S+T). In MRM analyses, pairwise Bray-Curtis indices computed for Hellinger-transformed abundance data and for presence-absence data separately were used as response distance matrices. Euclidean distances of the standardized environmental parameters selected using BIOENV approach (Clarke & Ainsworth, 1993) were applied as 'environmental distances' in MRM models. The 'spatial distances' were created by calculating pairwise geographic distances with earth.dist function of fossil R package (Vavrek, 2011). After transforming the sampling dates to Julian days, pairwise temporal distances (i.e., the days elapsed between two samplings) were computed and used as explanatory matrix in MRM analyses. The proportion of variance in community dissimilarities explained by the pure and shared fractions of environmental, spatial and temporal distances and the unexplained variation was calculated based on the R^2 values resulted from the MRM models (Jones et al., 2006). Variation partitioning computations were described in Appendix 7.

All statistical analyses were carried out separately for the two regions and were performed in R statistical and computing environment (R Development Core Team, 2017).

4.4. Results

A total of 163 diatom species were identified in the Fertő-Hanság (FH) region (n=29) and 117 in the Danube-Tisza (DT) Interfluve (n=47). Species richness per sample varied between 15 and 57 (mean and standard deviation: 34±11) in the FH region, and between 2 and 32 (mean and standard deviation: 17±7) in the DT region. Dissimilarity according to the abundance- and incidence-based multiple-site framework was fairly high in both regions (β_{BC} and β_{SOR} >0.90). Patterns of β-diversity in the epipelon were mainly attributed to the species replacement components ($\beta_{BC.BAL}$ and β_{SIM}), and subset components ($\beta_{BC.GRA}$ and β_{NES}) were considerably lower (Table 4). After limiting the total datasets in space and time, 143 species (mean and standard deviation: 35±12) were found in the FH region between February and July 2014, and 66 (mean and standard deviation: 15±6) in the DT region between February and July 2015. Compared to the one-year periods, overall β-diversity values did not reduce markedly in case of the data subsets and they were enhanced mainly by the species replacement components (Appendix 8).

Table 4 *β-diversity and its components of benthic diatom communities in the Fertő-Hanság region and in the Danube-Tisza Interfluve (β_{BC} = overall dissimilarity measured as Bray-Curtis multiple-site dissimilarity, $\beta_{BC.BAL}$ = balanced variation component, $\beta_{BC.GRA}$ = abundance gradient component, β_{SOR} = overall dissimilarity measured as Sørensen dissimilarity, β_{SIM} = turnover component, β_{NES} = nestedness component).*

		Fertő-Hanság (n = 29)	**Danube-Tisza Interfluve (n = 47)**
abundance-based β-diversity	β_{BC}	0.938	0.957
	$\beta_{BC.BAL}$	0.932	0.954
	$\beta_{BC.GRA}$	0.006	0.003
incidence-based β-diversity	β_{SOR}	0.902	0.942
	β_{SIM}	0.857	0.909
	β_{NES}	0.046	0.033

In the FH region, the abundance-based overall β-diversity (β_{bray}) and its balanced variation component ($\beta_{bray.bal}$) were positively correlated both to the expected β-diversity under ($\beta_{bray\text{-}null}$) and beyond ($\beta_{bray\text{-}diff}$) null model, however, the correlations with $\beta_{bray\text{-}diff}$ were much stronger (Fig. 9a-d). The abundance gradient component ($\beta_{bray.gra}$) was not related either to $\beta_{bray\text{-}null}$ or to $\beta_{bray\text{-}diff}$ (Fig. 9e, f).

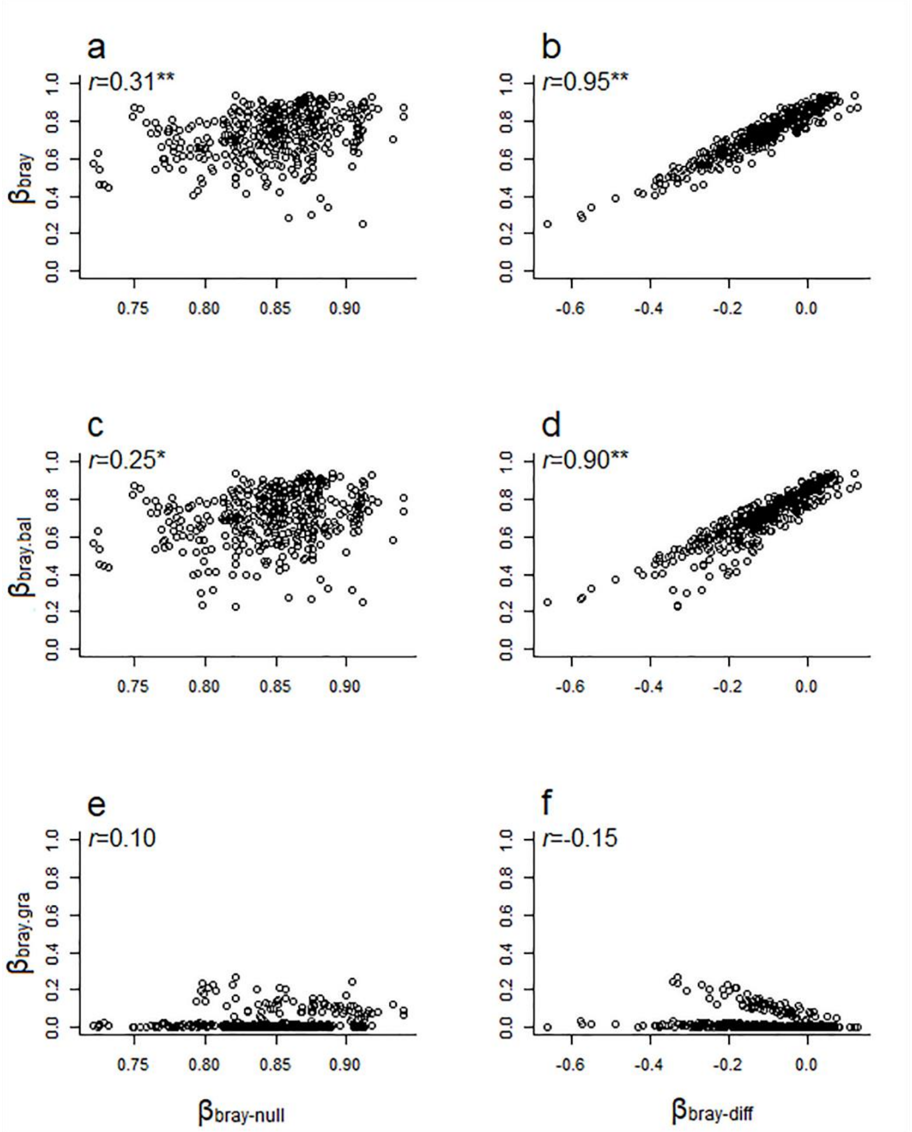

Figure 9 *The relationship of abundance-based overall β-diversity (β_{bray}; a, b), and its balanced variation ($\beta_{bray.bal}$; c, d) and abundance gradient ($\beta_{bray.gra}$; e, f) components with the overall β-diversity expected under ($\beta_{bray\text{-}null}$; a, c, e) and beyond null model ($\beta_{bray\text{-}diff}$; b, d, f) in the Fertő-Hanság region. Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance levels: ** = 0.01, * = 0.05.*

In contrast to the abundance-based analyses, neither the incidence-based total β-diversity (β_{sor}) nor its turnover component (β_{sim}) was related to the β-diversity values expected under the null model ($\beta_{sor\text{-}null}$), but they were strongly positively correlated to that of deviations beyond null model expectations ($\beta_{sor\text{-}diff}$) (Fig. 10a-d). The nestedness component (β_{nes}) did not display a significant relationship either with $\beta_{sor\text{-}null}$ or with $\beta_{sor\text{-}diff}$ (Fig. 10e, f).

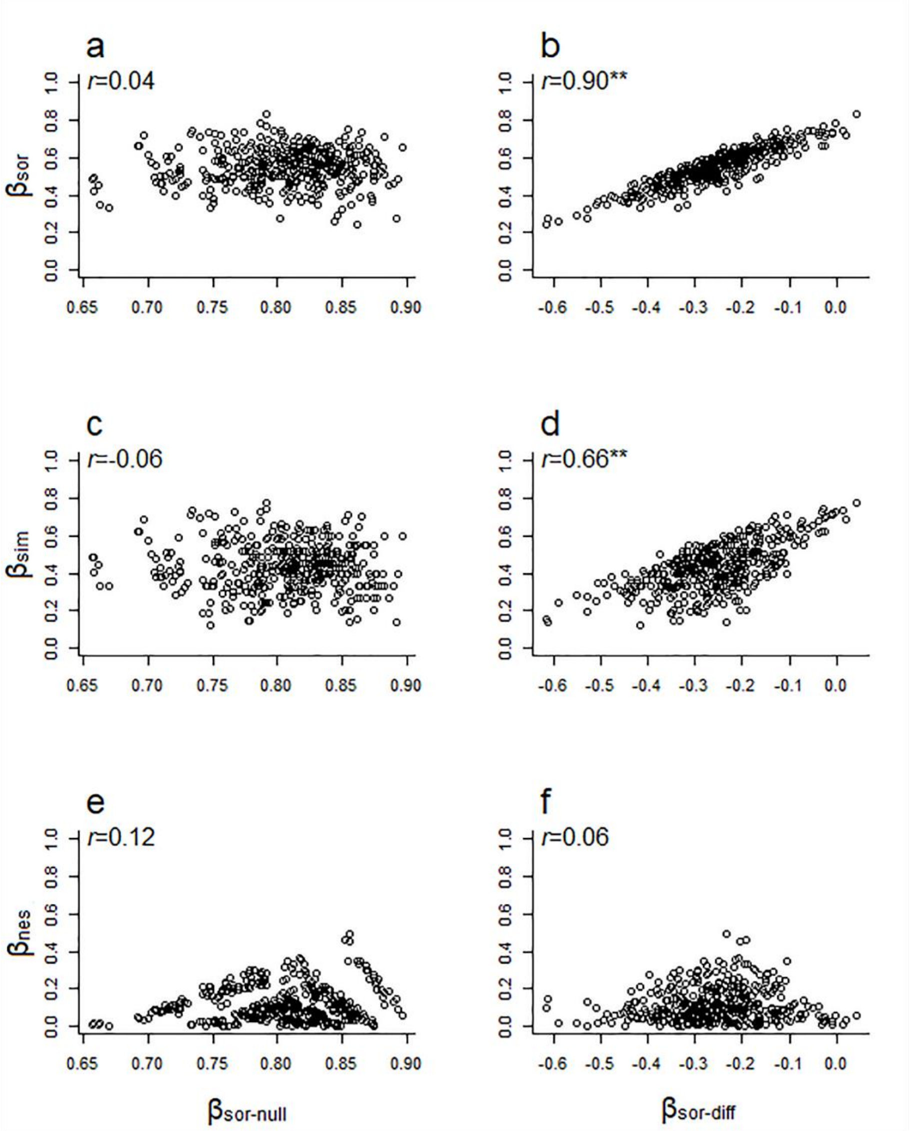

Figure 10 *The relationship of incidence-based overall β-diversity (β_{sor}; a, b), and its turnover (β_{sim}; c, d) and nestedness (β_{nes}; e, f) components with the overall β-diversity expected under ($\beta_{sor\text{-}null}$; a, c, e) and beyond null model ($\beta_{sor\text{-}diff}$; b, d, f) in the Fertő-Hanság region. Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance level: ** = 0.01.*

In the DT region, although both β_{bray} and $\beta_{bray.bal}$ were strongly correlated to $\beta_{bray\text{-}diff}$, they were not related significantly to $\beta_{bray\text{-}null}$ (Fig. 11a-d). However, similarly to the FH region, the relationship of $\beta_{bray.gra}$ with $\beta_{bray\text{-}null}$ and $\beta_{bray\text{-}diff}$ was not significant (Fig. 11e, f).

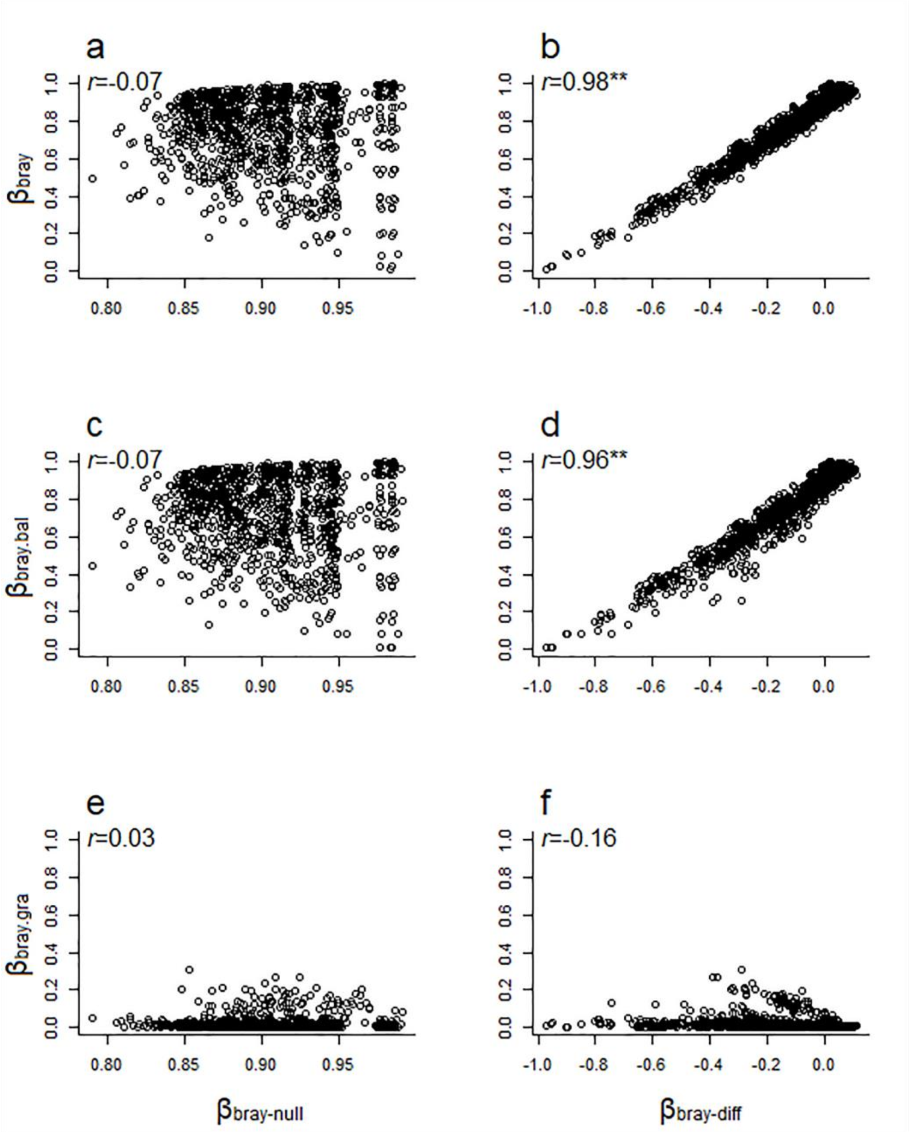

Figure 11 *The relationship of abundance-based overall β-diversity (β_{bray}; a, b), and its balanced variation ($\beta_{bray.bal}$; c, d) and abundance gradient ($\beta_{bray.gra}$; e, f) components with the overall β-diversity expected under ($\beta_{bray\text{-}null}$; a, c, e) and beyond null model ($\beta_{bray\text{-}diff}$; b, d, f) in the Danube-Tisza Interfluve. Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance level: ** = 0.01.*

Incidence-based calculations showed that β_{sor} values were significantly correlated to the predictions of the null model ($\beta_{sor\text{-}null}$) but β_{sor} showed a considerably stronger relationship with the residuals ($\beta_{sor\text{-}diff}$) (Fig. 12a, b). Regarding the turnover component, similar results were found as in the FH region: β_{sim} was strongly correlated to $\beta_{sor\text{-}diff}$ and it displayed a non-significant relationship with $\beta_{sor\text{-}null}$ (Fig. 12c, d). The nestedness component (β_{nes}) was related significantly both to $\beta_{sor\text{-}null}$ and $\beta_{sor\text{-}diff}$, but the positive correlation was stronger with the null expectations ($\beta_{sor\text{-}null}$) (Fig. 12e, f).

Conducting null model analyses on data subsets changed the results in the FH region at some points (Appendix 9, 10): in case of abundance-based indices, β_{bray} and $\beta_{bray.bal}$ were significantly correlated only to β-diversity of deviations beyond null model expectations ($\beta_{bray\text{-}diff}$), and in case of incidence-based analyses, the nestedness component (β_{nes}) showed a significant but relatively weak relationship with $\beta_{sor\text{-}null}$. In the DT region, results were not modified considerably compared to the results for total data set (Appendix 11, 12).

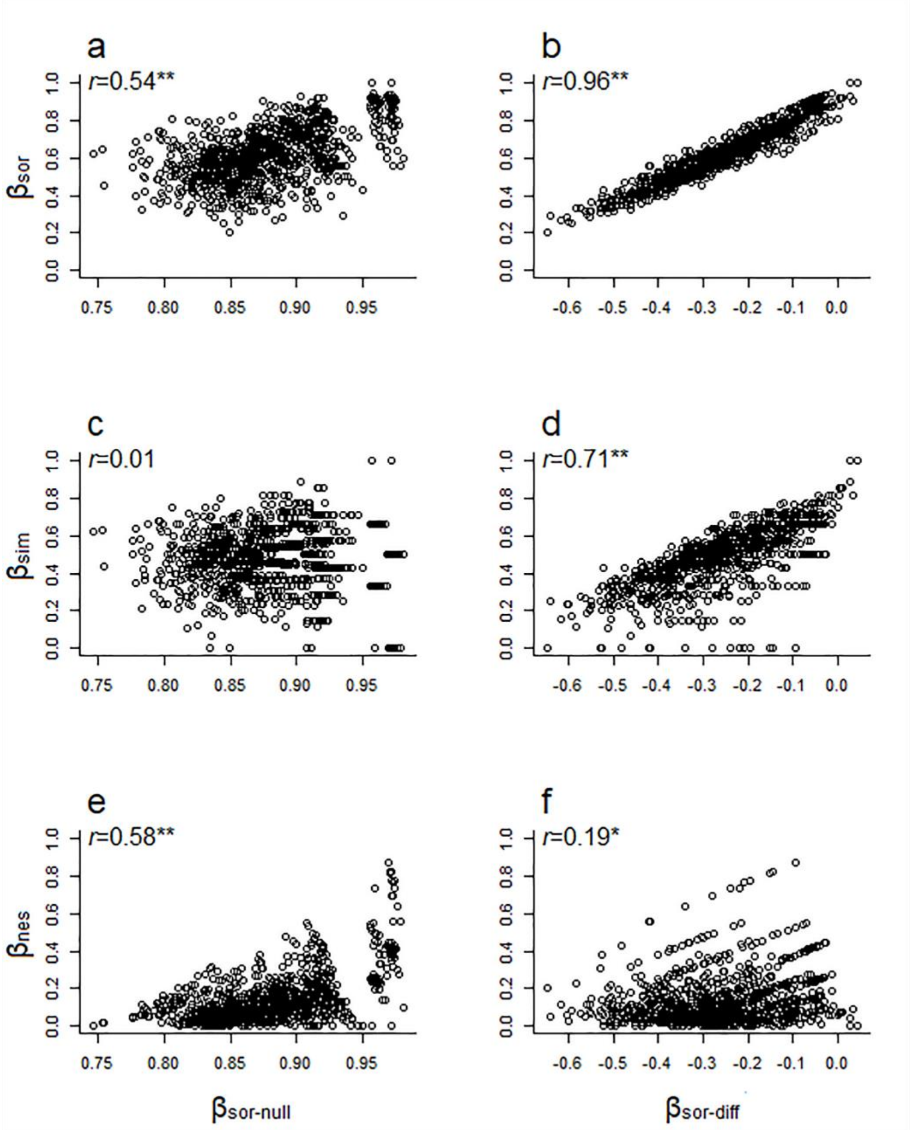

Figure 12 *The relationship of incidence-based overall β-diversity (β_{sor}; a, b), and its turnover (β_{sim}; c, d) and nestedness (β_{nes}; e, f) components with the overall β-diversity expected under ($\beta_{sor\text{-}null}$; a, c, e) and beyond null model ($\beta_{sor\text{-}diff}$; b, d, f) in the Danube-Tisza Interfluve. Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance levels: ** = 0.01, * = 0.05.*

The mean Euclidean distance of standardized environmental variables was 5.55 in the FH region and 5.32 in the DT region. The model selection procedure displayed a significant impact of SRP (Df=1, F=1.836, $P<0.05$) and SRSi (Df=1, F=1.724, $P<0.05$) in the FH region and that of COD (Df=1, F=2.7401, $P<0.01$), NO_3^- (Df=1, F=3.2104, $P<0.01$), CO_3^{2-} (Df=1, F=3.2473, $P<0.01$) and Cl^- (Df=1, F=2.6031, $P<0.05$) in the DT region. Variation partitioning for both regions revealed that establishment of community structure using either abundance or presence-absence data was related mainly to the pure environmental effect, which was significant in each case but explained a higher proportion of the variations in diatom communities in the DT (16% and 7.1%) than in the FH region (5.6% and 2.3%). In the FH region, the pure temporal variation also had a significant impact on the community structures, however, the explained variation was lower (3.9% and 2.2%). All the other fractions (pure and shared) of explanatory data sets were negligible in terms of variance explanation. In all models presented, variation in community structure was not fully explained, leaving a considerable portion of residuals unexplored. Furthermore, the amount of unexplained variation was higher using presence-absence data in both regions (Fig. 13).

According to BIOENV approach applied for the subsets of species abundance data in the FH region, the best subset of environmental variables (that showed the maximum Pearson correlation with community dissimilarities, $r_{ab}=0.39$, $P_{ab}<0.01$) consisted of only water temperature. However, sampling was conducted not at the same time of day in each case and the resulting differences in water temperature can not be excluded completely. In my opinion, subsequent MRM analyses would have led to deceptive results if temperature differences alone had been applied as explanatory distance matrix. Therefore, in this case, a subset of environmental parameters that showed the second highest correlation with community dissimilarities was used instead of the best subset. This subset contained SRSi and temperature ($r_{ab}=0.36$, $P_{ab}<0.01$). In the DT region, the best model included COD, CO_3^{2-}, temperature and pH. ($r_{ab}=0.39$, $P_{ab}<0.05$). For subsets of presence-absence data, the best model consisted of SRSi, temperature, conductivity and Pt colour in the FH region, whereas CO_3^{2-}, HCO_3^-, Cl^-, temperature and conductivity in the DT region. Similarly to the abundance-based results, community dissimilarity matrices and distance matrices of the best models were correlated significantly (FH region: $r_{p\text{-}a}=0.32$, $P_{p\text{-}a}<0.01$; DT region: $r_{p\text{-}a}=0.64$, $P_{p\text{-}a}<0.01$). Each MRM model regarding abundance data subset in the FH region which consisted of environmental and temporal distances individually or any combination of environmental, spatial and temporal distances was significant. However, when only spatial distance matrix was considered, the proportion of explained variation was statistically not significant. In case of incidence-based analyses, MRM displayed a marginally non-significant relationship between environmental distances and community dissimilarities, all other MRM models were not significant. In the DT region, variation in abundance-based community dissimilarities was explained significantly by the MRM model included either environmental and temporal distances as independent explanatory matrices or the combination of environmental and spatial distance matrices as well as that of spatial and temporal distance matrices. All other models were marginally non-significant or not significant. In contrast, each MRM model concerning incidence-based community dissimilarities in this region was statistically significant. Results of each MRM were summarized in Appendix 13. Variation partitioning calculations conducted for both regions' data subset showed that the explained variation in community dissimilarities between February and July was primarily related to the pure environmental distances or to the temporally structured environmental differences. Furthermore, in contrast to the variation partitioning results for the one-year period data set, the effect of pure temporal distances on community dissimilarities was negligible in the FH region. In each case, the variation explained by pure spatial distances or by spatially structured environmental differences was negligible, as well. The proportion of unexplained variances were relatively high; however, a remarkable decrease of residual variation was observed in case of the DT region's presence-absence data subset compared to those found for the entire data. Results of variation partitioning carried out for data subsets based on Jones et al.'s (2006) suggestions are presented in Appendix 14.

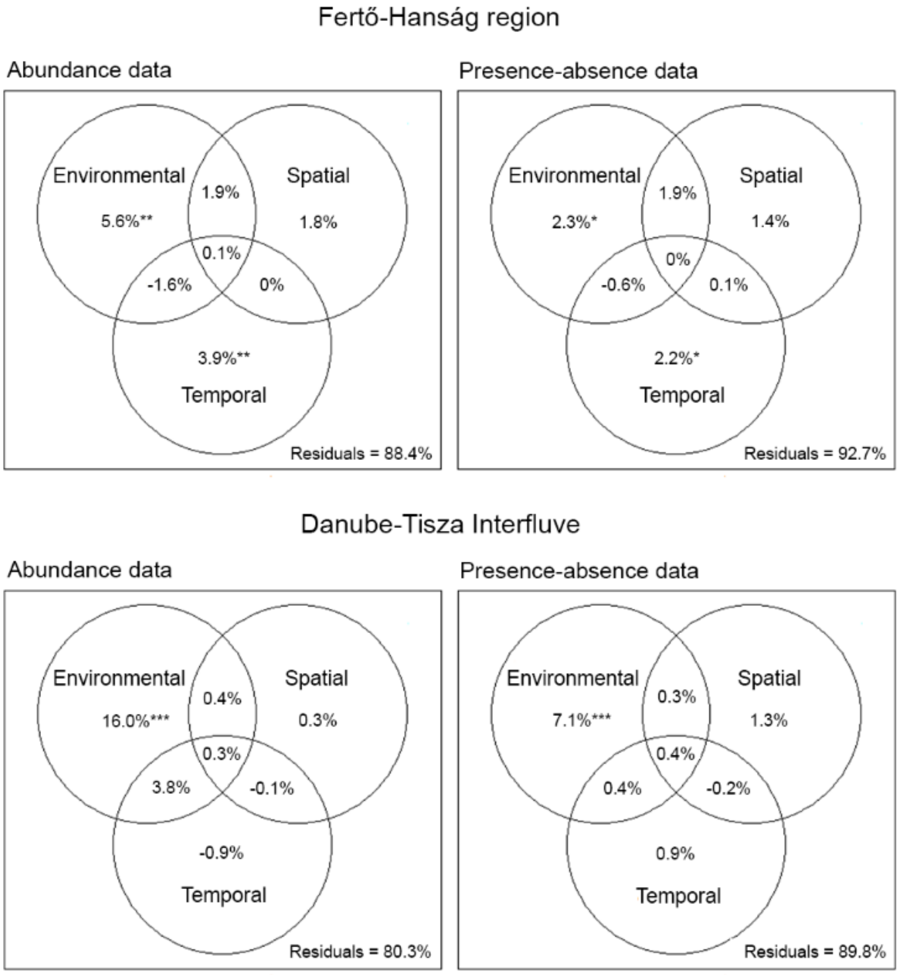

Figure 13 *Results of variation partitioning for Hellinger-transformed relative abundance and presence-absence data in the Fertő-Hanság region and in the Danube-Tisza Interfluve. Fractions are shown as percentages of total variation based on adjusted* R^2 *values (Environmental = environmental variables, Spatial = spatial distance, Temporal = temporal variation). P values for testable fractions were computed using ANOVA of RDA models. Residuals indicate the unexplained variances. Significance levels: *** = 0.001, ** = 0.01, * = 0.05.*

4.5. Discussion

In this study the diatom metacommunity across reconstructed soda pans in the Fertő-Hanság region and across natural soda pans in the Danube-Tisza Interfluve was examined. In both cases, high β-diversity enhanced mainly by species turnover was observed and within the explained community variance, the role of environmental variables was primary indicating the importance of deterministic processes. However, in the Fertő-Hanság region, temporal variations in community structure also appeared that might be related to that natural hydrological cycle of the pans is obstructed by restoration management, on the other hand, to the overrepresentation of the temporal scale in the one-year data set. The results of this research might be helpful in understanding which dynamics maintain diatom diversity at relatively small regional scale in such extreme environments as soda pans and in assessing how to preserve biodiversity by applying an appropriate management strategy in the future.

4.5.1. Main drivers in β-diversity

Soda pans located in Central Europe have a rather low α-diversity (species richness and Shannon diversity; Stenger-Kovács et al., 2016) in comparison to other lakes in the region with 'average' environmental characteristics (e.g. Stenger-Kovács et al., 2007). In the one-year periods, species richness showed a considerable variation in both regions, however, on average, the number of species was lower in the natural soda pans of the DT region. In addition, high overall β-diversity of diatom communities was observed in both study areas based on both abundance- and incidence-based dissimilarity measures. The high β-diversity might indicate that highly different communities (thus, a variety of species) are hosted by heterogeneous habitats that need to be maintained and considered during the development of conservation strategies, instead of focusing only on preserving high species richness (Samson & Knopf, 1982; Mumby, 2001). Partitioning of overall β-diversity revealed that dissimilarity in diatom communities originates mainly from the replacement of species in one community by different species in the other community. Gutiérrez-Cánovas et al. (2013) emphasized that lasting natural stress gradients can cause the selection of species according to their different environmental preferences leading to the dominance of turnover component. Algarte et al. (2016) reported 50% mean β-diversity for periphytic diatoms in lakes connected to the Paraná River, however, the authors calculated incidence-based pair-wise dissimilarity instead of multiple-site dissimilarity because they focused on β-diversity between each pair of lakes among the sampling years. Despite the difference of the applied dissimilarity measures, they also found that β-diversity was driven mainly by turnover (Algarte et al., 2016), similarly to the observations in the present study. Moreover, they found that damming of the studied area resulted in new environmental conditions forcing replacement processes between species with time, but each lake contributed equally to the regional species-pool as there was no significant richness difference. Maloufi et al. (2016) published extremely high β-diversity (>96%), which was also driven by high species turnover, using a multiple-site framework for phytoplankton from lakes in the Paris area, where the results were mainly explained by distinct local environmental conditions at a regional scale due to different anthropogenic impacts and landscape. Observations in present study provide a new insight into community ecology by applying null models in order to determine the role of deterministic and stochastic processes in diatom community variation. In both the Fertő-Hanság region and Danube-Tisza Interfluve, overall β-diversity indices (Bray-Curtis and Sørensen) and species replacement component (balanced variation and turnover) values matched much less to random expectations than to deviations beyond null model expectations, indicating that epipelic diatom communities are assembled predominantly by deterministic processes similarly to periphytic diatoms (Algarte et al., 2016) or to phytoplankton communities (Maloufi et al., 2016) in other studies. Nevertheless, the null model analyses in this study revealed also the role of stochasticity (a multitude of random processes) depending on whether abundance- or incidence-based indices were calculated: in the FH region, Bray-Curtis dissimilarity and balanced variation showed a weak correlation to null model expectations, whereas in the DT region, a moderate relationship was found between Sørensen dissimilarity and dissimilarity under null model. The components accounting for subsets (abundance gradient and nestedness) showed a different relationship to expectations with and beyond null models in the two areas: in the FH region, no correlation was observed, but in the DT region, nestedness showed a strong relation to the expectation with null model indicating a signal of stochastic processes. However, the subsets components (abundance gradient and nestedness) were quite low in both areas regarding the overall β-diversity. When the both regions' data subsets characterized by similar representation of temporal and spatial scales (implemented by reducing the number of soda pans in the DT region and considering the samples only from February to July in both regions) were investigated, diversity patterns were similar to those observed in case of the one-year periods: the mean species richness was appreciably lower in the DT region than in the FH region, but both areas were characterized by high β-diversity mainly due to species replacements. According to the null models, deterministic processes might have a primary role in development of community dissimilarities in case of the smaller data subsets as well, however, the effect of stochastic processes on nestedness component was also indicated.

4.5.2. Key components of deterministic mechanisms

In the DT region during the one-year investigation, the explained variation of community structures was associated merely with the pure environmental effects due to the unique environmental characteristics of the pans in conformity with the species-sorting. When metacommunity drivers for the data subset encompassing samples between February and July were examined, concordant patterns were observed: community dissimilarities were related mainly to the differences in environmental variables including the temporally structured environmental differences as well. These findings might originate from that these soda pans are in natural status, their hydrological cycle is undisturbed. As their water supply is provided solely by precipitation and groundwater (no man-made freshwater ingress), their natural saline features (the decisive physical and chemical parameters) can serve as environmental filters for diatom species.

In case of the one-year period, physical and chemical factors played a key role in the reconstructed soda pans of the FH region, but pure temporal variation also influenced the community structure. However, the effect of pure temporal distance has become negligible and community dissimilarities were driven chiefly by environmental differences and by the temporal variation of environmental differences when only the period between February and July was considered. It can be assumed that a possible reason for the significant temporal variation in diatom communities appeared during the one-year period might be the restoration management applied in this area aiming to re-establish migrating and nesting waterfowl population density. Legény-tó has a permanent linkage to one of the numerous drainage canals in the region, which results in a more or less constant water level and low conductivity. Lengyel et al. (2016) reported that the lack of a natural hydrological regime resulted in high diversity and dominance of freshwater diatoms in Legény-tó. Water level and surface area of Borsodi-dűlő and Nyéki-szállás are regulated by sluices built on the Hanság Main Canal and they receive a periodical water supply from Lake Fertő and the surrounding area. In addition, due to its proximity, water can occasionally be supplied from Lake Fertő by strong winds, when its water level is relatively high. Lengyel et al. (2016) stated that repeated shifts or reversions in the succession process can appear due to the water management and the occasional water supplied from Lake Fertő, which could also provide a reasonable explanation for the findings of the present study. Algarte et al. (2016) also reported that water management (namely damming) resulted in significant compositional changes in diatom communities due to variation of environmental characteristics in freshwater lakes connected to the Paraná River over a 10-year period. Thus, along with environmental changes, temporal variation was the most important in terms of assembly, similarly to the present observations in the FH region regarding the explained community variation. On the other hand, when subsets of the FH and DT regions' data were investigated where representation of spatial and temporal β-diversity was similar, the main drivers, considering the explained variation, were environmental and temporally structured environmental differences in each case. This suggests that in case of the reconstructed soda pans, the significant effect of pure temporal differences experienced during the one year might also be related to that temporal differences were overrepresented compared to spatial differences.

Different observations are presented in the literature regarding the key drivers of diatom metacommunities in freshwater ecosystems. Vilmi et al. (2016) found that diatom community structures in a large, well-connected lake system were determined by shared effects of both spatial and local environmental factors instead of pure environmental effects. They showed that the pure spatial effects interfered with environmental variables due to dispersal processes. Nevertheless, since communities are structured spatially mainly due to dispersal limitation at large scales (e.g. within a continent, a region or a watershed), they highlighted that spatial effects must be studied with caution in relatively smaller geographic scales (Vilmi et al., 2016). Dong et al. (2016) showed that in high-mountain streams, intense environmental gradients related to steep elevation affect the assembly of diatom metacommunities but spatial factors are also important, since mountains prevent stream corridors from facilitating the dispersal of species at a small spatial extent ($< 500\ \mathrm{km}^2$). In both areas investigated in this study, soda pans (within each region) are located relatively close to each other ($\leq$ 10 km). Therefore, there was no limitation of passive dispersal of diatom species, i.e., geographic distance did not play a key role. In such ecosystems with high and multiple stresses, where environmental parameters tend to reach extreme values (Stenger-Kovács et al., 2014; Lengyel et al., 2016), spatial distance did not affect the variation in community composition (i.e., the difference in community structure was not greater in more distant lakes than in those in close proximity): its effect was overcome by the physical and chemical properties of the water which supported a species-sorting mechanism.

Although, environmental variables played a key role in driving the composition of diatom communities, the most important parameters differed in the two regions either the total data sets or their subsets were examined. In the FH region, SRSi, SRP, temperature, conductivity and Pt colour were related mostly to community compositions. In the DT region, COD, NO_3^-, HCO_3^-, CO_3^{2-}, Cl^-, pH, and similarly to the reconstructed pans of the FH region, conductivity and temperature were the most important community drivers among environmental variables. A common feature of diatoms is that their cell wall (frustule) consists of biogenic silica therefore, diatoms play an important role in modifying the silica flux rates in waterbodies by assimilating large amount of silica. (Wetzel, 2001). Furthermore, it has been reported that the silica content of frustule (and thus Si uptake) can vary among species considerably (Paasche, 1973; Harrison et al., 1977) and it is dependent on size, frustule thickness (Durbin, 1977) and growth phase (Martin-Jézéquel et al., 2000). Although cell division and growth are thought to affect silicification in diatoms most directly, several environmental factors, such as external silicon concentration, nutrient content, salinity, temperature and light intensity regulate growth rate and thereby also have indirect effect on silicification (Martin-Jézéquel et al., 2000; Claquin et al., 2002; Shatwell et al., 2013). Soda pans can be classified based on to what extent suspended particles and dissolved coloured humic material contribute to the light extinction in the water. In turbid pans, light extinction is determined by suspended material to an extent of at least 55%, whereas in coloured pans, it is determined by humic material to an extent of at least 55%. In transitional type, both the suspended and the coloured humic material contribute with less than 55% to the light extinction (Boros et al., 2013). The sampled pans in the FH region are turbid (Legény-tó, Nyéki-szállás) and transitional (Borsodi-dűlő) (Boros et al., 2013), and it has been already reported that their Pt color, which represents the humic material content, is lower compared to the turbid (Bogárzó-szék, Böddi-szék, Kelemen-szék, Zab-szék) and coloured (Bába-szék, Sós-ér) natural pans investigated in the DT region (Stenger-Kovács et al., 2014). However, the types can alternate and more types can be found even within a given soda pan depending on the succession of the lacustrine sedimentation and the hydrological and biological status of the lake bed (Boros et al., 2013). The amount of humic material has an important effect on the spectral composition of light regime by changing the light attenuation in the water column (V.-Balogh et al., 2000). Diatoms have similar pigment profile which enables them to harvest light more efficiently compared to other algae (Falkowski & Knoll, 2007) but the ratio of pigments is variable among the species (Kuczynska et al., 2015). Consequently, a possible reason for the variation in diatom community composition driven partly by Pt color differences might be that the artificial water level regulation in the FH region resulted in changes of coloured humic material content and thus also in the light's spectral composition. Temperature is one of the most important environmental variables for periphyton, its effects can be manifested at several ecological scales, such as autecological, population, community, ecosystem and global scale. Temperature changes can cause shifts not only at the level of major algae groups but also at lower taxonomic levels (Stevenson et al., 1996). Due to their differences in temperature optimum and range, diatom species can differ in their distribution along the temperature gradients (Lowe, 1974; Hofmann et al., 2011). Nevertheless, it is important to note that due to the shallowness, the daily temperature fluctuation of soda pans can be also considerable in addition to the seasonal changes (Vörös & Boros, 2010, Boros et al., 2013). Similarly to the water temperature, diatom taxa can show considerably variability in their salinity, pH and trophic preferences (Schiefele & Schreiner, 1991; Håkansson, 1993; Van Dam et al., 1994, Hofmann et al., 2011). In line with this, Soininen (2007) summarized in her review that pH, conductivity, major ion concentrations and trophic level have been found to be the most important variables driving diatom communities. In temporary intermittent saline lakes, conductivity can vary related to the natural hydrological cycle (drying and filling phases) and tend to reach extreme values (Boros et al., 2014), however, "freshwater" supply can reduce the conductivity and moderate its variation (Lengyel et al., 2016). Conductivity can be used for estimating salinity (Boros et al., 2014) which influences directly or indirectly the diatom communities via causing osmotic stress, regulating cell wall thickness, nutrient uptake and transport (Bhattacharyya & Volcani, 1980; Tuchman et al., 1984; Stoermer & Smol, 1999). In alkaline, saline lakes, the ionic composition is strongly related to the groundwater's chemical characteristic (Simon et al., 2011) which is highly variable in time and space in the Carpathian Basin (Boros et al., 2013). Moreover, ionic composition of endorheic lakes can change with precipitation of minerals during evaporative concentration (Eugster & Jones, 1979). In the soda pans of the DT region, besides the dominance of Na^+, the dominant anions are HCO_3^-, CO_3^{2-} and Cl^-, however their relative proportion shows differences among the pans (Boros et al., 2013). The results experienced in the present study suggest, in line with previous findings (Stenger-Kovács et al., 2014; Lengyel et al., 2016), that diatom community composition may be affected not only by the variation of conductivity in soda pans but also by the differences in anionic composition. For diatoms, pH is also an important variable, since algae can utilize only free CO_2 and HCO_3^- (Hopkins & Hüner, 2004), and the proportion of CO_2, HCO_3^- and CO_3^{2-} in a given water is related to its pH (Wetzel, 2001). In soda pans, the amount of dissolved organic material is inherently high and dependent strongly upon the waterfowl populations (Boros et al., 2008). This can be reflected in the measured phosphorus content and COD. Although COD represents the amount of both organic and inorganic materials subjected to oxidation, the organic component is prevalent in most cases (APHA, 1998). Boros (2007) revealed that NO_3^--N:PO_4^{3-}-P ratio, which is typically low in alkaline waters, is related inversely to salinity in turbid soda pans. Moreover, phosphorus cycle is influenced by several factors, such as the sediment's phosphorus storage capacity related to pH, oxidation-reduction related to biological processes and the sediment's stirring up (Scheffer, 1998, Padisák, 2005).

In previous studies it has been recognized that proportion of the explained variance tend to be higher when weighted species occurrences are used rather than merely presence-absence data. The explanation for higher explained variance might be that the abundance data set magnified the response of abundant taxa to changes along environmental gradients to a greater extent (Beisner et al., 2006; Heino et al., 2010). In most cases of variation partitioning, the present observations were in line with this interpretation, except when incidence data of FH region between February and July was considered as environmental differences explained approximately half of the total community dissimilarities. Furthermore, it is important to note that although null model analyses highlighted the importance of deterministic processes that was reflected in the remarkable proportion of community variation explained by local environmental differences, most of the variance remained unexplained (in most cases ~80-90%). This might be resulted from both deterministic (e.g. further unmeasured environmental factors) or stochastic (demographic and patch stochasticity) processes, and from latent variance in residuals due to correlations among species (Leibold & Chase, 2018).

It is worth to note that the natural and reconstructed soda pans are located in two different regions (natural pans in the Danube-Tisza Interfluve and reconstructed pans in the Fertő-Hanság region) in this study. Therefore, metacommunity patterns observed across soda pans having a given ecological status apply to the given region where those pans are located. Consequently, the findings presented in recent dissertation do not imply that diversity and structuring mechanisms in case of one type of ecological status are the same in two different regions (e.g. metacommunity drivers in natural soda pans at the Austrian side of Lake Fertő might differ from those in the Danube-Tisza Interfluve), however this was not examined in the present study.

5. Benthic diatom metacommunity across small freshwater lakes in the Carpathian Basin[3]

5.1. Introduction

The current ecology- and conservation-oriented research tends to explore the possible drivers of community assembly by examining it at regional scale, rather than by investigation of groups of biota within a given habitat. That is, studies focusing on metacommunity processes as well as β-diversity and its component are gaining more and more attention.

In estimating the heterogeneity of communities and in unraveling the mechanisms acting behind metacommunity patterns, β-diversity analyses play a key role (Viana et al., 2016). It has been known for a few years that total dissimilarity, in case of either pairwise or multiple-site framework, can be partitioned into turnover and nestedness components (for incidence data) (Baselga et al., 2007; Baselga, 2010, 2012), and as its analogue, the partition into abundance balanced variation and abundance gradients components (for abundance data) has been introduced recently (Baselga, 2013b, 2017). In either terrestrial or aquatic community ecology, a myriad of studies conducted on different spatial and temporal scales has been published dealing with partitioning β-diversity into turnover and nestedness (e.g. Hortal et al., 2011; Maloufi et al., 2016; Alahuhta et al., 2017; Conradi et al., 2017; Wojciechowski et al., 2017; Soininen et al., 2018); application of β-diversity measures in indication of human impacts (Passy & Blanchet, 2007, Donohue et al., 2009; Conradi et al., 2017); environmental changes (Alahuhta et al., 2017); and planning conservation strategies (Angeler, 2013) is also widespread. However, total β-diversity (i.e., the total variation in community concerning binary or abundance matrix) can be divided according to another aspect as well: into the relative contribution of individual sampling units (Local Contribution to Beta Diversity - LCBD) and of individual species (Species Contribution to Beta Diversity - SCBD) to the overall β-diversity which targets the assessing of ecological uniqueness of sites and species (Legendre & De Cáceres, 2013). Large LCBD index might be an indicator of species poor habitats implying ecological restoration, or that of unusual community compositions or rare species combinations, which refer to high conservation value. In addition, it might indicate specific ecological conditions or the results of invasive species'

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[3] A part of this chapter was published in the following paper:
Szabó, B., Lengyel, E., Padisák, J. & Stenger-Kovács, C. (2019). Benthic diatom metacommunity across small freshwater lakes: driving mechanisms, β-diversity and ecological uniqueness. Hydrobiologia, 828: 183–198.

effects on the community (Legendre & De Cáceres, 2013). Furthermore, LCBD calculations have been extended to the measure of sites' uniqueness in terms of species replacement and nestedness (Legendre & De Cáceres, 2013). Estimation of local and species contributions to β-diversity is receiving increasing scientific interest (e.g., Lopes et al., 2014; Tonkin et al., 2016; Heino & Grönroos, 2017; Vad et al., 2017; Vilmi et al., 2017; Yang et al., 2018). Nevertheless, to my knowledge, diatom studies on LCBD in terms of replacement and nestedness as well as the comparison of their incidence- and abundance-based results are absent.

5.2. Aims

The first aim of this study was to estimate the regional β-diversity of diatom communities formed by metacommunity processes and to assess whether it is enhanced mainly by species turnover or nestedness related to the richness difference between sites. Similarly to the findings reported for most biota at low- or mid-latitude ecosystems (e.g., Tisseuil et al., 2012; Maloufi et al., 2016; Viana et al., 2016; Soininen et al., 2018), a high β-diversity of diatom communities due to the high degree of species turnover and a much smaller role of the nestedness component were expected.

The second goal was to investigate the driving mechanisms of benthic diatom communities in small freshwater lakes of the Carpathian Basin (Appendix 15): whether they are assembled merely due to the selection forces of the local environment or spatial variables are also important. Distances between the sampling sites can be considered as intermediate (2-400 km), they cover regional scale. Furthermore, environmental parameters vary reasonably across the sampled lakes (Appendix 16), however, they do not represent such extremely stressed environments as for instance, natural shallow saline lakes of the Carpathian Basin. Therefore, it was assumed that both spatial distance between sites and local environmental characteristics should equally affect the development of diatom communities.

Furthermore, it was assessed if sampled lakes contribute equally to β-diversity or some of them plays a particularly important role with its unique community composition and to determine which factors are responsible for the established patterns. Also, this issue was examined in terms of species turnover and nestedness, as well. It was assumed that sampling sites where one or more environmental parameters deviate considerably from the average, thereby resulting in unique species combinations and/or low species richness (Legendre, 2014), should have the largest contribution to β-diversity.

Finally, it was quantified to what extent the individual species contribute to β-diversity in the sampled region. It was hypothesized that species, which are characteristic of restricted environmental conditions should affect overall β-diversity to the greatest extent.

5.3. Material and methods

5.3.1. Study sites, sampling and processing of samples

In August 2010, a total of 38 small freshwater lakes were sampled in the Carpathian Basin (Fig. 14, Appendix 15). Each of them had a surface smaller than 3 km^2 and their altitude varied between 73 and 311 m. Altitude of sampling sites was measured in Google Earth Pro. Based on their surface, the lakes could be classified into three size categories: category 1 (< 1 km^2), category 2 (1-2 km^2), category 3 (2-3 km^2). Most of the lakes belonged to category 1, approximately one third to category 2, and four lakes to category 3. Following the Hungarian typological classification (OVF, 2016), the lakes were grouped into four depth categories according to their mean depth. A few lakes were very shallow (< 1 m), most lakes had shallow depth (1-3 m), five were moderately deep (3-5 m) and only one was deep (> 5 m). Following the recommendation of the OECD (1982), the lakes were classified into trophic classes based on their TP concentration. Most of them belonged to the category hypertrophic (> 100 $\mu g\ L^{-1}$ TP), one third was eutrophic (35-100 $\mu g\ L^{-1}$ TP) and only one was mesotrophic (10-35 $\mu g\ L^{-1}$ TP). In addition, habitat type of the investigated lakes also differed. Majority of the samples was collected either from oxbow- or natural lakes, and some of the waterbodies were reservoirs or wetlands. Code for the lakes, the date of sampling, the lakes' geographic location, altitude, size and depth category, and trophic classification were presented in Appendix 15. The geographical distance between two sampling sites ranged from 2 to 400 km.

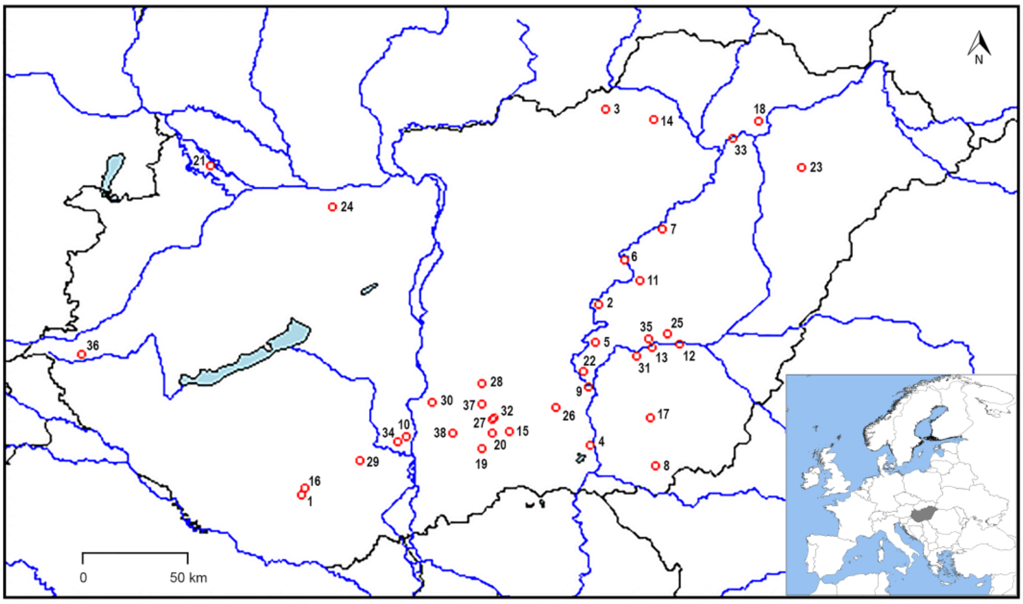

Figure 14 *Location and schematic map of Hungary and the sampling sites. Lake codes for the numbers are listed in Appendix 15.*

Phytobenthos samples were collected in the littoral region primarily from common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) or from other characteristic emergent macrophytes, such as sedge (*Carex* sp.) or bulrush (*Typha* sp.) (CEN, 2003; King et al., 2006). In each case, five macrophyte stems of the same species were chosen and starting ca. at 10 cm below the water surface, their 15-cm sections were cut. In some lakes, where macrophyte vegetation was not characteristic or was absent, benthic diatoms were taken from permanently-submerged natural stones, boughs or in case of their absence, from mud surface with pipette. In each lake, only one type of substrate was sampled. Sample preparation and light microscopic identification of species were carried out as described in Chapter 3.3.2. according to the standard taxonomic guides (Krammer & Lange-Bertalot, 1991, 1999a, 1999b, 2000; Krammer, 2000, 2002, 2003; Lange-Bertalot, 2001; Levkov, 2009; Hofmann et al., 2011; Lange-Bertalot et al., 2011; Bey & Ector, 2013; Levkov et al., 2013). All diatom taxa (identified at species or genera level) were regarded as individual species and were included in each subsequent statistical analysis.

Furthermore, physical and chemical characteristics were determined for each sampling site. Water temperature, oxygen saturation (DO%), conductivity, pH and turbidity were measured *in situ* using an HQ40d Hach Lange multimeter. In laboratory, concentration of HCO_3^-, Cl^- and COD were determined titrimetrically (APHA, 1998), whereas SO_4^{2-}, NO_2^-,

NO_3^-, NH_4^+, SRP, TP (APHA, 1998) and SRSi (Wetzel & Likens, 2000) spectrophotometrically.

5.3.2. Statistical analyses

Prior to the metacommunity-analyses, non-metric multidimensional scaling (NMDS) was performed to visualize whether community composition of benthic diatoms was separated according to the substrate types. NMDS was conducted based on the Hellinger-transformed species abundance data applying Bray-Curtis distance. The NMDS projection displayed that benthic diatom communities were not separated according to the substrate types and their distribution was relatively homogeneous (Appendix 17). Therefore, all samples were included in the subsequent statistical analyses.

Across the 38 sampling sites, β-diversity of diatom communities was estimated by multiple-site Bray-Curtis dissimilarity (β_{BC}) which was partitioned into its abundance balanced variation ($\beta_{BC.BAL}$) and abundance gradients ($\beta_{BC.GRA}$) component (Baselga, 2017); and by incidence-based multiple-site Sørensen dissimilarity index which was divided into its turnover (β_{SIM}) and nestedness (β_{NES}) component (Baselga et al., 2007; Baselga, 2010).

Variation partitioning was performed to quantify the relative contribution of pure and shared effect of environmental heterogeneity and spatial distance to variability of diatom communities (Peres-Neto et al., 2006). Prior to this, two explanatory data matrices were created. To generate the group ‘environmental heterogeneity’, a principal component analysis (PCA) on the correlation matrix of standardized physical and chemical parameters was performed in order to eliminate collinearity of variables, and the first two principal components’ scores were used as explanatory variables. The group ‘spatial distance’, distance-based Moran’s eigenvectors (dbMEMs) were included as explanatory variables. Variation partitioning was performed both for Hellinger-transformed species abundance (Legendre & Gallagher, 2001; Borcard et al., 2011) and species incidence data. ANOVA (permutations = 999) of RDA models were run to assess the significance of adjusted R^2 values for testable fractions (pure environmental heterogeneity and spatial distance).

Sampling locations in the region were not evenly distributed in space: eight lakes (ARL, HÁM, KEN, LIP, NAV, ÖRE, TDO, VAD) were located further away from the 30 that could be better clustered spatially. Therefore, β-diversity indices and the relative role of local environmental variables and spatial distance were assessed also for a data subset where the spatially more “isolated” eight lakes were not included.

The partitioning of variance in community dissimilarity was carried out in similar way as described in Chapter 4.3.4. First, a set of environmental variables showing the maximum correlation with community dissimilarities was determined using the bioenv function in vegan package (Oksanen et al., 2017). Then, permutation-based (permutations = 1000) multiple regressions on distance matrices (MRM) (Legendre et al., 1994; Lichstein, 2007) were run in three ways: where (i) environmental distances (E) and (ii) spatial distances (S) served as independent explanatory matrices; and where (iii) both groups of matrices were used in combination (E+S). The group ‘environmental distances’ included the Euclidean distances of the standardized environmental parameters selected by the BIOENV approach (Clarke & Ainsworth, 1993), whereas ‘spatial distances’ consisted of the geographic distance matrix calculated with the earth.dist function of fossil R package (Vavrek, 2011). To produce the two dependent distance matrices for MRM analyses, pairwise Bray-Curtis indices were computed both for Hellinger-transformed species abundance data and for incidence data. Finally, R^2 values produced by MRM models served as the base for determining the proportion of variance in community dissimilarities explained by the pure and shared fractions of environmental and spatial distances and the unexplained variation (Jones et al., 2006) (Appendix 7).

In case of the total data set (contained 38 sampling sites), local contribution to β-diversity was calculated for each sampling site to quantify their ecological uniqueness. The computation was carried out both for abundance ($LCBD_{D\%diff}$) and presence-absence ($LCBD_{DS}$) data based on indices from the Baselga-family, Sørensen group. Percentage different dissimilarity ($D_{\%diff}$) was used for quantitative (Baselga, 2013b) and Sørensen dissimilarity (D_S) for binary data (Baselga, 2010). To stratify Euclidean property, square-root transformation was applied for dissimilarity matrices ($D_{\%diff}$ and $D_{S)}$ (Legendre & De Cáceres, 2013). To assess how unique each site is in terms of species replacement and nestedness, LCBD values were computed for replacement ($LCBD_{ReplB\%diff}$, $LCBD_{ReplBS}$) and nestedness ($LCBD_{NesB\%diff}$, $LCBD_{NesBS}$) decomposing $LCBD_{D\%diff}$ and $LCBD_{DS}$ (Legendre & De Cáceres, 2013).

To describe the relative importance of individual species in affecting overall β-diversity, species contribution to β-diversity was calculated for Hellinger-transformed abundance data ($SCBD_{ab}$) and for species incidence data ($SCBD_{pa}$) (Legendre & De Cáceres, 2013).

Since LCBD and SCBD indices (response variables) exhibit relative contribution data with values between 0 and 1, generalized additive models (GAMs) using beta regression family with logit link function (Wood et al., 2016) were applied to investigate the relationship of $\text{LCBD}_{\text{D\%diff}}$, and LCBD_{DS} with the local species richness as well as the relationship of SCBD_{ab} and SCBD_{pa} with the number of sites occupied by a given species and with the total abundance of the species. Regression tree model analyses were run (Breiman et al., 1984) to find the most important environmental factors determining the variation in LCBD indices ($\text{LCBD}_{\text{D\%diff}}$, LCBD_{DS}, $\text{LCBD}_{\text{ReplB\%diff}}$, $\text{LCBD}_{\text{ReplBS}}$, $\text{LCBD}_{\text{ReplB\%diff}}$, $\text{LCBD}_{\text{ReplBS}}$). Furthermore, Pearson correlation coefficient was computed for each pair of LCBD indices to estimate the correlation between them.

R statistical software (R Development Core Team, 2017) was used to conduct statistical analyses. Codep (Guenard et al., 2017) and ape (Paradis et al., 2004) R packages were applied for dbMEM analysis and PCoA, and vegan (Oksanen et al., 2017) for variation partitioning. Multiple-site β-diversity indices were calculated in betapart (Baselga et al., 2017), LCBD and SCBD indices in adespatial (Dray et al., 2017), ade4 (Dray & Dufour, 2007) R packages and with beta.div function (Legendre & De Cáceres, 2013). Regression tree model analyses and GAMs were conducted and illustrated using rpart (Therneau et al., 2017), rpart.plot (Milborrow, 2017), mgcv (Wood, 2011) and ggplot2 (Wickham, 2009) R packages.

5.4. Results

In the 38 phytobenthos samples, 273 diatom taxa were identified. The number of species showed high variability: its lowest value was 20 and the highest was 66 (average and standard deviation: 42 ± 12). Considering either species' abundance or only their incidence, the overall diatom β-diversity was high (β_{BC}=0.956, β_{SOR}=0.934) which was due to the species substitutions ($\beta_{\text{BC.BAL}}$=0.953, β_{SIM}=0.914) and the components accounting for subsets ($\beta_{\text{BC.GRA}}$=0.003, β_{NES}=0.020) were negligible.

In the phytobenthos data subset which contained only the spatially "most clustered" 30 lakes, 248 diatom taxa were found. In α- and β-diversity, compared to the total data set, only negligible change was observed: the lowest species richness was 21 and the highest was 66 (average and standard deviation: 43 ± 12); the overall β-diversity was high mainly due to the species replacement considering either species' abundance or only their incidence (Appendix 18).

Physical and chemical parameters varied considerably among the 38 lakes. Many of them had a higher standard deviation than their average (Appendix 16), the mean Euclidean distance calculated for the standardized environmental variables was 4.97. According to the PCA results (Appendix 19), 33.7% of the variance in environmental factors is explained by PC1 axis and 17.3% by PC2 axis. In descending order, HCO_3^-, conductivity, TP and SRP showed the highest correlation with PC1 axis (absolute values of Pearson correlation coefficients were above 0.8) and had the highest PC1 loading. Variables correlated most with PC2 axis (absolute values of Pearson correlation coefficients were above 0.6) and possessing the highest PC2 loading were O_2 saturation and pH.

Based on the results of variation partitioning (Fig. 15), the establishment of diatom community composition was affected significantly by environmental heterogeneity and spatial distance among the sampling sites as well. However, either in case of species abundance or incidence data, the pure spatial distance explained a slightly higher proportion (7.3% and 3.4%) of community variation than environmental heterogeneity alone (2.8% and 2.1%).

According to the BIOENV approach, the best subset of environmental variables driving community dissimilarities included COD, SRSi, HCO_3^{2-} and pH for species abundance data ($r_{ab}=0.33$, $P_{ab}<0.01$), and only SRSi for species incidence data ($r_{p\text{-}a}=0.32$, $P_{p\text{-}a}<0.05$). MRM results revealed that spatial distances as well as environmental and spatial distances together affected significantly the community dissimilarities when species abundances were considered. Nevertheless, a marginally non-significant relationship was observed between community dissimilarities and environmental distances (Appendix 20). In case of presence-absence data, MRM models contained either environmental distances or both environmental and spatial distances together as explanatory matrices were significant, however, spatial distance as single explanatory matrix had no significant effect on community dissimilarities (Appendix 20). Based on variation partitioning (Appendix 21), either in case of species abundance or incidence data, pure environmental distances explained a higher proportion of variance in community dissimilarities than pure spatial distance. Spatially structured environmental distances (i.e., the shared fraction of environmental and spatial distances) explained negligible proportion of variance.

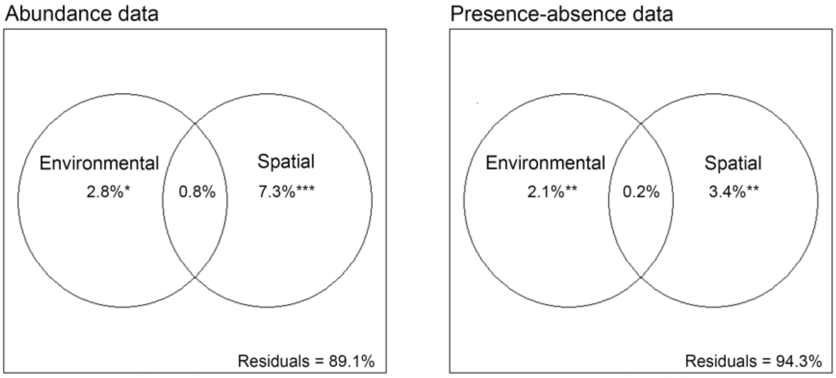

Figure 15 *Results of variation partitioning conducted on Hellinger transformed species abundance and presence-absence data from the 38 small freshwater lakes. Adjusted* R^2 *values are shown to indicate the relative importance of environmental heterogeneity (Environmental) and spatial distance (Spatial) in the total community variation. Unexplained variances are represented by the residuals. Significance of testable fractions is shown as follows: *** = 0.001, ** = 0.01, * = 0.05. P values were computed using ANOVA of RDA models.*

Strong positive correlation was found between $LCBD_{D\%diff}$ and $LCBD_{ReplB\%diff}$ as well as between $LCBD_{DS}$ and $LCBD_{ReplBS}$ (Pearson correlation coefficients were 0.98 and 0.94, respectively) furthermore, $LCBD_{NesB\%diff}$ correlated negatively with $LCBD_{D\%diff}$ and $LCBD_{ReplB\%diff}$ (Pearson correlation coefficients were -0.51 and -0.47, respectively). For any other pairs of indices, no significant correlation was displayed (Appendix 22). GAMs and regression tree model analyses revealed that distinct factors affect the LCBD indices using abundance and incidence data. There was no significant relationship between $LCBD_{D\%diff}$ and local species richness, but $LCBD_{DS}$ showed a significant decrease with the increase of species richness (Table 5, Fig. 16a-b).

Table 5 *Results of GAMs (beta regression family with logit link function) testing relationship of local contribution to β-diversity (LCBD$_{D\%diff}$, LCBD$_{DS}$) with local species richness (richness), and the relationship of species contribution to β-diversity (SCBD$_{ab}$, SCBD$_{pa}$) with the number of sites occupied by a given species (occup) and the species' total abundance (abund). edf = The estimated degrees of freedom accounting for smoothing function, Ref. df. = Reference degrees of freedom, χ^2 = Chi-square test statistic, adj. R^2 = The proportion of variance explained by the model, Dev. expl. = The proportion of the null deviance explained by the model, P = P value.*

	smooth term	edf	Ref. df	χ^2	adj. R^2	Dev. expl. (%)	P
LCBDD%diff	s(richness)	1.000	1.000	2.09	0.032	5.6	0.148
LCBDDS	s(richness)	4.034	4.915	68.06	0.644	64.6	<0.001
SCBDab	s(occup)+s(abund)	8.155	8.795	281.40			<0.001
		8.918	8.996	4171.20	0.996	99.1	<0.001
SCBDpa	s(occup)+s(abund)	8.437	8.891	4687.79			<0.001
		1.002	1.003	0.11	0.963	96.2	0.741

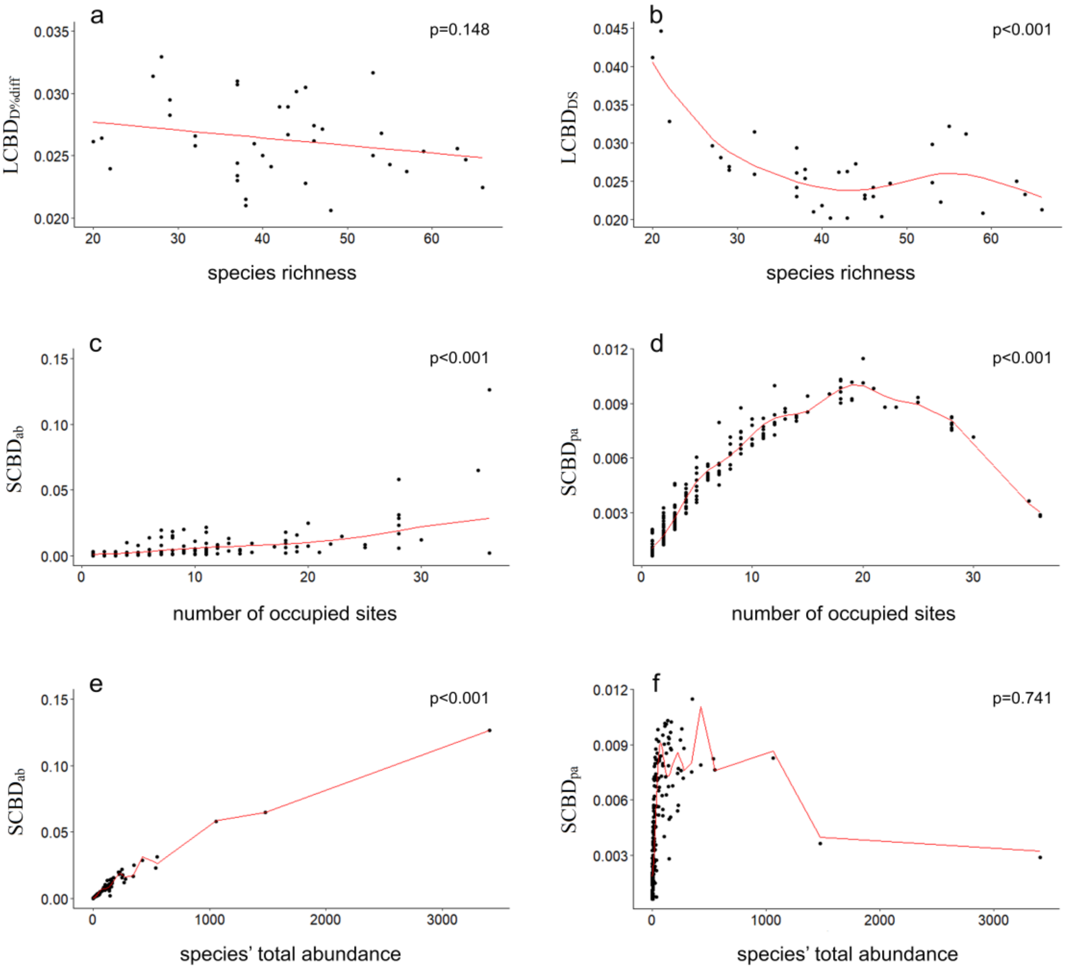

Figure 16 *The relationship of local contribution to β-diversity (LCBD$_{D\%diff}$, LCBD$_{DS}$) with local species richness and the relationship of species contribution to β-diversity (SCBD$_{ab}$, SCBD$_{pa}$) with the number of occupied sampling sites and with the total abundance of a given species. Solid lines show the fitted GAM using beta regression family with logit link function.*

Sites with the highest local contribution to β-diversity were different when conducting computations on species abundance and presence-absence matrix. These two types of data revealed different results also during the investigation of sampling sites' uniqueness in terms of species replacement and nestedness. Sites possessing the highest $\mathrm{LCBD}_{\mathrm{D\%diff}}$ index (>0.030) were CSA, CSI, HAR, ÖRE and SZT (Appendix 23a), and according to the regression tree model analyses, environmental variables driving $\mathrm{LCBD}_{\mathrm{D\%diff}}$ were TP and NO_3^- (Fig. 17a). Similarly, sampling sites with the highest $\mathrm{LCBD}_{\mathrm{ReplB\%diff}}$ value (>0.034) were CSA, CSI, HAR, ÖRE and SZT (Appendix 23b) where SRP and COD were the most decisive (Fig. 17b). Lakes HAR, ÖRE, SZT had relatively high concentrations of nutrient forms (501.9–732.5 μg L^{-1} NO_3^-, 95.9–412.5 μg L^{-1} SRP, 208–541.5 μg L^{-1} TP) and low COD (9.2 – 29.9 mg L^{-1}); CSI had high nutrient concentrations (3137.8 μg L^{-1} NO_3^-, 313.8 μg L^{-1} SRP, 522.4 μg L^{-1} TP) and COD (165.5 mg L^{-1}); and CSA had slightly lower nutrient load (108.5 μg L^{-1} NO_3^-, 24.4 μg L^{-1} SRP, 110.5 μg L^{-1} TP) and low COD (7.4 mg L^{-1}). Sites represented by the highest $\mathrm{LCBD}_{\mathrm{NesB\%diff}}$ (>0.115) were KHT, TDO, VDK and MÁM (Appendix 23c) determined primarily by TP, COD and pH (Fig. 17c). Lakes KHT, VDK, MÁM had moderate to high TP (89.2–214.5 μg L^{-1}), relatively low COD (11–14.9 mg L^{-1}) and slightly alkaline (8–8.8) pH; whereas TDO had higher TP (364 μg L^{-1}), COD (49.4 mg L^{-1}) and lower (7.7) pH. In case of the incidence-based data, the highest $\mathrm{LCBD}_{\mathrm{DS}}$ indices (>0.031) were found at sites HÁM, KEN, KFT, SÁR, VAD and PIR (Appendix 24a), where SRP, COD and SRSi had the most important effect (Fig. 18a). HÁM, KEN, KFT, SÁR and VAD (Appendix 24b) achieved the highest $\mathrm{LCBD}_{\mathrm{ReplBS}}$ value (>0.036) affected mainly by SRP and NH_4^+ (Fig. 18b). Each of the lakes KEN, KFT, SÁR, VAD could be characterized by low SRP (3.3–20.7 μg L^{-1}), COD (3.2–26 mg L^{-1}), NH_4^+ (6–33 μg L^{-1}) and low to relatively high SRSi (0.7–19.5 mg L^{-1}). HÁM had low SRP (22.7 μg L^{-1}), COD (3.2 mg L^{-1}), moderate SRSi (8.5 mg L^{-1}) and high NH_4^+ (456 μg L^{-1}); whereas PIR had relatively high SRP (164 μg L^{-1}), COD (40.8 mg L^{-1}), SRSi (31.1 mg L^{-1}) and low NH_4^+ (19 μg L^{-1}). Sites with outstanding $\mathrm{LCBD}_{\mathrm{NesBS}}$ index (>0.095) were PIR, TÚR and TOL (Appendix 24c) driven by SRP and TP concentration (Fig. 18c). TÚR had high concentrations of phosphorus forms (266 μg L^{-1} SRP, 369.5 μg L^{-1} TP); whereas TOL had lower (36.6 μg L^{-1} SRP, 57.3 μg L^{-1} TP).

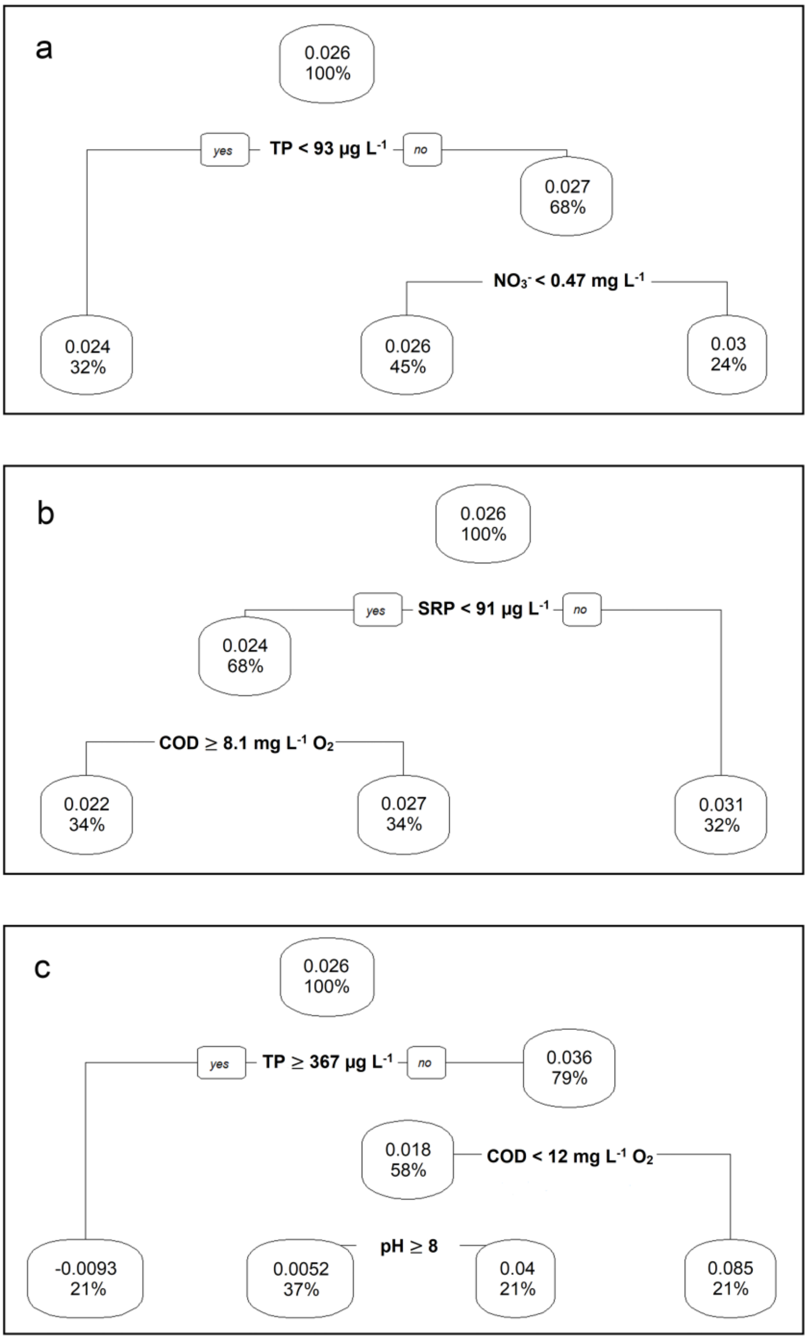

Figure 17 *Regression trees for predicting a)* $LCBD_{D\%diff}$*, b)* $LCBD_{ReplB\%diff}$ *and c)* $LCBD_{NesB\%diff}$ *from the set of environmental parameters. Each node shows the predicted LCBD value (i.e., the mean LCBD value) and the percentage of observations in the node.*

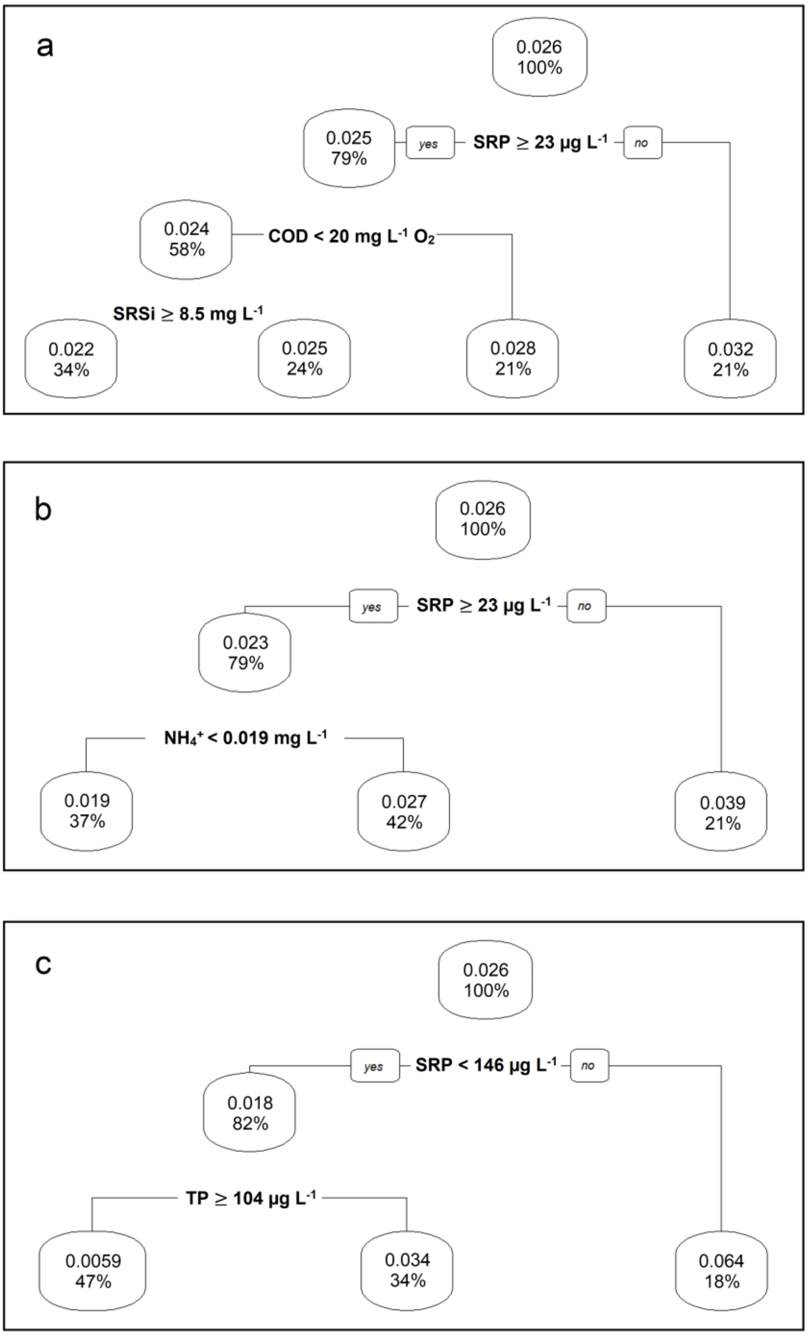

Figure 18 *Regression trees for predicting a)* $LCBD_{DS}$*, b)* $LCBD_{ReplBS}$ *and c)* $LCBD_{NesBS}$ *from the set of environmental parameters. Each node shows the predicted LCBD value (i.e., the mean LCBD value) and the percentage of observations in the node.*

Contribution of the individual species to β-diversity depended on the type of the applied data matrix (abundance- or incidence-based). According to the GAMs' results, SCBD using abundance data ($SCBD_{ab}$) depended both on the number of sites occupied by the given species and on the total abundance of the species (Table 5, Fig. 16c, e): it showed an increasing trend with the increase of both explanatory variables. In turn, SCBD based on incidence data ($SCBD_{pa}$) was significantly related only to the number of occupied sites and a unimodal (hump-shaped) relationship was revealed between them (Table 5, Fig. 16d, f): $SCBD_{pa}$ increased up to 20 occupied sites and then, it started to decrease. Species with the highest $SCBD_{ab}$ value (>0.05) were *Achnanthidium minutissimum* (Kützing) Czarnecki, *Amphora pediculus* (Kützing) Grunow and *Cocconeis placentula* Ehrenberg, all of which occupied high number of samples (≥28) and were present with high total abundance (≥1060 individuals counted during the study). In contrast, *Eolimna minima* (Grunow) Lange-Bertalot, *Halamphora veneta* (Kützing) Levkov, *Nitzschia palea* var. *tenuirostris* Grunow, *Nitzschia palea* var. *debilis* (Kützing) Grunow and *Nitzschia supralitorea* Lange-Bertalot had the highest $SCBD_{pa}$ (>0.01). These species occurred at intermediate proportion of sites (at 18-20 sites) and with moderate total abundance (110-354 individuals).

5.5. Discussion

5.5.1. Structuring drivers and β-diversity of diatom communities

In accordance with the preliminary hypothesis, when all the 38 lakes were considered at intermediate regional scale, the composition of benthic diatom communities depended significantly on both the spatial variables and the local environmental characteristics. Using variation partitioning to unravel metacommunity mechanisms, Cottenie (2005) developed a general sheme which assumes i) species-sorting if solely the "environmental variables" fraction explains significantly the community structures; ii) neutral theory or patch dynamics if only the "spatial variables" fraction is significant and iii) mass-effect concept or the combination of species-sorting and mass-effect if both fractions have significant explanatory power. If the investigated metacommunity should be classified as one of the four paradigms according to Cottenie's (2005) postulates, the mass-effect should be chosen based on the variation partitioning results. However, mass-effect is very rare in natural communities, only week evidence for it has been found even at high dispersal rates (Kunin, 1998; Kadmon & Tielborger, 1999; Michels et al., 2001; Harrison et al., 2010; Howeth & Leibold, 2010). The present study also supported that diatom metacommunity was driven by dispersion limitation inherent to neutral theory and patch dynamics and by environmental filtering complying with the species-sorting, rather than conforming mass-effect. In turn, when only the spatially "more clustered" lakes were investigated, community dissimilarities, either abundance- or incidence-based, were more related to environmental differences than to spatial distance. That is, species-sorting became more prevalent. This observation might be related to that the investigated area was reduced and on the other hand, to that the spatially more “isolated” sampling sites were omitted from the analysis.

Nevertheless, the four archetypes are not mutually exclusive, it is impossible to firmly determine the boundaries between them due to several interfering factors (Logue et al., 2011; Leibold & Chase, 2018). Consequently, instead of regarding metacommunity concepts as distinct alternatives, considering them as continuum is suggested (Alonso et al., 2006; Gravel et al., 2006; Leibold & McPeek, 2006; Adler et al., 2007; Chase, 2007). One of the factors which influences metacommunity patterns is the number of measured environmental variables. For instance, if an originally unmeasured variable were spatially structured, the importance of the “spatial variables” fraction would increase, whereas if it were not spatially structured, residuals would be higher, leading to different conclusions regarding metacommunity theories (Leibold & Chase, 2018). Furthermore, the amount of encompassed habitat heterogeneity is also influential: the proportion of variation explained by environmental variables decreases, the proportion of variation explained by spatial variables increases slightly, whereas residuals show a great increase with reduction of the amount of sampled habitat types (Leibold & Chase, 2018).

The traits of species, such as size and dispersal rate, can also greatly influence the relative role of environmental and spatial variables. Among passively dispersing organisms, the relatively large species with low dispersal rates are assumed to be structured according to spatial variables due to their limited dispersal complying with the neutral theory and patch dynamics rather than by environmental characteristics. In contrast, smaller species with better dispersal abilities are likely driven by habitat heterogeneity because they might be able to respond more sensitively even to the minor environmental differences (Hájek et al., 2011; De Bie et al., 2012; Heino, 2013). At low dispersal rates, spatial factors have more important role in development of communities due to dispersal limitation, rather than environmental heterogeneity. In case of intermediate dispersal rates, dispersal limitation is not probable and environmental heterogeneity inherent to species-sorting mechanisms is the most decisive. When dispersal rate is very high, the role of local environmental variables declines, the importance of spatial variables increases and the strength of these two factors become approximately equal. The latter is assumed to occur when dispersal into adjacent less favorable habitats is high resulted from mass-effect (Leibold & Chase, 2018). Despite that diatoms have small size are regarded as relatively well, passively dispersing organisms

(Kristiansen, 1996; Finlay, 2002), within large areas (e.g., at continental or global scale) geographic separation tend to limit their ubiquitous dispersal thus showing pure spatial patterns which can be explained by the neutral theory (Heino et al., 2010). The recent study can confirm this observation, since at intermediate spatial scale, a proportion of the explained variation in diatom communities was related significantly to spatial variables.

Similarly to previous studies (Heino et al., 2010; Vilmi et al., 2016), the unexplained variation in community structure was slightly lower when abundance of diatom species was considered, however, it was above 80% in each case of variation partitioning. This high proportion of unexplained variation (residuals) probably deriving from unmeasured environmental parameters, undersampling of rare species, correlations among species and stochastic processes should not be ignored during the interpretation of the observed patterns. Moreover, demographic stochasticity and colonization-extinction stochasticity (predicted by the neutral theory and patch dynamics, respectively) might also increase residual variation (Hubbell, 2001; Vellend, 2010, 2016; Leibold & Chase, 2018).

Either the entire region was considered or only the spatially “most clustered” sampling sites, high average of local diatom species richness and high β-diversity were experienced primarily due to the high degree of species turnover among the sampling sites which is in agreement with the initial expectations and with previous findings from the mid-latitudes (Tisseuil et al., 2012; Maloufi et al., 2016; Viana et al., 2016; Soininen et al., 2018). In turn, nestedness resulted from richness differences was inconsiderable. In the meta-analysis by Soininen et al. (2018), species turnover and total β-diversity showed strong correlation as both quantify the compositional dissimilarities between samples, whereas nestedness is represented with several times smaller proportion (even close to zero) than turnover and it may only measure the bias caused by richness differences. They also described that β-diversity and its turnover component are slightly smaller near the poles, which could be explained by the more homogeneous environment, less limited dispersal of species (Mouquet & Loreau, 2003; Leibold et al., 2004) and less pronounced biotic interactions (Willig et al., 2003; Schemske et al., 2009). Towards higher latitudes, where glaciation might have played an important role in the local and regional extinction and recolonization processes, the increase of nestedness was found (Soininen et al., 2018).

5.5.2. Local contribution of sampling sites to β-diversity

Calculation of LCBD is suitable for quantifying which sites contribute more (or less) to β-diversity than the mean and thereby for evaluating the ecological uniqueness of communities at each site (Legendre & De Cáceres, 2013). Local contribution to β-diversity and local contribution in terms of species replacement showed a strong positive relationship applying either abundance- or incidence-based data. However, in case of using abundance data, LCBD for nestedness decreased significantly with increasing LCBD and LCBD for replacement. Accordingly, sites with highest uniqueness in terms of replacement contributed to the greatest extent to total β-diversity of diatom communities, as well. This may be related to the fact that in general, total β-diversity also correlates positively with its turnover component and negatively with its nestedness component (Soininen et al., 2018). It is supposed that species-rich sites exhibit low LCBD due to the greater chance of sharing species with other communities (Maloufi et al., 2016). Nevertheless, the preliminary assumption that sites with low diatom species richness have greater contribution to the regional β-diversity than sites with higher richness, was only partly confirmed by the results. The declining trend in LCBD with increasing local richness was observed both for abundance and presence-absence data, but the relationship was significant only for species incidences. A part of former studies confirms, whereas some of them contradicts the recent findings depending on the organisms and the habitat type targeted. Applying abundance data for stream (Vilmi et al., 2017) and pond (Teittinen et al., 2017) diatom communities, negative correlation between LCBD and species richness was reported, however, this relationship was not evident for lake benthic diatoms (Vilmi et al., 2017). In case of dung beetles (Da Silva & Hernández, 2014) and stream insect assemblages (Heino & Grönroos, 2017), LCBD decreased significantly with increasing local species richness if calculations were conducted on presence-absence data, which is in line with the findings of the present research. Consequently, it can be concluded that sites sustaining less diverse communities have greater ecological uniqueness, however, this coherence varies among different groups of organisms and ecosystems, furthermore also depends largely on the data type applied.

The results of this study revealed that local environmental variables affected sampling sites' contribution to β-diversity, including its extension to replacement and nestedness, as well. Although sites with highest LCBD indices were different based on abundance- and incidence-based community data, no explicit contrasts were found in their main driving variables. Most decisive factors were phosphorus forms for each LCBD index, which corroborates the hypothesis, since these parameters displayed relatively high variance among the sites. Additionally, nitrogen forms, pH, COD and SRSi were also crucial in evolving sites' ecological uniqueness for diatom communities. Abundance-based analyses revealed that each lake with the highest contribution to β-diversity and to species replacement was hypertrophic based on TP concentration, however, they showed variability in their COD, NO_3^- and SRP concentration. Lakes with the highest contribution to abundance-based nestedness were also variable regarding nutrient content, they belonged to the eutrophic or hypertrophic category, and their slightly alkaline pH also differed within a relatively narrow range of gradient. Lakes with the highest contribution to incidence-based β-diversity and to species replacement were also variable regarding their nutrient loads. They covered the trophic scale ranging from mesotrophic to hypertrophic, however, the most of them could be characterized with relatively low COD, SRP and NH_4^+ concentration. In turn, they were rather variable concerning their SRSi content. Lakes contributed to the highest extent to nestedness belonged to the eutrophic or hypertrophic category and they also showed difference in the concentrations of their phosphorus forms. Consequently, lakes which were the most important in the development of β-diversity (and its turnover and nestedness components, as well) had different environmental characteristics suggesting that environmental filtering played a key role in the formation of community composition. Phosphorus and nitrogen forms, COD and SRSi have already been emphasized as master variables for freshwater lake diatom communities in several previous studies (e.g., Hall & Smol, 1992; King et al., 2000; Lim et al., 2001; Soininen, 2007). Nutrient supply plays a key role in establishment of autotrophic algal communities and trophic status is also related, for instance, to oxygen conditions and pH, thereby, it affects indirectly the physiological processes of aquatic organisms (Soininen, 2007). In addition, pH was found as one of the most influential variables for subarctic ponds' contribution to β-diversity of diatom communities (Teittinen et al., 2017). In turn, some publications targeting β-diversity assessments reported that LCBD was not well determined by local environmental characteristics, for instance, in case of stream insects (Heino & Grönroos, 2017) and invertebrates (Tonkin et al., 2016). Contribution to β-diversity and to its components seemed to be independent of the surface and depth of the given waterbody since rather very shallow lakes with small surface area as well as moderately deep or deep lakes had high LCBD indices. Furthermore, considering the geographical location of lakes, lakes with high LCBD indices were found that are relatively close to each other and that are located quite far from each other. Accordingly, it can not be concluded obviously that the most distant sites had the greatest contribution to β-diversity (or to its components).

5.5.3. Species contribution to β-diversity

With respect to species contribution to β-diversity, results published for different biota and ecosystems are congruent, however, abundance- and incidence-based calculations displayed fundamentally distinct patterns similarly to the findings of this study. Gaston et al. (2006) emphasized the tight link between abundance, its spatial variation and the number of occupied sites by a given species, which may be related to the observations of the present study that diatom species occupying a high number of lakes and represented by high abundance contributed the most to overall β-diversity. That is, contrary to the initial hypothesis, common diatom species such as *Achnanthidium minutissimum*, *Amphora pediculus* and *Cocconeis placentula* with wide ecological amplitude (Hofmann et al., 2011) and variable abundance at different sites exerted the greatest impact on β-diversity. However, this pattern prevailed only in case of abundance-based SCBD similarly to observations by Heino & Grönroos (2017) for stream insects and by Vilmi et al. (2017) for stream and lake diatom communities. The incidence-based calculations of this study revealed that species with intermediate occupancy had the largest contribution to β-diversity, which was also observed by Heino & Grönroos (2017). This may be due to the fact that occupancy of these species can vary largely across the sites (Gaston et al. 2006). Species with the highest incidence-based SCBD were *Eolimna minima*, *Halamphora veneta*, *Nitzschia palea* var. *tenuirostris, N. palea* var. *debilis* and *N. supralitorea,* which are relatively common and possess intermediate-sized niches (Hofmann et al., 2011). Also, their total abundance was intermediate in the present data set, but in this case, the relationship between SCBD and species' abundance was statistically not significant. However, it is important to note that both dependent (SCBD index) and explanatory variables (occupancy and species' total abundance) of the models are not independent mathematically, since each of them is conducted from the same raw community data (even abundance or presence-absence), which might have affected the strong relationship between them (Legendre & De Cáceres, 2013; Heino & Grönroos, 2017).

6. Conclusions

Within the oligo-mesotrophic Lake Stechlin, no spatial segregation of α-diversity and composition of benthic diatom community was revealed according to the basins. However, moderate changes in nutrient forms along the shoreline seem to induce relatively high β-diversity enhanced by species replacement, even if species' autecological preferences did not differ considerably. The temporal variation of communities was more prominent compared to the spatial patterns, owing largely to the dominance of centric species settled from the phytoplankton and to the lower species richness in spring.

In ecosystems affected by multiple stressors such as soda pans (high conductivity, pH, TP, turbidity and daily temperature fluctuation), high β-diversity of diatom metacommunities due to species turnover was observed, and the explained variation of communities was related primarily to the environmental differences, which refers to the role of underlying deterministic processes. Within both small investigated regions (Danube-Tisza Interfluve and Fertő-Hanság region), environmental filtering overrode the effect of spatial variables, and the species richness (α-diversity) of communities in single soda pans was low in the DT region and moderate in the FH region. Although α-diversity is relatively low regarding the individual pans, the high β-diversity might indicate that the single pans are inhabited by different communities (consisted of different species combinations) that raises their conservation value. Climate change and anthropogenic interventions (e.g. water drainage, dredging, pumping of groundwater) induce irreversible changes in the natural hydrological cycle of soda pans, thus threatening their good ecological status and even their existence (Williams, 2002; Boros et al., 2013). In the FH region, significant temporal changes in diatom communities were experienced which is probably due to the restoration activities supplying water permanently or periodically for the pans. However, it can not be ruled out that the overrepresentation of temporal scale might have resulted in the significant proportion of community variance explained by pure temporal differences, as this pattern became negligible when data subset having similar representation of spatial and temporal scales was examined. Since diatoms proved to be suitable for indicating the changes in the limnological characteristics of soda pans, continuous monitoring of diatoms (including β-diversity studies) is suggested and they should be considered during ecological status assessment and the development of conservation management.

Environmental heterogeneity across small freshwater lakes in a mid-latitude region, estimated by the mean Euclidean distance of all environmental parameters, was considerably higher than along the littoral region of Lake Stechlin but only slightly lower compared to the values measured across natural and reconstructed soda pans. However, the calculated values can be affected by the number of measured environmental factors, the number of samples considered and the spatial and temporal scales. At intermediate spatial scale, the explained variation in benthic diatom communities was related both to spatial distance and to the differences in local environmental factors. Accordingly, development of communities was driven both by dispersal limitation complying with the neutral theory and patch dynamics and by environmental filtering inherent to species-sorting perspective. After omitting some spatially more "isolated" sampling sites and focusing on the "more clustered" ones within a reduced area, the effect of spatial distance (i.e., the dispersal limitation) became negligible and the importance of species-sorting increased. Nevertheless, because the patterns are largely dependent on several factors (such as scale of heterogeneity, environmental variables considered during the study, dispersal rates, size of species pool and stochastic processes) and most of the community variance was unexplained, conclusions should be drawn with caution. For both the entire and the reduced region in the Carpathian Basin, high α-diversity (average of local species richness) and high β-diversity enhanced mainly by species turnover were observed. The most important lakes regarding the establishment of β-diversity and its components differed considerably in their environmental characteristics confirming the important role of environmental filtering. Lakes with the highest contribution to overall β-diversity (and with the highest ecological uniqueness in terms of turnover, too) hosted a lower number of diatom species than the average, however, biodiversity conservation, in general, focuses on preserving species-rich sites. Furthermore, β-diversity was related mainly to the regionally common species that have medium-sized or broad niches, instead of the ecologically restricted ones. This confirmed the previous suggestions made by Heino & Grönroos (2017) and Vilmi et al. (2017) that if a study aims comprehensive conservation planning, a simultaneous application of LCBD and SCBD indices combining with the focus on species-rich ecosystems and rare species would be sufficient.

Abundance-based and incidence-based analyses revealed similar results and led to the same conclusions regarding the metacommunity concepts and the estimated β-diversity in case of all spatial scales. However, they highlighted differences in null model analyses when the role of deterministic and stochastic processes was assessed in case of soda pans: basically, the key role of deterministic mechanisms was emphasized in both areas but in natural soda pans of the DT region, incidence-based β-diversity and nestedness were related strongly to random expectations indicating that stochastic processes might have induced changes in species occurrences. Nevertheless, proportion of unexplained variances resulted from variation partitionings was high which can be the result of both deterministic and stochastic processes. Furthermore, different patterns of species' ecological uniqueness were displayed depending on whether their abundance or only their incidence was taken into account. Consequently, for assessing species' ecological uniqueness during an extensive research of metacommunities, conducting the analyses both on species abundance and binary data is recommended, especially in case of conservation objectives.

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Additionally, present thesis could not be prepared without the teamwork of the Department of Limnology's colleagues and students in field and in laboratory, and without the laboratory assistance of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries' colleagues.

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8. Contribution to the research

Samples from Lake Stechlin were collected with Dr Géza Balázs Selmeczy's help. The sampling of soda pans was conducted primarily by Dr Edina Lengyel, Dr Csilla Stenger-Kovács, Dávid Németh and István Kacsala with the assistance of colleagues of the Fertő-Hanság National Park: Attila Pellinger, Dr András Ambrus, Péter Kugler, Gábor Takács; and of the Kiskunság National Park: Tamás Sápi, Dr Csaba Pigniczki, Sándor Kovács. The sampling of small freshwater lakes was teamwork of the Department of Limnology's colleagues and students: Dr Katalin Eszter Hubai, Dr Viktória Üveges, Dr Kata Karádi-Kovács, Dr Géza Balázs Selmeczy, Dr Tamás Kucserka, Dávid Németh, Máté Vass, István Kacsala, Réka Molnár.

The preparation of diatom samples collected from the Carpathian Basin was carried out mainly by Dávid Németh and Dr Edina Lengyel.

Diatom taxa found in saline and freshwater lakes of the Carpathian Basin were identified by Dr Edina Lengyel and Dr Csilla Stenger-Kovács with Dr Krisztina Buczkó's help in scanning electron microscopic analyses. Scanning electron microscopic analysis of diatom samples from Lake Stechlin was conducted with Reingard Rossberg's assistance.

Laboratory analyses of water samples collected in the Carpathian Basin were performed as teamwork of the Department of Limnology's colleagues and technicians: Dr Katalin Eszter Hubai, Dr Viktória Üveges, Dr Edina Lengyel, Dr Kata Karádi-Kovács, Dr Csilla Stenger-Kovács, Dr Géza Balázs Selmeczy, Dr Tamás Kucserka, Tamás Pálmai, Dávid Németh, István Kacsala and many BSc and MSc students. Water chemical parameters of Lake Stechlin were measured by Uta Mallok.

The collection of epilithon and water samples from Lake Stechlin, diatom sample preparation, species identification and all statistical analyses presented in the recent dissertation were my own work. I participated in the samplings conducted in the Carpathian Basin and in the laboratory analyses of the water samples furthermore, I helped Dr Edina Lengyel in the identification of diatom species collected from small freshwater lakes.

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10. Results in thesis points

10.1. Community patterns of benthic diatom flora in Lake Stechlin

10.1.1. In most samples of the pelagic and along the littoral zone of Lake Stechlin, TP concentration indicated mesotrophic status. In line with this, mainly meso-eutraphentic and eutraphentic species were identified in the shoreline, or those that tolerate a wide range of trophic levels. Consequently, both nutrients and community composition pointed at the change of the lake from the originally oligotrophic to mesotrophic status.

10.1.2. Although no significant difference of Shannon diversity was found between 2013 spring and 2014 autumn, species richness was lower in spring and community composition also differed in the two years. In the spring communities, the remarkable proportion of Mediophyceae taxa was recognized due to predominance of *Stephanodiscus rugosus* and *S. neoastraea* sunk from the phytoplankton at the beginning of summer stratification, whereas the autumn communities were characterized by Bacillariophyceae species. As a consequence, due to the high relative abundance of centric species in the phytobenthos, sampling for ecological quality assessment in spring is not suggested.

10.1.3. Significant spatial segregation of α-diversity metrics (species richness and Shannon diversity) and community composition based on the three basins was not observed. However, in 2014 September, both abundance- and incidence-based analyses showed that the spatially structured environmental differences explained community variation to some extent, and high β-diversity was enhanced mainly by species replacement. In conclusion, moderate spatial change of environmental parameters might have caused species replacement along the littoral region resulting in relatively high β-diversity. However, variation of nutrient forms covered only a relatively narrow range thus, autecological preferences of species did not differ considerably.

10.2. Benthic diatom metacommunities across natural and reconstructed soda pans in the Carpathian Basin

10.2.1. Species richness observed in the natural soda pans of the Danube-Tisza Interfluve was remarkable lower than in the reconstructed soda pans of the Fertő-Hanság region. However, β-diversity due to species replacement was fairly high in both regions according either to the abundance- or the incidence-based approach.

10.2.2. Within the metacommunity of the DT region where the natural hydrological cycle of soda pans is inviolate, the explained variance in diatom communities were related mainly to the environmental differences referring to species-sorting mechanisms. In the soda pans located in the habitat reconstruction area of the FH region, considering the one-year period, significant temporal variation in community structure also appeared besides the environmental filtering. One possible explanation for this might be that water management and periodic water supply caused community changes. On the other hand, the significant effect of pure temporal distance might have been resulted also from the overrepresentation of temporal scale in the one-year data set.

10.2.3. It was revealed that deterministic mechanisms, such as environmental filtering, played an important role in establishment of β-diversity, however, the high proportion of unexplained variances indicates that the development of communities might have been affected by both deterministic and stochastic processes.

10.3. Benthic diatom metacommunity across small freshwater lakes in the Carpathian Basin

10.3.1. Across small freshwater lakes, both local species richness and regional β-diversity estimated from abundance and presence-absence community data were high. As observed in case of Lake Stechlin and soda pans as well, community dissimilarity among the lakes was maintained predominantly by species replacement, whereas the subsets components of total β-diversity were negligible.

10.3.2. It was experienced that the structure of diatom metacommunity was affected both by dispersal limitation inherent to neutral theory and patch-dynamics and by species-sorting mechanism. The elimination of the spatially “isolated” lakes from the investigation implied that in case of the “more clustered” sampling sites within a spatially reduced area, species-sorting became prevalent.

10.3.3. Although lakes with the highest local contribution to β-diversity and to its species replacement and nestedness components were different in case of abundance and incidence community data, their environmental drivers did not differ considerably: phosphorus and nitrogen forms, pH, COD and SRSi were the most decisive. Furthermore, the ecologically most unique sites in terms of replacement had the highest contribution to overall β-diversity in the region, and the more species a given site hosted, the lower its ecological uniqueness was.

10.3.4. Based on abundance data, the regionally common diatom species with broad ecological niche and high abundance variation contributed to β-diversity to the greatest extent. However, based on incidence data, species occupied intermediate number of sites and have intermediate-sized niches had the highest contribution to β-diversity, indicating their high ecological uniqueness.

11. List of publications

11.1. Papers related to the dissertation

Szabó, B., Padisák, J. & Stenger-Kovács, C. (2014). A Stechlin-tó (Németország) kovaalga összetétele. Hidrológiai Közlöny, 94: 79–81.

Szabó, B., Padisák, J., Selmeczy, G.B., Krienitz, L., Casper, P. & Stenger-Kovács, C. (2017). Spatial and temporal patterns of benthic diatom flora in Lake Stechlin, Germany. Turkish Journal of Botany, 41: 211–222. ***IF: 1.066, SJR: Q2.***

Szabó, B., Lengyel, E., Padisák, J., Vass, M. & Stenger-Kovács, C. (2018). Structuring forces and β-diversity of benthic diatom metacommunities in soda pans of the Carpathian Basin. European Journal of Phycology, 53: 219–229. ***IF: 2.481, SJR: Q1.***

Szabó, B., Lengyel, E., Padisák, J. & Stenger-Kovács, C. (2019). Benthic diatom metacommunity across small freshwater lakes: driving mechanisms, β-diversity and ecological uniqueness. Hydrobiologia, 828: 183–198. ***IF: 2.165, SJR: Q1.***

11.2. Other papers

Pálmai T., Selmeczy G.B., **Szabó B.**, G.-Tóth L., Padisák J. (2016). A *Microcystis flos-aquae* fotoszintetikus aktivitása a Balaton keleti medencéjében 2015 nyarán. Hidrológiai közlöny, 96: 75–78.

Lengyel, E., Padisák, J., Hajnal, É., **Szabó, B.**, Pellinger, A. & Stenger-Kovács, C. (2016). Application of benthic diatoms to assess efficiency of conservation management: a case study on the example of three reconstructed soda pans, Hungary. Hydrobiologia, 777: 95–110. ***IF: 2.165, SJR: Q1.***

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Selmeczy, G.B., Kajan, K., **Szabó, B.**, Casper, P. & Padisák, J. (2017). A fitoplankton közösség hosszútávú változásainak értékelése a fitoplankton funkcionális csoportjainak összetétele alapján a Stechlin-tóban (Németország). Hidrológiai közlöny, 97: 21–23.

Pálmai, T., **Szabó, B.**, Hubai, K.E. & Padisák, J. (2018). Photosynthetic performance of two freshwater red algal species. Acta Botanica Croatica, 77: 135–140. ***IF: 0.580, SJR: Q3.***

Stenger-Kovács C., Körmendi K., Lengyel E., Abonyi A., Hajnal É., **Szabó B.**, Buczkó K. & Padisák J. (2018). Expanding the trait-based concept of benthic diatoms: Development of trait- and species-based indices for conductivity as the master variable of ecological status in continental saline lakes. Ecological Indicators, 95: 63–74. ***IF: 3.983, SJR: Q1.***

11.3. Congress attendances related to the dissertation

Szabó, B., Padisák, J. & Stenger-Kovács, C. (2013). A Stechlin-tó (Németország) kovaalga összetétele. LV. Hidrobiológus Napok, Tihany (Hungary), 2-4 October 2013, ***poster presentation***

Szabó, B., Selmeczy, G.B., Krienitz, L., Padisák, J. & Stenger-Kovács, C. (2015). Benthic diatom composition of Lake Stechlin (Germany). 4th Fresh Blood for Freshwater Conference, Research Institute for Limnology in Mondsee, University of Innsbruck, Mondsee (Austria), 15-17 April 2015, ***oral presentation***

Szabó, B., Lengyel, E., Padisák, J. & Stenger-Kovács, C. (2015). Kis szikes tavak kovaalga diverzitásának mintázata stressz gradiensek mentén. 10. Magyar Ökológus Kongresszus, Pannon Egyetem, Veszprém (Hungary), 12-14 August 2015, ***oral presentation***

Szabó, B., Selmeczy, G.B., Padisák, J., Stenger-Kovács, C. (2015). A Stechlin-tó kovaalga összetételének tér- és időbeli változása. III. Aktuális Eredmények a Kriptogám Növények Kutatásában Konferencia, Eger (Hungary), 17-18 November 2015, ***oral presentation***

Stenger-Kovács, C., Lengyel, E., Buczkó, K., Abonyi, A., Kovács, W.A., Körmendi, K., Lázár, D., Hajnal, É., **Szabó, B.** & Padisák, J. (2015). Szikes tavak kovaalgáinak szerepe az ökológiai állapotbecslésben és a klímaváltozás hatásainak megértésében. III. Aktuális Eredmények a Kriptogám Növények Kutatásában Konferencia, Eger (Hungary), 17-18 November 2015, ***oral presentation***

Szabó, B., Lengyel, E., Padisák, J. & Stenger-Kovács, C. (2016). Beta diversity of benthic diatom communities in soda pans in the Carpathian basin. 5th Interdisciplinary Doctoral Conference, Pécs (Hungary), 27-29 May 2016, ***oral presentation***

Szabó, B., Lengyel, E., Padisák, J. & Stenger-Kovács, C. (2017). Beta-diversity and the main drivers of benthic diatom communities in soda pans of the Carpathian Basin. 5th Fresh Blood for Freshwater Conference, Institute of Hydrobiology, Biology Centre CAS, České Budějovice (Czech Republic), 9-13 April 2017, ***oral presentation***

Szabó, B., Lengyel, E., Stenger-Kovács, C. & Padisák, J. (2017). Beta-diversity and structuring forces of diatom communities in small lakes of the Carpathian Basin. 4th Conference on Cryptogams, Eger (Hungary), 30 November - 1 December 2017, ***oral presentation***

Szabó, B., Lengyel, E., Stenger-Kovács, C., Vass, M. & Padisák, J. (2018). Kárpát-medencei kis tavak kovaalga metaközösségeinek béta-diverzitása és alakító tényezőik. XI. Algológiai Találkozó és Továbbképzés, Budapest (Hungary), 17 May 2018, ***oral presentation***

Szabó, B., Lengyel, E., Padisák, J. & Stenger-Kovács, C. (2018). Édesvízi kis tavak kovaalga metaközössége a Kárpát-medencében. LX. Hidrobiológus Napok, Tihany (Hungary), 3-5 October 2018, ***oral presentation***

11.4. Other congress attendances

Szabó, B., Fuchs, A., Selmeczy, G.B., Stenger-Kovács, C., Zsuga-Biró, R. & Padisák, J. (2014). A Stechlin-tavon végzett mezokozmosz kísérlet üledékcsapdáinak kovaalga közössége. Tavaszi Szél Konferencia, Henkel Kémiai és Környezettudományi Szekció, Debrecen (Hungary), 22 March 2014, ***oral presentation***

Pálmai, T., **Szabó, B.** & Padisák, J. (2015). Különböző divízióba tartozó algafajok ökofiziológiai plaszticitásának jellemzése. 10. Magyar Ökológus Kongresszus, Pannon Egyetem, Veszprém (Hungary), 12-14 August 2015, ***oral presentation***

Pálmai, T., Selmeczy, G.B., **Szabó, B.**, G.-Tóth, L. & Padisák, J. (2015). A *Microcystis flos-aquae* fotoszintetikus aktivitása a Balaton keleti medencéjében 2015 nyarán. LVII. Hidrobiológus Napok, Tihany (Hungary), 7-9 October 2015, ***oral presentation***

Pálmai, T., **Szabó, B.** & Padisák, J. (2015). Kerti tavak szerepe az algakutatásban és az ökofiziológiai vizsgálatokban. III. Aktuális Eredmények a Kriptogám Növények Kutatásában Konferencia, Eger (Hungary), 17-18 November 2015, ***oral presentation***

Pálmai, T., **Szabó, B.** & Padisák, J. (2015). Comparison of the photosynthesis of a stream and a lake red alga. 5th Interdisciplinary Doctoral Conference, Pécs (Hungary), 27-29 May 2016, ***oral presentation***

Selmeczy, G.B., Kajan, K., **Szabó, B.**, Casper, P. & Padisák, J. (2016). A fitoplankton közösség hosszútávú változásainak értékelése a fitoplankton funkcionális csoportjainak összetétele alapján a Stechlin-tóban (Németország). LVIII. Hidrobiológus Napok, Tihany (Hungary), 5-7 October 2016, ***poster presentation***

Pálmai, T., **Szabó, B.**, Hubai, K. E., Selmeczy, G.B. & Padisák, J. (2017). Temperature- and light intensity preference of four freshwater green algae from different habitats. 5th Fresh Blood for Freshwater Conference, Institute of Hydrobiology, Biology Centre CAS, České Budějovice (Czech Republic), 9-13 April 2017, ***oral presentation***

Pálmai, T., **Szabó, B.** & Padisák, J. (2017). Plaszticitás. X. Algológiai Találkozó és Továbbképzés, Budapest (Hungary), 3 May 2017, ***oral presentation***

Pálmai, T., **Szabó, B.** & Padisák, J. (2017). A *Picocystis salinarum* ökofiziológiai vizsgálata folyamatos algatenyésztőben. X. Algológiai Találkozó és Továbbképzés, Budapest (Hungary), 3 May 2017, ***oral presentation***

Appendix

Appendix 1 *Formulation of the pairwise and multiple-site Sørensen and Bray-Curtis dissimilarity indices and that of their components (*a *= the number of species common to both sites,* b *= the number of species unique to the first site,* c *= the number of species unique to the second site,* b_{ij} *= the number of species unique to site i,* b_{ji} *= the number of species unique to site j,* S_i *= total number of species at site i,* S_T *= total number of species in the data set,* A *= the number of individuals of each species that exists in both sites j and k,* B *= the number of individuals that are unique to site j,* C *= the number of individuals that are unique to site k,* x_{ij} *= the number of individuals of species i at site j,* x_{ik} *= the number of individuals of species i at site k,* S *= total number of species at sites j and k,* T_{AB} *= total abundance in the data set).*

Index	Formula	Reference
β_{sor}	$\frac{b+c}{2a+b+c}$	Sørensen (1948), Koleff et al. (2003)
β_{sim}	$\frac{\min(b,c)}{a+\min(b,c)}$	Simpson (1943), Lennon et al. (2001), Koleff et al. (2003)
β_{nes}	$\frac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)}\times\frac{a}{a+\min(b,c)}$	Baselga (2010)
β_{bray}	$\frac{\sum_i \lvert x_{ij}-x_{ik}\rvert}{\sum_i x_{ij}+x_{ik}}=\frac{B+C}{2A+B+C}$	Bray & Curtis (1957)
$\beta_{bray.bal}$	$\frac{\min(B,C)}{\mathrm{A}+\min(B,C)}$	Baselga (2013b)
$\beta_{bray.gra}$	$\frac{\lvert B-C\rvert}{2A+B+C}\times\frac{A}{A+\min(B,C)}$	Baselga (2013b)
β_{SOR}	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}max(b_{ij},b_{ji})]}{2[\sum_i S_i-S_T]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}max(b_{ij},b_{ji})]}$	Baselga (2010)
β_{SIM}	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]}{[\sum_i S_i-S_T]+[\sum_{i<j}\min(b_{ij},b_{ji})]}$	Baselga et al. (2007), Baselga (2010)
β_{NES}	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}max(b_{ij},b_{ji})]}{2[\sum_i S_i-S_T]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}max(b_{ij},b_{ji})]}\times\frac{\sum_i S_i-S_T}{[\sum_i S_i-S_T]+[\sum_{i<j}\min(b_{ij},b_{ji})]}$	Baselga (2010)
β_{BRAY}	$\frac{\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])+\sum_{j<k}max(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}{2[T_{AB}-\sum_i^S max(x_{ij},x_{ik},x_{il},x_{im},x_{in}\ldots)]+\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])+\sum_{j<k}max(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}$	Baselga (2017)
$\beta_{BRAY.BAL}$	$\frac{\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}{[T_{AB}-\sum_i^S max(x_{ij},x_{ik},x_{il},x_{im},x_{in}\ldots)]+\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}$	Baselga (2017)
$\beta_{BRAY.GRA}$	$\frac{\sum_{j<k}max(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])+\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}{2[T_{AB}-\sum_i^S max(x_{ij},x_{ik},x_{il},x_{im},x_{in}\ldots)]+\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])+\sum_{j<k}max(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}\times\frac{[T_{AB}-\sum_i^S max(x_{ij},x_{ik},x_{il},x_{im},x_{in}\ldots)]}{[T_{AB}-\sum_i^S max(x_{ij},x_{ik},x_{il},x_{im},x_{in}\ldots)]+\sum_{j<k}min(\sum_i^S[x_{ij}-min(x_{ij},x_{ik})],\sum_i^S[x_{ik}-min(x_{ij},x_{ik})])}$	Baselga (2017)

Appendix 2 *List of diatom taxa found in Lake Stechlin in 2013 spring and 2014 autumn. RL = Red List species (Lange-Bertalot, 1996), 3 = endangered, V = decreasing, R = extremely rare, D = data scarce, * = at present not considered threatened, ** = surely not threatened. B = Basin where the taxon was counted, n = north basin, s = south basin, w = west basin. S = season, SP = spring, A = autumn. Ecological preferences according to Van Dam et al. (1994), pH = pH preferences. 3 = circumneutral, 4 = alkaliphilous, 5 = alkalibiontic. T = trophic preferences, 1 = oligotraphentic, 2 = oligo-mesotraphentic, 3 = mesotraphentic, 4 = meso-eutraphentic, 5 = eutraphentic, 6 = hypereutraphentic, 7 = oligo to eutraphentic (hypereutraphentic). + = species listed by Casper (1985).*

Taxa	**RL**	**B**	**S**	**pH**	**T**	**Casper (1985)**
Achnanthidium minutissimum (Kützing) Czarnecki	**	n,s,w	SP,A	3	7	+
Achnanthidium rosenstockii (Lange-Bertalot) Lange-Bertalot	3	n	A	4	2	
Amphipleura pellucida (Kützing) Kützing	*	s	SP	4	2	+
Amphora aequalis Krammer	*	w	A			
Amphora indistincta Levkov		n,s	A			
Amphora pediculus (Kützing) Grunow	**	n,s,w	SP,A	4	5	+
Amphora stechlinensis Levkov & Metzeltin		s	A			
Aneumastus minor Lange-Bertalot		n,s,w	SP,A	5		
Aneumastus stroesei (Østrup) D.G. Mann	3	s	A	5	4	
Asterionella formosa Hassall	**	n,s	A	4	4	+
Brebissonia lanceolata (C. Agardh) R.K. Mahoney & Reimer	V	n,s,w	SP			+
Caloneis lancettula (Schulz) Lange-Bertalot & Witkowski		w	SP,A			
Cavinula scutelloides (W. Smith) Lange-Bertalot	V	n,w	SP,A	5	5	+
Cocconeis neodiminuta Krammer	R	s,w	SP,A			+
Cocconeis neothumensis Krammer	V	n,s,w	A	5		
Cocconeis pediculus Ehrenberg	**	n,s,w	SP,A	4	5	
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow	**	n,s,w	SP,A	4	5	+
Cocconeis placentula var. *lineata* (Ehrenberg) van Heurck	**	n,s,w	A	4	5	+
Cocconeis pseudolineata (Geitler) Lange-Bertalot	D	n,s,w	A	4		
Craticula cuspidata (Kützing) D.G. Mann	**	n	SP	4	5	+
Cyclotella radiosa (Grunow) Lemmermann	*	n,s	A	4	5	
Cymbella compacta Østrup	*	n,s	SP,A			
Cymbella excisa Kützing		n,s,w	SP,A	4	5	
Cymbella neocistula Krammer		s,w	SP	4	5	
Cymbellafalsa diluviana (Krasske) Lange-Bertalot & Metzeltin	V	s,w	SP,A			

Appendix 2 *List of diatom taxa found in Lake Stechlin in 2013 spring and 2014 autumn (continued).*

Taxa	RL	B	S	pH	T	Casper (1985)
Cymbopleura inaequalis (Ehrenberg) Krammer		w	A			
Denticula kuetzingii Grunow	*	n	A	4	3	+
Diatoma ehrenbergii Kützing	**	n,s,w	SP,A	5	4	
Diatoma moniliformis (Kützing) D.M. Williams	**	n,s,w	SP	5	5	
Diatoma tenuis C. Agardh	**	n,s,w	SP	4	5	+
Diploneis oculata (Brébisson) Cleve	*	s	A	3		
Diploneis parma Cleve	3	s	A			
Discostella stelligera (Cleve & Grunow) Houk & Klee	*	n	A			
Encyonema cespitosum Kützing	**	n,s,w	SP,A		7	
Encyonema lacustre (C. Agardh) Pantocsek	V	s	A	4	4	
Encyonema leibleinii (C. Agardh) W.J. Silva, R. Jahn, T.A. Veiga Ludwig & M. Menezes	**	n,s,w	SP,A	4	5	+
Encyonema reichardtii (Krammer) D.G. Mann	*	s	A			
Encyonema silesiacum (Bleisch) D.G. Mann	*	n,s,w	SP,A	3	7	
Encyonopsis subminuta Krammer & E. Reichardt		n,s,w	SP,A	3	1	
Epithemia adnata (Kützing) Brébisson	**	s,w	A	5	4	+
Epithemia frickei Krammer		n,s,w	SP,A	4		
Epithemia gibba (Ehrenberg) Kützing	*	n,s,w	A	5	5	+
Epithemia sorex Kützing	**	n,s,w	SP,A	5	5	+
Epithemia turgida (Ehrenberg) Kützing	*	n,s,w	SP,A	5	4	+
Eucocconeis laevis (Østrup) Lange-Bertalot	*	s,w	SP	3	1	
Fallacia subhamulata (Grunow) D.G. Mann	*	s	A	3	4	
Fragilaria acus (Kützing) Lange-Bertalot	*	s	SP	4	5	+
Fragilaria mesolepta Rabenhorst	**	n,s,w	SP	4		+
Fragilaria perminuta (Grunow) Lange-Bertalot	*	n,s,w	SP,A	3		
Fragilaria vaucheriae (Kützing) J.B. Petersen	**	n,s,w	SP,A	4	5	+
Gomphoneis sp.		s,w	SP			
Gomphonema acuminatum Ehrenberg	**	n,s,w	SP,A	4	5	+
Gomphonema angusticephalum E. Reichardt & Lange-Bertalot		s,w	SP,A			
Gomphonema italicum Kützing		n,w	SP			
Gomphonema olivaceolacuum (Lange-Bertalot & E. Reichardt) Lange-Bertalot & E. Reichardt	*	n,s	SP			
Gomphonema olivaceum (Hornemann) Brébisson	**	n,s,w	SP,A	5	5	+

Appendix 2 *List of diatom taxa found in Lake Stechlin in 2013 spring and 2014 autumn (continued).*

Taxa	RL	B	S	pH	T	Casper (1985)
Gomphonema olivaceum var. *olivaceoides* (Hustedt) Lange-Bertalot	*	n,s,w	SP	3	3	
Gomphonema pala E. Reichardt		n,s,w	SP,A			
Gomphonema parvulum (Kützing) Kützing	**	n,s,w	SP,A	3	5	+
Gomphonema pumilum var. *rigidum* E. Reichardt & Lange-Bertalot		n,s,w	SP,A			
Gomphonema truncatum Ehrenberg	*	s	SP	4	4	
Gyrosigma sciotoense (W.S. Sullivant) Cleve		s,w	SP	4	5	
Halamphora thumensis (A. Mayer) Levkov	*	s	A	5		
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski	*	n,s	SP,A	4	4	
Hippodonta lueneburgensis (Grunow) Lange-Bertalot, Metzeltin & Witkowski		w	SP			
Karayevia clevei (Grunow) Bukhtiyarova	*	n,s,w	SP,A	4	4	+
Karayevia laterostrata (Hustedt) Bukhtiyarova	3	n,s,w	A	3	1	
Kolbesia gessneri (Hustedt) Aboal		s,w	SP,A	4	4	
Lemnicola hungarica (Grunow) Round & Basson	**	s	A	4	6	
Navicula antonii Lange-Bertalot		n,s,w	SP,A	4	5	
Navicula capitatoradiata H. Germain	**	n,s,w	SP,A	4	5	
Navicula cari Ehrenberg	**	s	A		7	+
Navicula cryptotenella Lange-Bertalot	**	n,s,w	SP,A	4	7	
Navicula cryptotenelloides Lange-Bertalot	*	n,s,w	SP,A	4	7	
Navicula hofmanniae Lange-Bertalot	R	n,s,w	A			
Navicula jakovljevicii Hustedt		n,s,w	SP,A			
Navicula radiosa Kützing	**	n,s,w	SP,A	3	4	+
Navicula reichardtiana Lange-Bertalot	**	n,s,w	SP,A	4		
Navicula reinhardtii (Grunow) Grunow		n,s,w	SP,A	5	5	+
Navicula subalpina E. Reichardt	V	n,s,w	SP,A			
Navicula tripunctata (O.F. Müller) Bory	**	n,s,w	SP,A	4	5	
Navigeia decussis (Østrup) Bukhtiyarova	**	n,s,w	SP,A	4	4	
Neidium dubium (Ehrenberg) Cleve	*	s,w	SP,A	3	4	
Nitzschia archibaldii Lange-Bertalot	*	n,s,w	A	3	5	
Nitzschia dissipata (Kützing) Rabenhorst	**	n,s,w	SP,A	4	4	+
Nitzschia dissipata var. *media* (Hantzsch) Grunow	D	n,s,w	SP,A	4		
Nitzschia lacuum Lange-Bertalot	*	n,s,w	SP,A	4	3	

Appendix 2 *List of diatom taxa found in Lake Stechlin in 2013 spring and 2014 autumn (continued).*

Taxa	RL	B	S	pH	T	Casper (1985)
Nitzschia sociabilis Hustedt	**	n,s,w	A	3	5	
Nitzschia sublinearis Hustedt	*	n,s,w	SP,A			
Pantocsekiella ocellata (Pantocsek) K.T. Kiss & E. Ács	*	n,s,w	SP,A	4	4	+
Paraplaconeis minor (Grunow) Lange-Bertalot		n	SP			
Placoneis clementis (Grunow) E.J. Cox	*	s	SP			
Planothidium frequentissimum (Lange-Bertalot) Lange-Bertalot	**	n,s,w	SP,A	4	7	
Planothidium joursacense (Héribaud-Joseph) Lange-Bertalot	3	n,s	A	4	2	
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot	**	w	SP	4	5	+
Planothidium rostratum (Østrup) Lange-Bertalot	D	n,s,w	SP,A	4	5	+
Platessa conspicua (Ant. Mayer) Lange-Bertalot	**	n,s,w	SP,A	3	7	+
Platessa ziegleri (Lange-Bertalot) Lange-Bertalot	*	s,w	SP,A			
Psammothidium bioretii (H. Germain) Bukhtiyarova & Round	V	n,s	SP,A	3	3	
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	**	n,s,w	SP,A	4	7	+
Pseudostaurosira subconstricta (Grunow) Kulokovskiy & Genkal	**	n,w	SP,A	4	4	
Reimeria sinuata (W. Gregory) Kociolek & Stoermer	**	n,s,w	SP,A	3	3	
Rhoicosphenia tenuis Z. Levkov & T. Nakov	**	n,s,w	SP,A			
Sellaphora pupula (Kützing) Mereschkovsky	**	s,w	SP,A	3	4	+
Sellaphora utermoehlii (Hustedt) C.E. Wetzel & D.G. Mann	*	s	A	3	3	
Simonsenia delognei (Grunow) Lange-Bertalot	**	s	A		5	
Stauroneis gracilis Ehrenberg	V	w	A			
Staurosira binodis (Ehrenberg) Lange-Bertalot	*	s,w	A	4	4	+
Staurosira construens Ehrenberg	**	n,s,w	A	4	4	+
Staurosira venter (Ehrenberg) Cleve & J.D. Möller	**	n,s,w	SP,A	4	4	+
Staurosirella martyi (Héribaud-Joseph) E.A. Morales & K.M. Manoylov	*	s	A	4	4	+
Staurosirella pinnata (Ehrenberg) D.M. Williams & Round	**	n,s,w	SP,A	4	7	+
Stephanodiscus binatus H. Håkansson & H.J. Kling		n,s,w	SP			
Stephanodiscus neoastraea Håkansson & Hickel	**	n,s,w	SP,A	5	5	
Stephanodiscus rugosus J. Sieminska & D. Chudybowa		n,s,w	SP,A			
Tabularia fasciculata (C. Agardh) D.M. Williams & Round		s	SP			
Tryblionella angustata W. Smith	*	s	SP	3	3	
Ulnaria ulna (Nitzsch) Compère	*	n,s,w	SP	4	7	+

Appendix 3 *Red List species found in Lake Stechlin. Scale bar = 10 µm.*

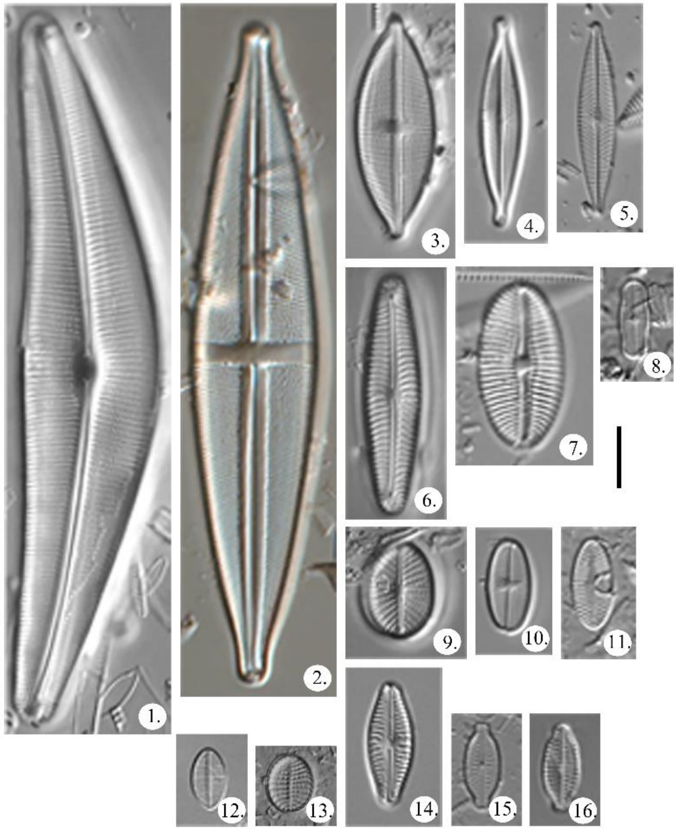


Fig 1 *Brebissonia lanceolata* (C. Agardh) R.K. Mahoney & Reimer

Fig 2 *Stauroneis gracilis* Ehrenberg

Fig 3 *Aneumastus stroesei* (Østrup) D.G. Mann

Fig 4 *Navicula hofmanniae* Lange-Bertalot

Fig 5 *Navicula subalpina* E. Reichardt

Fig 6 *Encyonema lacustre* (C. Agardh) Pantocsek

Fig 7 *Diploneis parma* Cleve

Fig 8 *Achnanthidium rosenstockii* (Lange-Bertalot) Lange-Bertalot

Fig 9 *Cavinula scutelloides* (W. Smith) Lange-Bertalot

Fig 10 *Psammothidium bioretii* (H. Germain) Bukhtiyarova & Round

Fig 11 *Planothidium joursacense* (Héribaud-Joseph) Lange-Bertalot

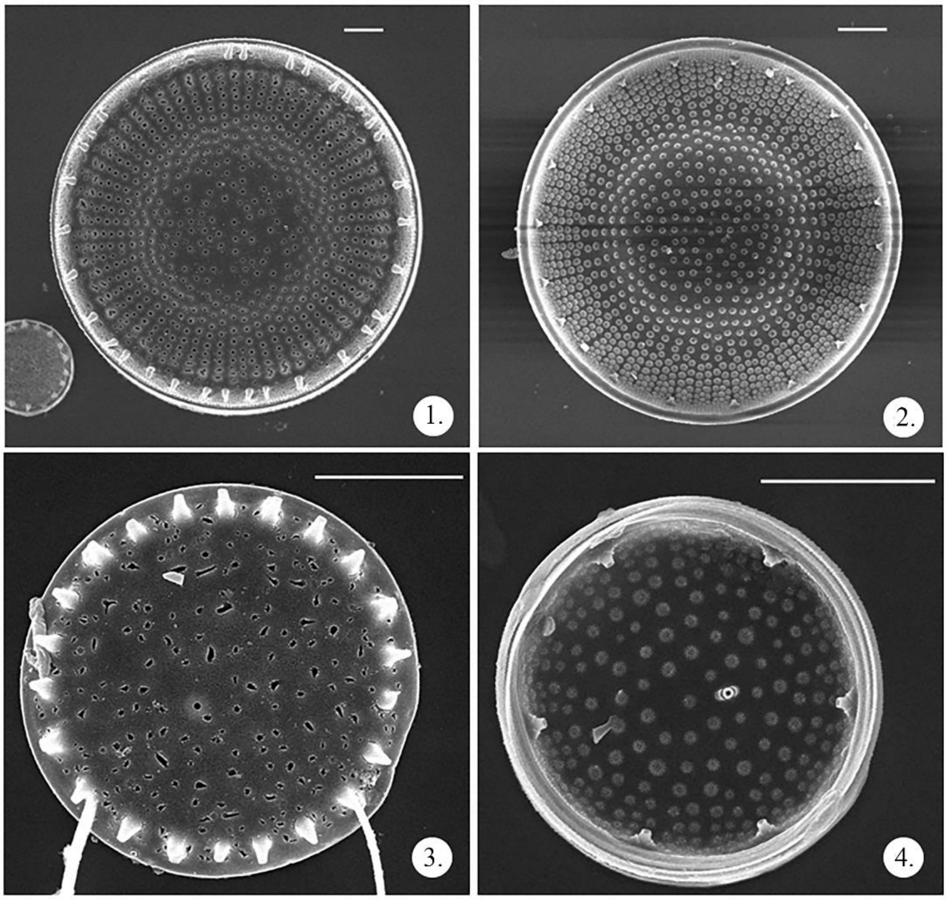
Fig 12 *Cocconeis neothumensis* Krammer

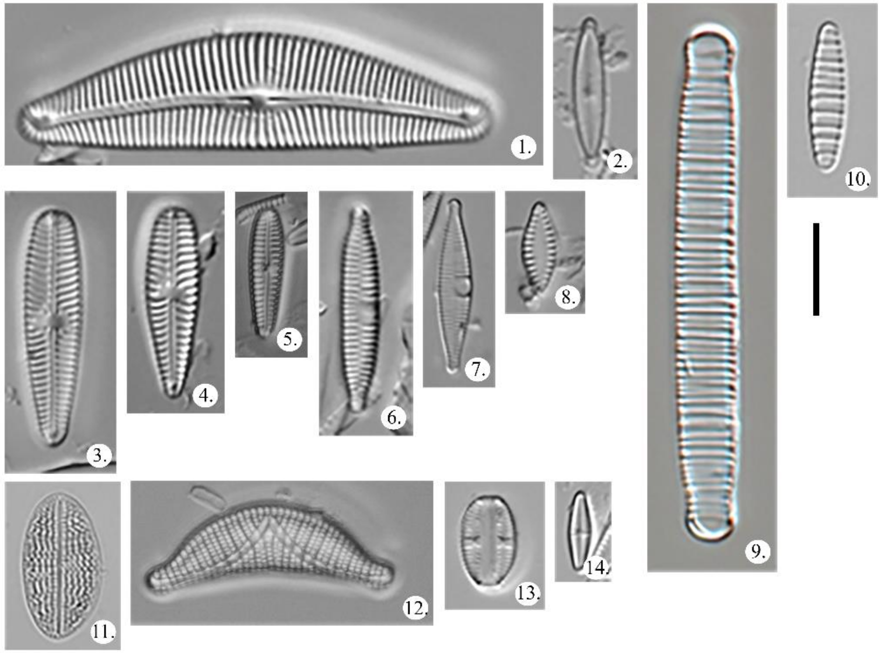
Fig 13 *Cocconeis neodiminuta* Krammer

Fig 14 *Cymbellafalsa diluviana* (Krasske) Lange-Bertalot & Metzeltin

Figs 15–16 *Karayevia laterostrata* (Hustedt) Bukhtiyarova

Appendix 4 *SEM pictures of two dominant Mediophyceae species in spring. Figs. 1–2: Stephanodiscus neoastraea; Figs 3–4: Stephanodiscus rugosus. Scale bar = 3 μm.*





Appendix 5 *Most frequent and abundant Bacillariophyceae species in Lake Stechlin. Scale bar = 10 µm.*

Fig 1 *Cymbella compacta* Østrup

Fig 2 *Encyonopsis subminuta* Krammer & E. Reichardt

Fig 3 *Gomphonema olivaceum* var. *olivaceoides* (Hustedt) Lange-Bertalot

Fig 4 *Gomphonema olivaceum* (Hornemann) Brébisson

Fig 5 *Gomphonema pumilum* var. *rigidum* E. Reichardt & Lange-Bertalot

Fig 6 *Fragilaria vaucheriae* (Kützing) J.B. Petersen

Fig 7 *Fragilaria perminuta* (Grunow) Lange-Bertalot

Fig 8 *Pseudostaurosira brevistriata* (Grunow) D.M. Williams & Round

Fig 9 *Diatoma ehrenbergii* Kützing

Fig 10 *Diatoma moniliformis* (Kützing) D.M. Williams

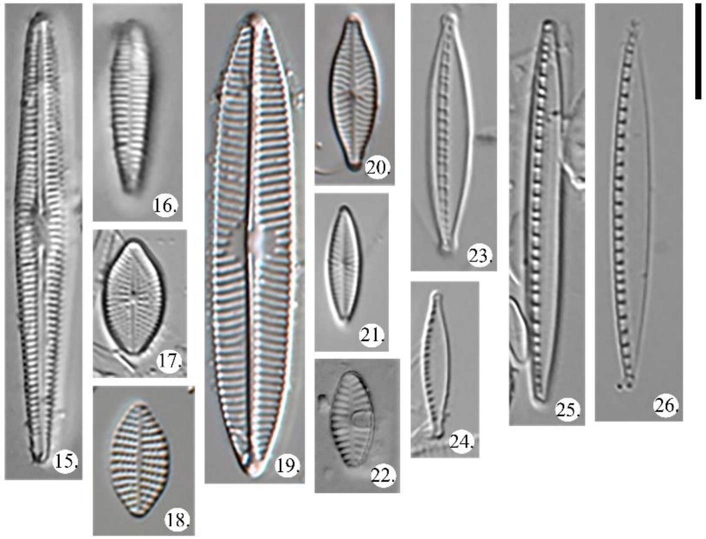
Fig 11 *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow

Fig 12 *Epithemia sorex* Kützing

Fig 13 *Amphora pediculus* (Kützing) Grunow

Fig 14 *Achnanthidium minutissimum* (Kützing) Czarnecki

Appendix 5 *Most frequent and abundant Bacillariophyceae species in Lake Stechlin (continued). Scale bar = 10 µm.*



Figs 15–16 *Rhoicosphenia tenuis* Z. Levkov & T. Nakov

Figs 17–18 *Karayevia clevei* (Grunow) Bukhtiyarova

Fig 19 *Navicula tripunctata* (O.F. Müller) Bory

Fig 20 *Navicula reichardtiana* Lange-Bertalot

Fig 21 *Navicula cryptotenelloides* Lange-Bertalot

Fig 22 *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot

Fig 23 *Nitzschia dissipata* (Kützing) Rabenhorst

Fig 24 *Nitzschia lacuum* Lange-Bertalot

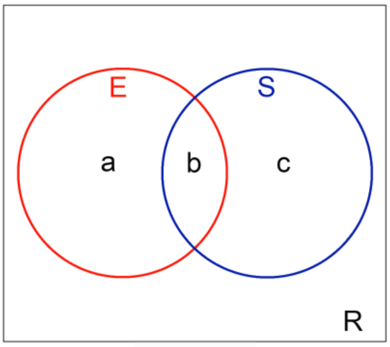
Fig 25 *Nitzschia dissipata* var. *media* (Hantzsch) Grunow

Fig 26 *Nitzschia sociabilis* Hustedt

Appendix 6 *The investigated soda pans, their region, GPS coordinates and the number of samples (FH = Fertő-Hanság region, DT = Danube-Tisza Interfluve).*

Soda pans	Region	GPS coordinates		No. of samples
1. Borsodi-dűlő	FH	N 47.6815	E 16.8400	10
2. Legény-tó	FH	N 47.6632	E 16.8134	12
3. Nyéki-szállás	FH	N 47.6770	E 16.8328	7
4. Bába-szék	DT	N 46.7405	E 19.1503	8
5. Bogárzó-szék	DT	N 46.8048	E 19.1408	7
6. Böddi-szék	DT	N 46.7608	E 19.1437	9
7. Kelemen-szék	DT	N 46.7974	E 19.1831	9
8. Sósér	DT	N 46.7892	E 19.1470	7
9. Zab-szék	DT	N 46.8375	E 19.1698	7

Appendix 7 *Scheme for calculation of the amount of variance in community dissimilarities explained by the pure and shared fractions of Environmental (E) and Spatial (S) distances as well as that of Environmental (E), Spatial (S) and Temporal (T) distances.*

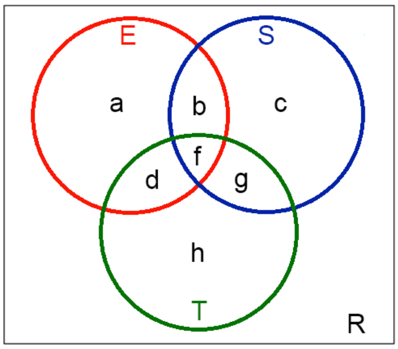


$R^2_a = R^2_{E+S} - R^2_S$

$R^2_c = R^2_{E+S} - R^2_E$

$R^2_b = (R^2_E + R^2_S) - R^2_{E+S}$

$R^2_R = 1 - R^2_{E+S}$



$R^2_a = R^2_{E+S+T} - R^2_{S+T}$

$R^2_c = R^2_{E+S+T} - R^2_{E+T}$

$R^2_h = R^2_{E+S+T} - R^2_{E+S}$

$R^2_b = (R^2_{E+S+T} - R^2_T) - (R^2_a + R^2_c)$

$R^2_d = (R^2_{E+S+T} - R^2_S) - (R^2_a + R^2_h)$

$R^2_g = (R^2_{E+S+T} - R^2_E) - (R^2_c + R^2_h)$

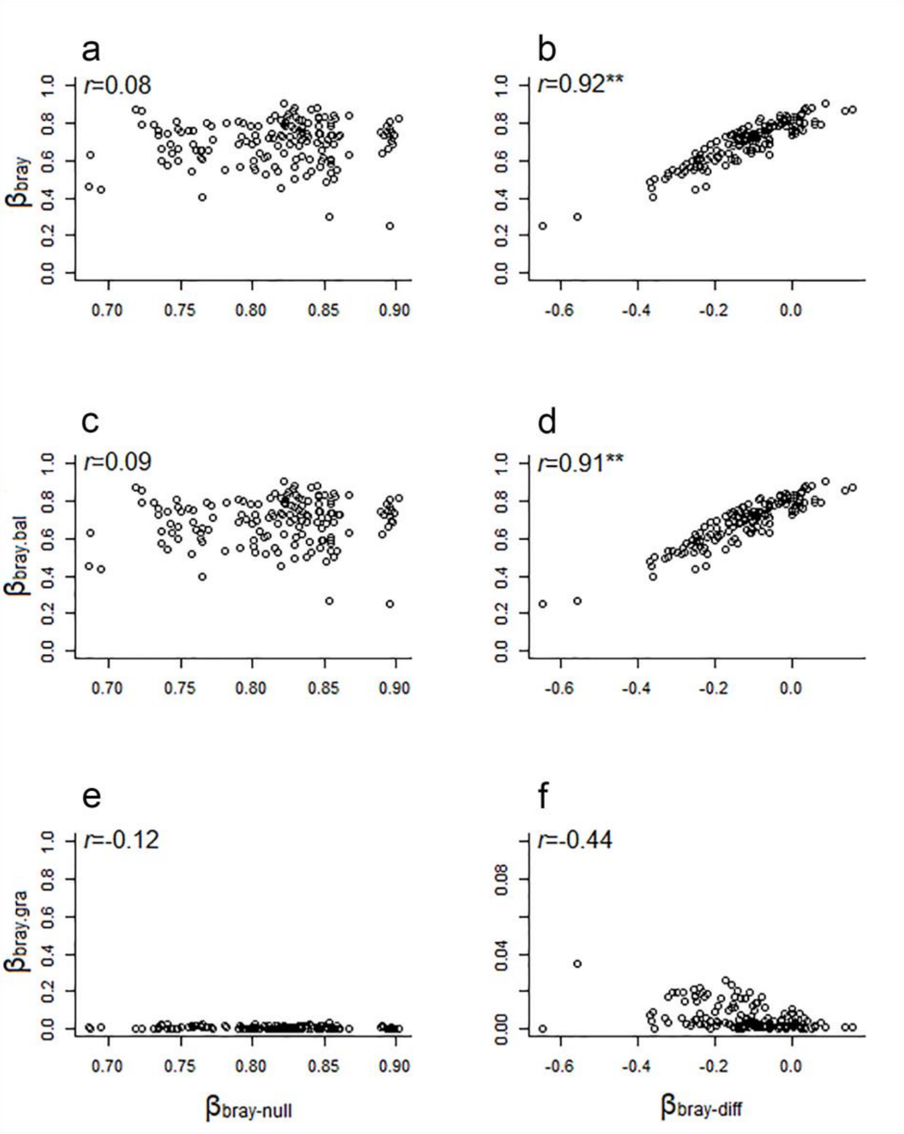
$R^2_f = R^2_E - (R^2_a + R^2_b + R^2_d)$

$R^2_R = 1 - R^2_{E+S+T}$

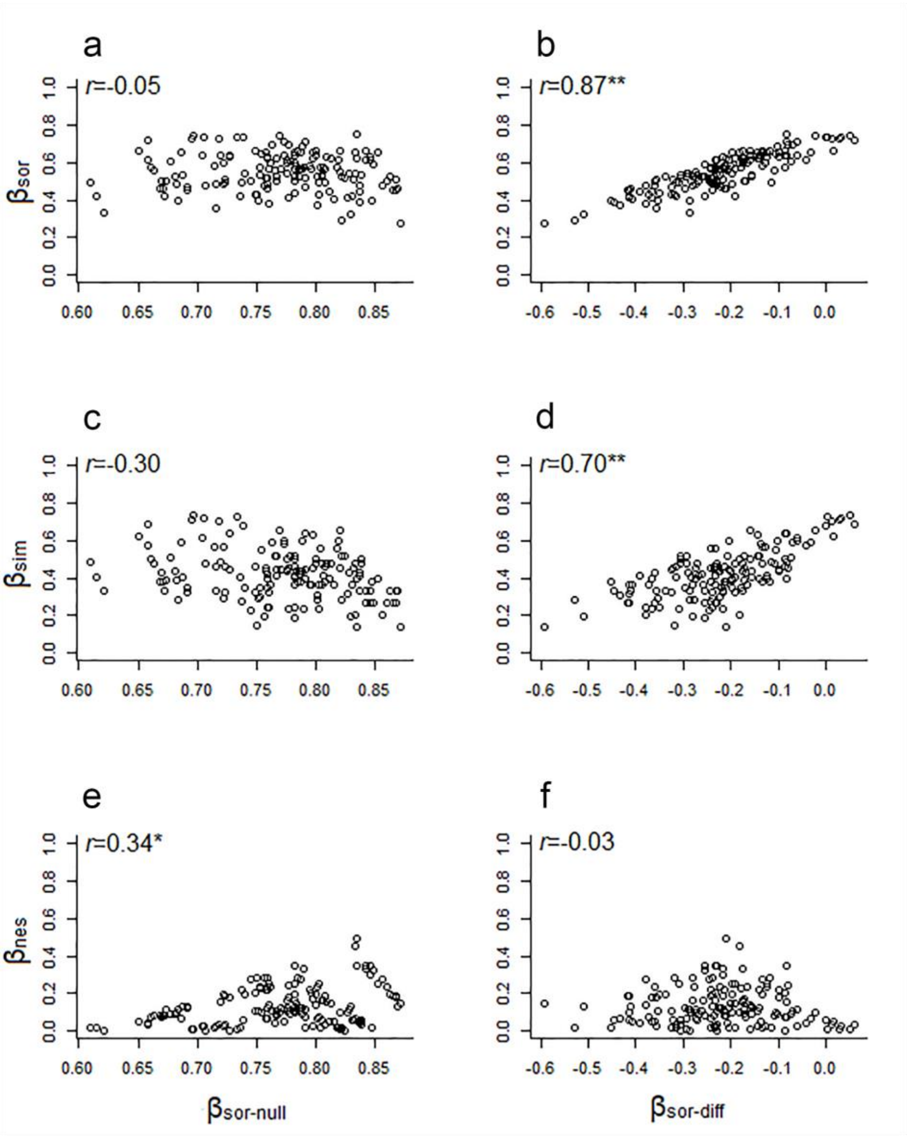
Appendix 8 *β-diversity and its components (β_{BC} = overall dissimilarity measured as Bray-Curtis multiple-site dissimilarity, $\beta_{BC.BAL}$ = balanced variation component, $\beta_{BC.GRA}$ = abundance gradient component, β_{SOR} = overall dissimilarity measured as Sørensen dissimilarity, β_{SIM} = turnover component, β_{NES} = nestedness component) of benthic diatom communities in the Fertő-Hanság region and in the Danube-Tisza Interfluve calculated for data subsets (see details in Chapter 4.3.4.).*

		Fertő-Hanság (n = 18)	**Danube-Tisza Interfluve (n = 20)**
abundance-based β-diversity	β_{BC}	0.904	0.890
	$\beta_{BC.BAL}$	0.902	0.881
	$\beta_{BC.GRA}$	0.002	0.009
incidence-based β-diversity	β_{SOR}	0.859	0.867
	β_{SIM}	0.792	0.794
	β_{NES}	0.067	0.073

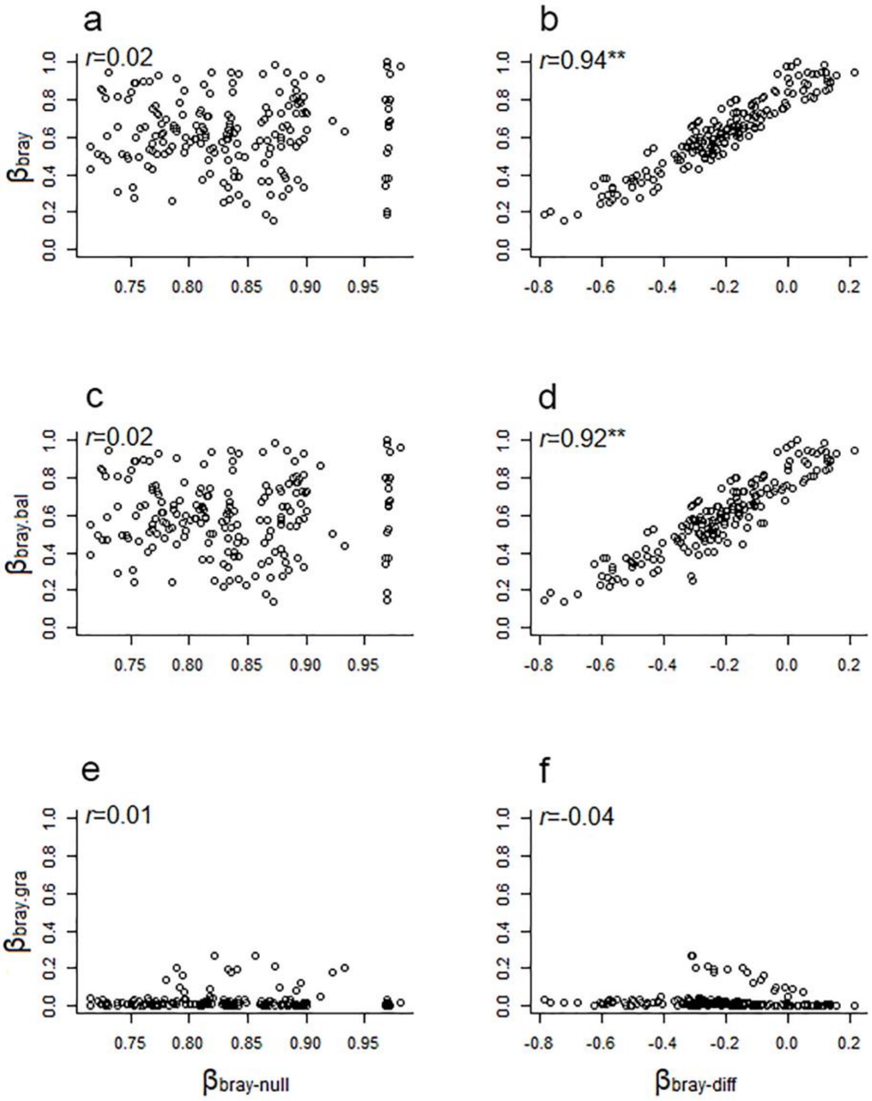
Appendix 9 *The relationship of abundance-based overall β-diversity (β_{bray}; a, b), and its balanced variation ($\beta_{bray.bal}$; c, d) and abundance gradient ($\beta_{bray.gra}$; e, f) components with the overall β-diversity expected under ($\beta_{bray\text{-}null}$; a, c, e) and beyond null model ($\beta_{bray\text{-}diff}$; b, d, f) in case of data subset of the Fertő-Hanság region (see details in Chapter 4.3.4.). Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance level: ** = 0.01.*



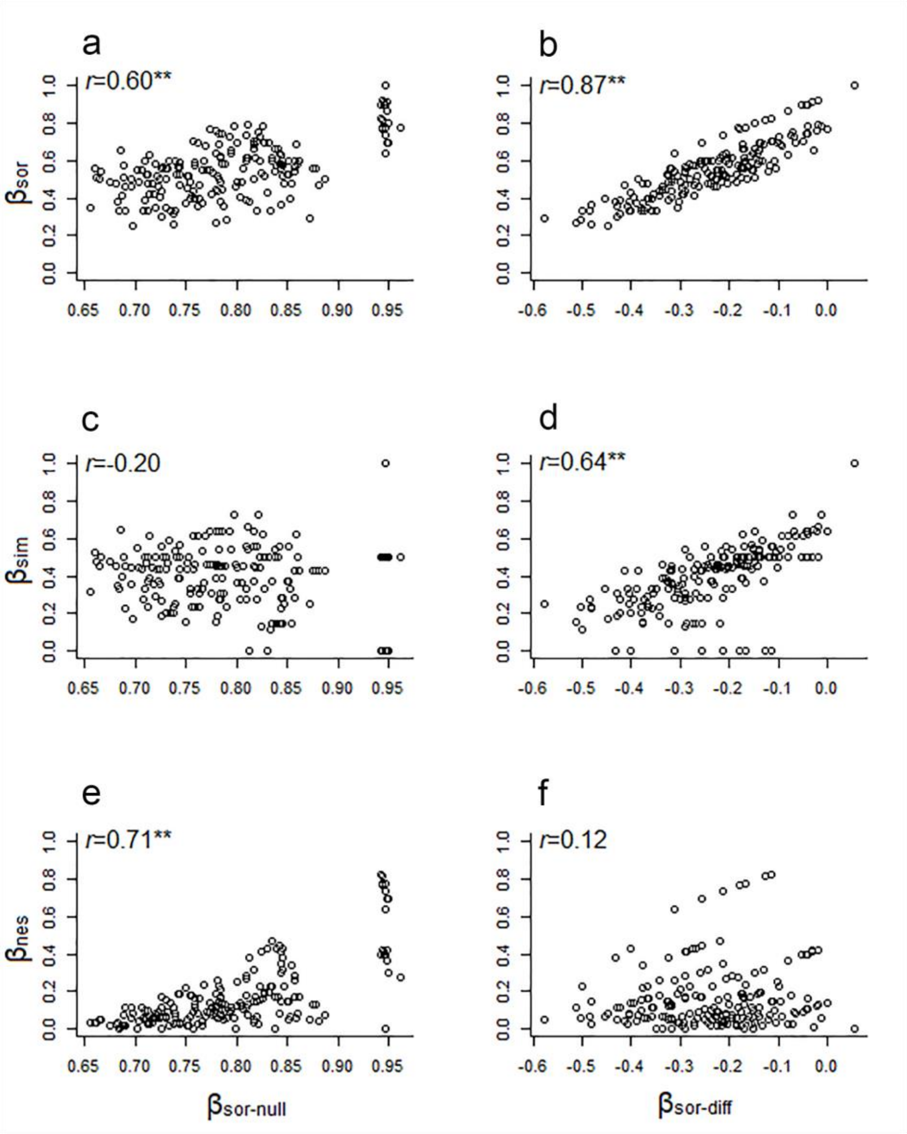
Appendix 10 *The relationship of incidence-based overall β-diversity (β_{sor}; a, b), and its turnover (β_{sim}; c, d) and nestedness (β_{nes}; e, f) components with the overall β-diversity expected under ($\beta_{sor\text{-}null}$; a, c, e) and beyond null model ($\beta_{sor\text{-}diff}$; b, d, f) in case of data subset of the Fertő-Hanság region (see details in Chapter 4.3.4.). Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance levels: ** = 0.01, * = 0.05.*



Appendix 11 *The relationship of abundance-based overall β-diversity (β_{bray}; a, b), and its balanced variation ($\beta_{bray.bal}$; c, d) and abundance gradient ($\beta_{bray.gra}$; e, f) components with the overall β-diversity expected under ($\beta_{bray\text{-}null}$; a, c, e) and beyond null model ($\beta_{bray\text{-}diff}$; b, d, f) in case of data subset of the Danube-Tisza Interfluve (see details in Chapter 4.3.4.). Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance level: ** = 0.01.*



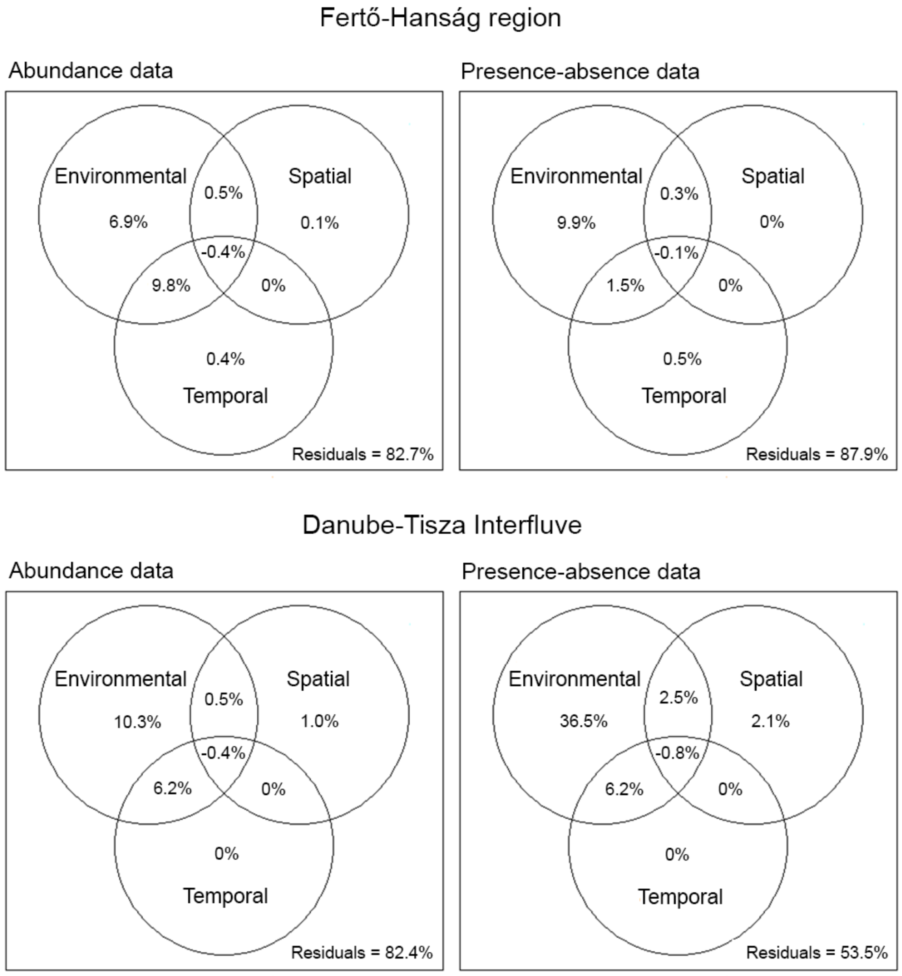
Appendix 12 *The relationship of incidence-based overall β-diversity (β_{sor}; a, b), and its turnover (β_{sim}; c, d) and nestedness (β_{nes}; e, f) components with the overall β-diversity expected under ($\beta_{sor\text{-}null}$; a, c, e) and beyond null model ($\beta_{sor\text{-}diff}$; b, d, f) in case of data subset of the Danube-Tisza Interfluve (see details in Chapter 4.3.4.). Pearson correlation coefficients (r) are shown. P values were computed using Mantel tests. Significance level: ** = 0.01.*



Appendix 13 *Results of multiple regressions on distance matrices (MRM) conducted on data subsets of the Fertő-Hanság region and the Danube-Tisza Interfluve (see details in Chapter 4.3.4.). Community dissimilarities were computed applying Bray-Curtis index based on Hellinger transformed species abundance and presence-absence data. The listed* R^2 *values served as the basis of variation partitioning procedure detailed in Appendix 7. Results of variation partitioning are presented in Appendix 14 (*R^2 *= the amount of variation in community dissimilarities explained by the model, P = P value).*

	Explanatory distance matrices	$\mathbf{R^2}$	**P**
Abundance	Environmental (SRSi+temperature)	0.168	0.001
	Spatial	0.002	0.583
	Temporal	0.098	0.001
	Environmental+Spatial	0.169	0.003
	Environmental+Temporal	0.172	0.003
	Spatial+Temporal	0.104	0.004
	Environmental+Spatial+Temporal	0.173	0.005
Presence-absence	Environmental (SRSi+temperature+conductivity+Pt)	0.116	0.081
	Spatial	0.002	0.593
	Temporal	0.019	0.144
	Environmental+Spatial	0.116	0.107
	Environmental+Temporal	0.121	0.111
	Spatial+Temporal	0.022	0.255
	Environmental+Spatial+Temporal	0.121	0.144
Abundance	Environmental (COD+CO_3^{2-}+temperature+pH)	0.166	0.049
	Spatial	0.011	0.165
	Temporal	0.058	0.015
	Environmental+Spatial	0.176	0.047
	Environmental+Temporal	0.166	0.071
	Spatial+Temporal	0.073	0.014
	Environmental+Spatial+Temporal	0.176	0.068
Presence-absence	Environmental (CO_3^{2-}+HCO_3^{-}+Cl^{-}+temperature+conductivity)	0.409	0.001
	Spatial	0.038	0.010
	Temporal	0.054	0.020
	Environmental+Spatial	0.437	0.001
	Environmental+Temporal	0.416	0.001
	Spatial+Temporal	0.100	0.001
	Environmental+Spatial+Temporal	0.441	0.001

Appendix 14 *Proportion of variation in community dissimilarities in case of data subsets of the Fertő-Hanság region and the Danube-Tisza Interfluve (see details in Chapter 4.3.4.) that can be explained by environmental distance (Environmental), spatial distance (Spatial), temporal distance (Temporal), spatially and temporally structured environmental distance. Unexplained variances are represented by the residuals.*



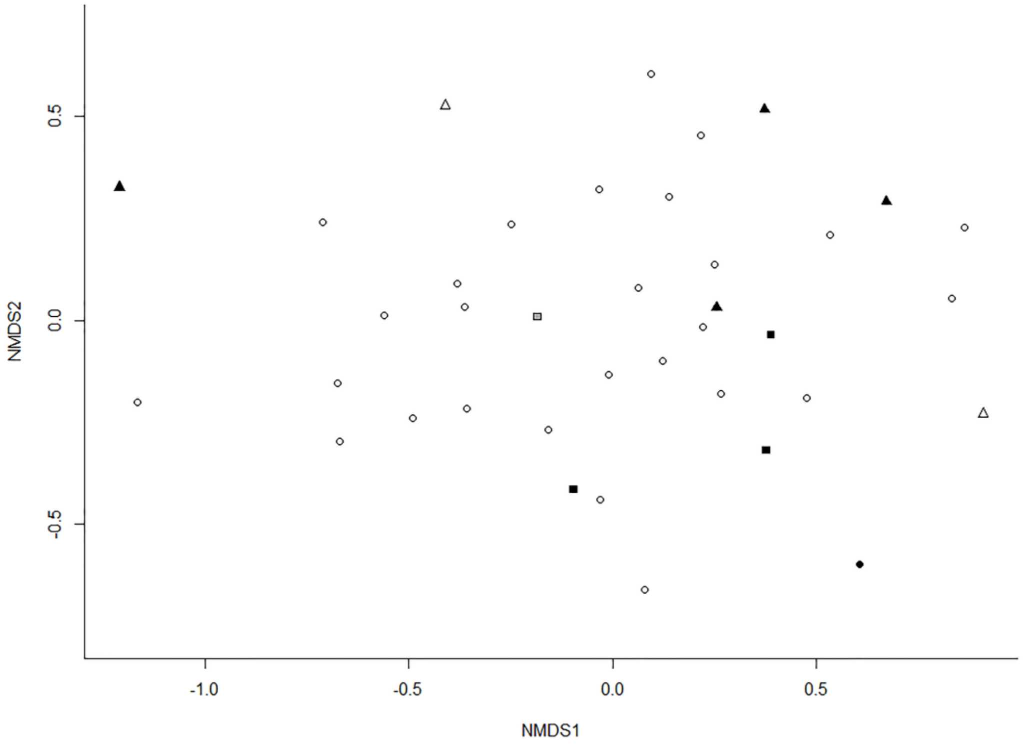
Appendix 15 *Codes for the 38 small freshwater lakes sampled in 2010, their GPS coordinates, altitude, size and depth category, trophic classification based on TP concentration proposed by the OECD (1982), habitat type and date of sampling.*

Lake code	Lake	Sampling date	GPS coordinates		Altitude (m)	Size category	Depth category	Trophic classification	Habitat type
1. ABA	Abaligeti Csónakázótó	16.08.2010	N 46.1398056	E 18.1138611	208	1	shallow	hypertrophic	reservoir
2. ALC	Alcsi Holt-Tisza	09.08.2010	N 47.1336111	E 20.2205528	84	2	moderately deep	hypertrophic	oxbow lake
3. ARL	Arlói-tó	02.08.2010	N 48.1640194	E 20.2684167	210	1	moderately deep	eutrophic	natural
4. ATK	Atkai Holt-Tisza	23.08.2010	N 46.3958056	E 20.1589167	73	2	moderately deep	hypertrophic	oxbow lake
5. CIB	Cibakházi Holt-Tisza	09.08.2010	N 46.9411111	E 20.1944417	77	3	shallow	eutrophic	oxbow lake
6. CSA	Csatlói Holt-Tisza	10.08.2010	N 47.3671611	E 20.4044528	83	1	shallow	hypertrophic	oxbow lake
7. CSER	Cserőközi Holt-Tisza	25.08.2010	N 47.5341667	E 20.6766889	85	1	very shallow	hypertrophic	oxbow lake
8. CSI	Csikóspusztai-tó	24.08.2010	N 46.2908333	E 20.6318333	87	1	very shallow	hypertrophic	natural
9. CSO	Csongrádi Holt-Tisza	23.08.2010	N 46.6997500	E 20.1475556	78	2	shallow	hypertrophic	oxbow lake
10. FAD	Fadd-Dombori Holt-Duna	16.08.2010	N 46.4467222	E 18.8568611	87	3	shallow	eutrophic	oxbow lake
11. FEG	Fegyverneki Holt-Tisza	09.08.2010	N 47.2611083	E 20.5208306	82	2	shallow	eutrophic	oxbow lake
12. FŰZ	Fűzfászugi Holt-Körös	24.08.2010	N 46.9325833	E 20.8039444	80	1	shallow	hypertrophic	oxbow lake
13. HAL	Nagyfoki-holtág	24.08.2010	N 46.9068889	E 20.5991111	79	1	shallow	eutrophic	oxbow lake
14. HÁM	Hámori-tó	02.08.2010	N 48.1108472	E 20.6143222	311	1	deep	hypertrophic	reservoir
15. HAR	Harkai-tó	17.08.2010	N 46.4709722	E 19.5863056	113	2	shallow	hypertrophic	natural
16. HMT	Herman Ottó-tó	16.08.2010	N 46.1706667	E 18.1295833	168	1	shallow	hypertrophic	reservoir
17. KAK	Kakasszéki-tó	24.08.2010	N 46.5464444	E 20.5875000	83	1	shallow	hypertrophic	natural
18. KEN	Kengyel Horgásztó	03.08.2010	N 48.0962694	E 21.3568167	93	1	shallow	eutrophic	oxbow lake
19. KFT	Kun-Fehér-tó	17.08.2010	N 46.3798056	E 19.3946944	133	1	shallow	mesotrophic	natural
20. KHT	Kiskunhalasi Sóstó	17.08.2010	N 46.4591667	E 19.4640556	127	1	shallow	eutrophic	natural
21. LIP	Lipóti Morotva-tó	02.08.2010	N 47.8641667	E 17.4638889	115	1	very shallow	hypertrophic	oxbow lake
22. MÁM	Mámai Holt-Tisza	09.08.2010	N 46.7841639	E 20.1188861	77	2	shallow	hypertrophic	oxbow lake
23. NAV	Nagy-Vadas-tó	25.08.2010	N 47.8598528	E 21.6600972	113	2	very shallow	hypertrophic	natural
24. ÖRE	Öreg-tó	11.08.2010	N 47.6483889	E 18.3263611	130	3	shallow	hypertrophic	reservoir
25. PER	Peresi Holt-Körös	24.08.2010	N 46.9840861	E 20.7103639	79	2	shallow	hypertrophic	oxbow lake
26. PÉT	Péteri-tó	23.08.2010	N 46.5979444	E 19.9133333	88	2	very shallow	hypertrophic	natural
27. PIR	Pirtói Nagy-tó	17.08.2010	N 46.5313333	E 19.4649167	115	2	shallow	hypertrophic	wetland
28. SÁR	Páhi Sárkány-tó	17.08.2010	N 46.7193889	E 19.3923611	99	1	very shallow	eutrophic	natural
29. SCS	Szecska-tó	16.08.2010	N 46.3133528	E 18.5208556	139	1	shallow	eutrophic	reservoir
30. SDI	Szelidi-tó	17.08.2010	N 46.6231667	E 19.0394722	88	1	moderately deep	eutrophic	natural
31. SZAR	Szarvasi-Holt-Körös	24.08.2010	N 46.8701278	E 20.4924750	80	2	shallow	hypertrophic	oxbow lake
32. SZT	Szarvas-tó	17.08.2010	N 46.5445306	E 19.4838750	111	1	very shallow	hypertrophic	natural
33. TDO	Tiszadobi Holt-Tisza	03.08.2010	N 48.0077222	E 21.1729333	95	2	moderately deep	hypertrophic	oxbow lake
34. TOL	Tolnai Holt-Duna	16.08.2010	N 46.4178889	E 18.7944722	89	1	shallow	eutrophic	oxbow lake
35. TÚR	Túrtői Holt-Körös	24.08.2010	N 46.9546389	E 20.5813333	80	2	shallow	hypertrophic	oxbow lake
36. VAD	Vadása-tó	03.08.2010	N 46.8765556	E 16.5513778	217	1	shallow	eutrophic	reservoir
37. VDK	Vadkerti-tó	17.08.2010	N 46.6137222	E 19.3879444	109	1	shallow	hypertrophic	natural
38. VÖR	Vörös-mocsár	17.08.2010	N 46.4625278	E 19.1877500	91	3	very shallow	hypertrophic	wetland

Appendix 16 *Mean, standard deviation, minimum and maximum value of the physical and chemical parameters measured in the 38 small freshwater lakes of the Carpathian Basin.*

variable	**unit**	**mean±SD**	**min**	**max**
NO_2^-	µg L^{-1}	9.4±18.9	0.0	98.1
NO_3^-	µg L^{-1}	554.5±812.7	49.7	4326.9
NH_4^+	µg L^{-1}	46.5±87.8	0.0	456.0
COD	mg L^{-1} O_2	18.4±27.5	2.9	165.5
SRP	µg L^{-1}	102.7±137.1	3.3	632.3
TP	µg L^{-1}	212.2±195.2	31.9	872.8
SRSi	mg L^{-1}	11.1±8.2	0.0	34.8
SO_4^{2-}	mg L^{-1}	67.0±82.6	0.0	393.1
HCO_3^-	mg L^{-1}	351.7±248.9	39.7	1183.4
Cl^-	mg L^{-1}	48.1±66.6	0.3	386.6
temperature	°C	26.0±1.6	22.1	28.5
conductivity	µS cm^{-1}	792.6±534.3	91.8	2650.0
O_2 saturation	%	99.7±45.8	16.1	200.0
turbidity	FNU	22.6±16.0	3.1	53.9
pH		8.4±0.5	7.5	9.3

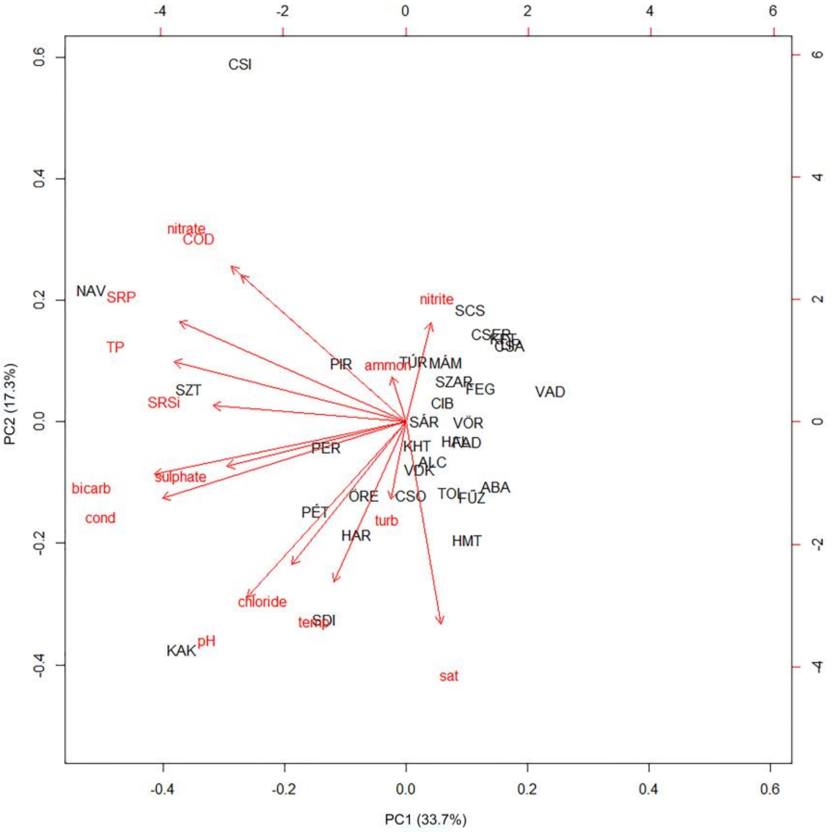
Appendix 17 *NMDS projection (Bray-Curtis distance, stress 0.191) of phytobenthos samples based on Hellinger transformed species abundance data (open circle = reed, black triangle = sedge, grey square = bulrush, open triangle = stone, black square = bough, black circle = mud).*



Appendix 18 *β-diversity and its components (β_{BC} = overall dissimilarity measured as Bray-Curtis multiple-site dissimilarity, $\beta_{BC.BAL}$ = balanced variation component, $\beta_{BC.GRA}$ = abundance gradient component, β_{SOR} = overall dissimilarity measured as Sørensen dissimilarity, β_{SIM} = turnover component, β_{NES} = nestedness component) of benthic diatom communities in small freshwater lakes in the Carpathian Basin calculated for data subsets (see details in Chapter 5.3.2.).*

abundance-based β-diversity	β_{BC}	0.947
	$\beta_{BC.BAL}$	0.943
	$\beta_{BC.GRA}$	0.004
incidence-based β-diversity	β_{SOR}	0.917
	β_{SIM}	0.892
	β_{NES}	0.025

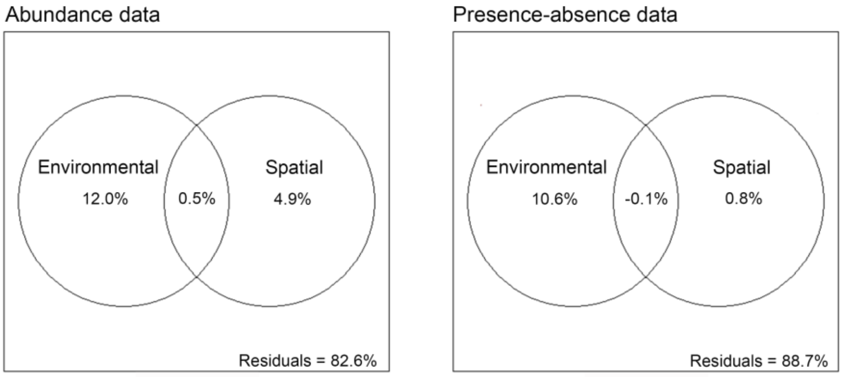
Appendix 19 *PCA biplot representing sample codes of the 38 small freshwater lakes and environmental variable vectors (cond = conductivity, sat = O_2 saturation, temp = water temperature, turb = turbidity, bicarb = HCO_3^-, chloride = Cl^-, sulphate = SO_4^{2-}, COD = chemical oxygen demand, nitrite = NO_2^-, nitrate = NO_3^-, ammon = NH_4^+, SRP = soluble reactive phosphorus, TP = total phosphorus, SRSi = soluble reactive silica). Proportion of variance explained by PC1 and PC2 axes are indicated.*



Appendix 20 *Results of multiple regressions on distance matrices (MRM) conducted on data subset of small freshwater lakes (see details in Chapter 5.3.2.). Community dissimilarities were computed applying Bray-Curtis index based on Hellinger transformed species abundance and presence-absence data. The listed* R^2 *values served as the basis of variation partitioning procedure detailed in Appendix 7. Results of variation partitioning are presented in Appendix 21 (*R^2 *= the amount of variation in community dissimilarities explained by the model, P = P value).*

	Explanatory distance matrices	$\mathbf{R^2}$	**P**
Abundance	Environmental (COD+SRSi+HCO_3^{2-}+pH)	0.125	0.051
	Spatial	0.054	0.006
	Environmental+Spatial	0.174	0.028
Presence-absence	Environmental (SRSi)	0.105	0.015
	Spatial	0.007	0.378
	Environmental+Spatial	0.113	0.016

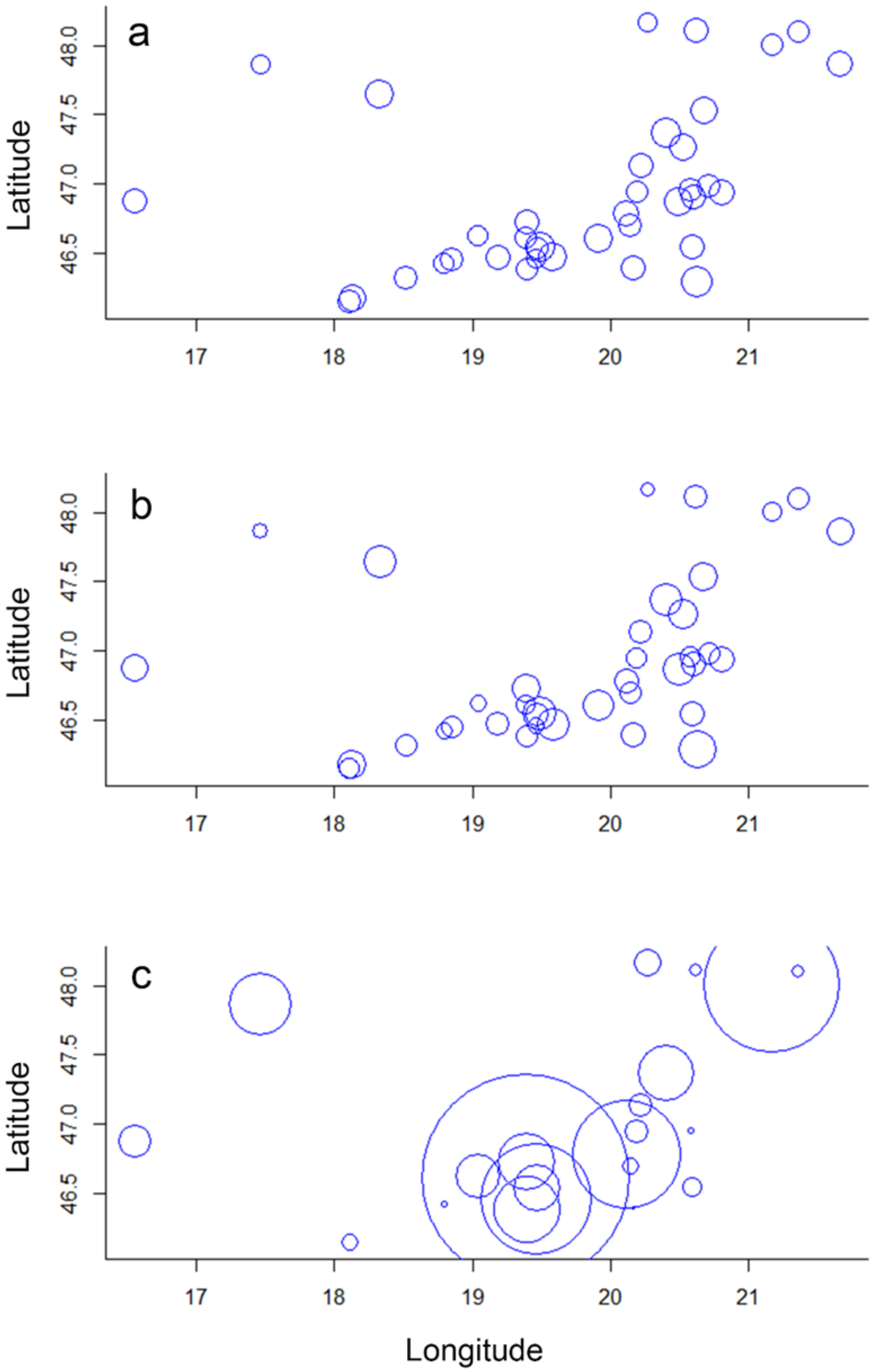
Appendix 21 *Proportion of variation in community dissimilarities of small freshwater lakes (see details in Chapter 5.3.2.) that can be explained by environmental distances (Environmental), spatial distances (Spatial) and spatially structured environmental distances. Unexplained variances are represented by the residuals.*



Appendix 22 *Correlation matrix of LCBD indices. Pearson correlation coefficients and the associated significance are displayed. Significance is shown as follows: *** = 0.001, ** = 0.01.*

	$\mathbf{LCBD_{D\%\,diff}}$	$\mathbf{LCBD_{ReplB\%\,diff}}$	$\mathbf{LCBD_{NesB\%\,diff}}$	$\mathbf{LCBD_{DS}}$	$\mathbf{LCBD_{ReplBS}}$	$\mathbf{LCBD_{NesBS}}$
$\mathbf{LCBD_{D\%\,diff}}$	1					
$\mathbf{LCBD_{ReplB\%\,diff}}$	0.98***	1				
$\mathbf{LCBD_{NesB\%\,diff}}$	-0.51**	-0.47**	1			
$\mathbf{LCBD_{DS}}$	0.11	0.27	0.17	1		
$\mathbf{LCBD_{ReplBS}}$	0.11	0.26	0.23	0.94***	1	
$\mathbf{LCBD_{NesBS}}$	-0.04	-0.02	-0.21	0.08	-0.24	1

Appendix 23 *Maps of a)* $LCBD_{D\%diff}$*, b)* $LCBD_{ReplB\%diff}$ *and c)* $LCBD_{NesB\%diff}$*. Sizes of circles are proportional to the index value.*



Appendix 24 *Maps of a)* $LCBD_{DS}$*, b)* $LCBD_{ReplBS}$ *and c)* $LCBD_{NesBS}$*. Sizes of circles are proportional to the index value.*