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Groups of small lakes maintain larger microalgal diversity than large ones

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Abstract

The question of whether one large, continuous area, or many smaller habitats maintain more species is one of the most relevant questions in conservation ecology and it is referred to as SLOSS (Single Large Or Several Small) dilemma in the literature. This question has not yet been raised in the case of microscopic organisms, therefore we investigated whether the SLOSS dilemma could apply or not to phytoplankton and benthic diatom metacommunities. Benthic diatom and phytoplankton diversity in pools and ponds of different sizes (ranging between 10^{-2} - 10^{7} m^{2}) was studied. Species richness of water bodies belonging the neighbouring size categories was compared step by step across the whole size gradient. With the exception of the compared 10^{4}–10^{5} m^{2} and 10^{5} – 10^{6} m^{2} size categories, where phytoplankton and benthic diatom richness values of the SL water bodies were higher than that of the SS ones, diversity of several smaller (SS) sized waters was higher than that in single large ones (SL) throughout the whole studied size range. The rate of the various functional groups of algae, including both the benthic diatoms and phytoplankton, showed remarkable changes from the smaller water bodies to large sized ones.

Keywords: SLOSS-dilemma, lakes, benthic diatom, phytoplankton, wide size scale

1. Introduction

The question of how cumulative species richness in several small habitats relates to that in one large area (where cumulative area of SS is equivalent to that of SL) became known as the SLOSS-debate (Single Large Or Several Small) in ecology. Several studies on the SLOSS dilemma were triggered by the frightening rate of habitat fragmentations which became an important issue in nature conservation (Foley et al., 2005). Since understanding the SLOSS-dilemma may help to find the optimal size of nature reserves it has been studied for decades by many authors since the seventies (Diamond, 1975; Wilson and Willis, 1975; Simberloff and Abele, 1976). While many studies demonstrated, that from the conservational point of view, several small habitats can be as valuable as a single larger-sized one (Turner and Corlett, 1996; Honnay et al., 1999; Gibb and Hochuli, 2002), there are many opposing results in the literature, which stress the importance of a single large habitat (Matias et al., 2010; Le Roux et al., 2015). The contradictory findings of these studies indicate that this debate is still unresolved (Tjørve, 2010; Rösch et al., 2015).

The size of the suitable habitat is largely determined by the characteristics of the species, which tries to settle and establish residence. Those species that are typically generalists or opportunists can easily adapt to the conditions of different-sized habitats (Gibb and Hochuli, 2002). High dispersal capability, that is characteristic for birds, allows them to survive in small habitats in the same way as in larger ones (Lindenmayer et al., 2015). On the other hand, the single large habitat ensures appropriate conditions by minimizing the extinction rate (Gaz and Garcia-Boyero, 1996; Le Roux et al., 2015). Besides the specific characteristics of the studied taxa, contradictory findings can also be traced back to statistical uncertainties. Theoretically, the SLOSS debate is in close connection with the species-area relationship (SAR). Essence of the SAR's theory is that the species richness increases with the increasing area size. This relation has been demonstrated for various organisms both on macro- (Connor and McCoy, 1979; Tjørve, 2003; Báldi, 2008; Lindenmayer et al., 2015; Matthews et al., 2016) and micro-scale (Smith et al., 2005; Bolgovics et al., 2016) and now, the SAR has become an accepted conceptual framework for ecological researches. Besides its theoretical importance, the species-area relationship (SAR) has substantial relevance from a nature conservation point of view. Although on a large spatial scale SAR can be described well by power function (Arrhenius, 1921), it becomes stochastic when only a small part of the size-scale is studied. It is especially true for the lower end of the size scale, where, because of the so called Small Island Effect (SIE) (Triantis and Sfenthourakis, 2011; Gao and Perry, 2016), diversity changes in an unpredictable way.

Moreover, species-area relationship can also be interpreted within the framework of the metacommunity theory (Gilpin and Hanski, 1991). This theory argues that local communities are linked by dispersal of many potentially interactive species, and thus create a metacommunity (Leibold et al., 2004). It means that, besides the local constraints, regional processes (e.g. dispersal) have pronounced influence on the composition of local communities. The most common distributional patterns in meta-communities are nestedness and species turnover (Baselga, 2010). Nestedness means that within a metacommunity, species of some local communities are the subsets of the larger, species rich communities; while species turnover is the rate of species replacement in communities, which is a reflection of habitat heterogeneity (Wiens, 1974; Astorga et al., 2014). These mechanisms shape the β-diversity of communities (Harrison et al., 1992), which, however, can be partitioned by the appropriate statistical tools (Baselga, 2010).

Majority of the above mentioned findings were obtained from studies on macroscopic taxa, but investigations of the SAR or the SLOSS debate on microscopic organisms may have similar relevance for the understanding of the compositional structure and functioning of microbial ecosystems. Diverse microbial primary producer communities in the pelagic and benthic zone sustain diverse grazer assemblages, have an impact on their composition and growth rate, and have far-reaching consequences for the structure and functioning of the whole aquatic food web (Liess and Hillebrand, 2004; Striebel et al., 2012).

Lakes and ponds are ideal objects to investigate the SLOSS-dilemma across a large spatial scale, because they can be considered as aquatic islands on a terrestrial landscape and their size range may cover several orders of magnitude even within a small geographic area (Dodson, 1992). These habitats provide suitable conditions for various aquatic organisms from the microscopic to the macroscopic ones. Among these organisms, algae represent a group which is usually characterized by high species richness and consists of taxa that are relatively easy to identify. These attributes make them suitable to answer various ecologically relevant questions (Soininen et al., 2016; Török et al,. 2016; Várbíró et al., 2017). In the last decades, functional approaches were increasingly used in algal researches (Reynolds et al., 2002; Padisák et al., 2009; Rimet and Bouchez, 2012; B-Béres et al., 2016, 2017; Tapolczai et al., 2016). They can provide detailed information about the ecosystem functioning and ensure a deep knowledge about ecosystem vitality. Thus, they have a remarkable role in conservation and environmental management (Padisák et al., 2006; Borics et al., 2007; B-Béres et al., 2019). In phytoplankton ecology, the functional group concept, proposed by Reynolds et al. (2002), has become the most widely used classification system (Salmaso et al., 2015). Here, algae and cyanobacteria are classified into more than 40 FGs based on their habitat preferences and environmental tolerances (Padisák et al., 2009; Salmaso et al., 2015). In diatom ecology, the use of functional classifications is based on morphological, behavioral and physiological criteria (Passy, 2007; Rimet and Bouchez, 2012; Berthon et al., 2011). Merging these approaches enabled the establishment of 20 combined eco-morphological functional groups (CEMFGs) by B-Béres et al. (2016). The feasibility and utility of this system have been studied under different environmental conditions (lowland rivers and streams - B-Béres et al., 2017; continental saline lakes and ponds - Stenger-Kovács et al., 2018).

While the relationship between nutrients and phytoplankton biomass has been well demonstrated, nutrient-diversity relationships might potentially exist only in oligotrophic or oligo-mesotrophic range (Soininen and Meier, 2014), where the low nutrient concentration might act as an environmental filter. In nutrient- enriched aquatic environments, causal relationship between nutrient availability and species richness could not be proved (Várbíró et al., 2017). In these systems the number of within-lake microhabitats has pronounced influence on species diversity (Görgényi et al., 2019). Eutrophic lakes of the Carpathian Basin therefore are appropriate objects to study the size-related aspects of diversity. Studying the SLOSS debate on microbial aquatic organisms is not just a theoretical issue but it might also have conservational relevance. In this study, we have performed an extensive analysis of the SLOSS debate on a large spatial scale in Hungary using both benthic diatoms and phytoplankton.

We addressed the following hypotheses:

(i) since we expect higher complexity in the larger water body categories, species richness of single large (SL) water bodies will be higher than species richness of several small (SS) ones

(ii) in accordance with the small island effect (SIE) species richness in smaller size categories (10^{-2}-10^{2} m^{2}) will change randomly, and clear patterns in the SLOSS dilemma will not be observed,

(iii) since increasing complexity is expected with the increasing habitat size, this complexity will result in higher number of functional groups in the case of both studied group.

2. Material and methods

2.1 Study area

Testing the research hypotheses eutrophic pools, ponds and lakes of varying sizes were selected in the whole area of Hungary (Central Europe). The area of the studied lakes covered 10 orders of magnitude, extending from 10^{-2} to 10^{7} m^2.

The data are partly derived from the National Hungarian Database, which contains phytoplankton and phytobenthon data for shallow lakes (mean depth <3m) and ponds between 10^{3}-10^{7} m^2 areas. To acquire the surface area of these ponds, oxbows and other larger standing water bodies we used the data of the national Hungarian database (database 1).

Samples belonging to the five smaller size categories (10^{-2}-10^{2} m^2) were collected from an extended area that was used as a bombing and gunnery training range between 1940 and 1990 and later for pasturing. This area is situated in the Hungarian Great Plain (Hungary, 47° 27' 00.36″ N and 20° 59' 44.09″), and the intensive bombing created thousands of bomb crater ponds of different sizes (10^{0}-10^{2} m^2) during the decades. In this area, very small pools were also created by grazing of the animals. Their sizes varied from 10^{-1} to 10^{-2} m^2. To calculate the area of the small pools (10^{-2}-10^{2} m^2) at the bombing range we measured their linear dimensions by a tape measure. Limnological characteristics of studied lakes can be seen in Table A.1.

2.2 Sampling and sample processing

2.2.1 Diatoms

The sampling and sample processing of benthic diatoms were done according to international standards (EN 13946, EN 14407). From shallow lakes and ponds with 10^{3}-10^{7} m^2 area, and from the bomb crater ponds with 10^{0}-10^{2} m^2 area samples were collected from reed stems. At those sites where macrophytes were unavailable (10^{-2} – 10^{-1} m^2 size range), samples were taken from the psammon. Although differences in substrata types might cause differences in the relative abundance of the occurring elements but the species composition of psammon to the harder substrates is similar (Townsend and Gell, 2005). Similar results were found by Szabó et al. (2018) studying the benthic diatom flora of lakes and ponds in Hungary: They found no significant differences in the composition and diversity of algal assemblages collected from different substrates.

Samples from shallow lakes and ponds ($10^3 - 10^7$ m^2 size range) were collected in the growing season between 2001 and 2012, while samples from small ponds in the bombing range were taken in September 2011.

In order to make the diatom valves clearly visible in benthic samples, 2 cm^3 H_2O_2 were added to 1 cm^3 sample. In addition, a few drops of HCl were also added to remove calcium carbonate. In the next step, the samples were placed in a water bath for one day at 70 °C. Finally, permanent slides were made with Cargille-Meltmount mounting medium (refractive index = 1.704). Diatom species were identified with Zeiss Axioimager A2 upright microscope at 1000 × magnification. Additionally, oil immersion and differential interference contrast (DIC) technique were applied. A minimum of 400 valves were counted per slides.

2.2.2 Phytoplankton

The sampling and sample processing of phytoplankton were done according to international standards (EN 16698, EN 16695, EN 15204). In the case of smaller sized pools (10^{-2}-10^2 m^2) phytoplankton samples were taken from the middle of the pools by a plastic dish in the second half of the vegetation period 2011. In the case of the shallow lakes and ponds (10^3-10^7 m^2) samples were collected in the vegetation period between 2001 and 2012. In these water bodies more sample sites were designated in the representative points of the lakes. Samples were collected from the euphotic layer with tube sampler. The euphotic layer was considered as 2.5 times of the Secchi depth. These subsamples were mixed in a larger plastic container, from which 0.5 L of water was taken and fixed with formaldehyde solution (concentration of 4%) and stored in darkness at 4 °C.

Phytoplankton samples were settled in 5 ml sedimentation chambers for 24 hours, and then analysed by inverted microscopes (Utermöhl, 1958), applying 400× magnification. To estimate the relative abundance of smaller algal units a minimum of 400 specimens were counted. The entire area of each chamber was investigated to estimate the number of large sized taxa. The list of the studied lakes and the observed number of samples are shown in Table 1.

2.3 Area of the SL and SS lakes

Since we hypothesised that the values of the metrics used for representing the SLOSS depend on the size of the water bodies, all adjacent size categories were separately compared within the studied size range (10^{-2} - 10^{7} m^2) (Fig. 1). More precisely it means, that taxonomical and functional diversities of the smaller water body category were compared to metrics of waters in the next larger category.

In an ideal case the sum of the area of small water bodies is equal with the area of the single large one. However, our database did not make possible that the area of SS lakes would be equal to that of the SL one. As it is illustrated in Fig. 2, in the majority of cases, the sum of the area of the SS lakes was smaller.

Within this smaller size range (10^{-2}-10^{2} m^2), where we had five pools in each size category, the size of SL pools was twice as large as that of the SS pools. In the larger size categories (10^{3}-10^{7} m^2) the area covered by the SS lakes also showed differences.

2.4 Species richness estimations - ESR

The observed number of species occasionally might give a biased estimate of the real species richness, and the bias is mostly related to differences in the sampling effort, therefore one major challenge in SLOSS studies is how to compare the species richness of the different areas. Since in the smallest size categories (10^{-2}-10^{2} m^2) single samples were collected from every water body, in the case of these waters statistical richness estimations cannot be applied. However, with respect to the small size of these water bodies, the sample volume/ habitat volume ratios were high, which increased the detectability of an individual algal unit. Since higher individual detectability increases the detection of species (Buckland et al., 2011), the observed number of species well represented the real species richness in these small habitats. In these size categories richness values of the SS lakes were considered as the sum of the observed species numbers of the 5 small pools. Species richness of the SL lake (i.e. lake in one order of magnitude larger size category) was considered as the mean of the observed richness values of the 5 pools belonging to the given category.

In the case of larger size categories (10^{3}-10^{7} m^2), data for longer time periods were available. Although we had different numbers of samples from each lake in all size categories (Fig. 3A), these sample numbers were sufficient to apply a more rigorous statistical comparison between the richness of SL and SS lakes.

Since the species numbers increase with the number of the samples studied, our aim was that in the pairwise comparisons between SL and SS lakes the number of samples considered would be equal. To achieve this, we applied Chao's sample-based extrapolation technique (Chao et al., 2014), which is a non-asymptotic approach, that enables us to compare diversity estimates by using seamless rarefaction and extrapolation (R/E) sampling curves. In the case of phytoplankton, the databases usually contain species specific biomass data, which do not enable the application of individual-based rarefactions. However Chao's method is an incidence-based technique, which considers the occurrences of species within the given sample, but ignores relative abundances.

Increasing lake size means decreasing individual and species detectability, therefore parallel with an increase in the lake size, we proposed to consider increasing sample numbers in richness comparisons (Table 1). To estimate the richness in SL lakes (ESR_{SL}) using the extrapolation curves, we calculated the species richness for the proposed sample numbers for each lake in the given size category (Fig. 3C), and means of these values were considered as ESR_{SL} values.

When estimating the species richness of SS lakes (ESR_{SS}), as a first step, species occurrence matrices of all lakes within the given size category were stacked. In the next step, applying the sample numbers that were considered for calculations of ESR_{SL} in the one order of magnitude larger size category, we calculated estimated species richness of the SS lakes (Fig. 4C).

These procedures were repeated in the case of each pairwise comparison. Finally, to represent the SLOSS dilemma, the quotient ESR_{SL}/ESR_{SS} was plotted against the area of water bodies (Fig. 5).

2.5 Evaluation of functional group richness and functional redundancy

The observed differences between the functional group richness values of adjacent size categories can be partly explained by functional differences between the compared water bodies (see in subsection 2.3). These limnological and/or biological differences between water bodies in adjacent size categories can result differences in the number of occurring functional groups (FG) of benthic diatoms and phytoplankton (Table A.2 and A.3). Studying these functional differences, taxa observed both in the benthic diatom and phytoplankton samples were assigned to the appropriate FGs (Tables A.2 and A.3). Diatom species were assigned to twenty combined eco-morphological functional groups according to B-Béres et al. (2016). Functional classification of phytoplankton was based on the concept proposed by *sensu* Reynolds et al. (2002); which was supplemented by Borics et al. (2007) and reviewed by Padisák et al. (2009).

2.6 Programs used for statistical analysis

Rarefaction curves were drawn using the iNEXT (Hsieh et al. 2013, ver. 1.0) packages available in R Studio (2012).

3. Results

Altogether 189 benthic diatom and 181 phytoplankton samples were collected from 36 different sized standing waters in Hungary. We identified 312 benthic diatom and 498 phytoplankton species in the samples.

The species richness of diatom assemblages in the SS lakes was higher at most size categories (ESR_{SL}/ESR_{SS} values<1), except in the case of 10^5 m^2 size range (Fig. 6 A). At the 10^5 m^2 size category more species could be observed in the SL lakes than in several smaller ones (ESR_{SL}/ESR_{SS} value>1). The ESR_{SL}/ESR_{SS} values showed large variation in the small size categories (from 10^{-2} m^2 to 10^2 m^2), while they were more consistent in the case of larger lakes (lake area>10^3 m^2).

The results showed similar patterns in the case of the phytoplankton. The species richness of SS lakes was higher in almost every size category, except in 10^4 m^2 area size (Fig. 6 B). The values showed large variation across the whole size scale, but the data showed no discernible trends or regularities. In contrast to benthic diatoms where ESR_{SL}/ESR_{SS} ratio showed only small changes in the larger lake categories, phytoplankton richness of this lake size category was considerably smaller than that in the sum of the lakes in the adjacent smaller lake size category.

3.1 Functional groups

The number of functional groups showed similar patterns in the case of both benthic diatoms and phytoplankton. Smaller values characterized the water bodies in the 10^{-2} m^2 to 10^2 m^2 size range, while larger ones in the 10^3-10^7 m^2 range (Fig. 7 A-B, and Table A.2 and A.3).

Smaller differences could be observed in the larger lake categories where the number of benthic diatom FGs was almost identical (~20), the phytoplankton FGs displayed a peak at 10^5 m^2 range and decreased thereafter.

The functional redundancies of benthic diatoms (i.e. number of species within the FGs) showed characteristic changes along the size gradient (Fig. 8 A and Table A.2).

Richness of the motile groups decreased with water body size. An opposing tendency was observed in the case of high profile groups which showed increasing redundancy from 10^3 m^2 to the largest size categories.

The ratios of the phytoplankton functional groups also differed from each other in the case of smaller and larger size categories (Fig. 8B and Table A.3).

In small sized water bodies (10^{-2} m^2 – 10^2 m^2), the W1 functional group was dominant, that mostly consists of euglenoid algae. In contrast to W1 group, richness of X1, N and Lo FGs were higher in the larger size categories (for more information on functional groups see in Table A.3).

4. Discussion

Our results clearly demonstrated that several small water bodies can maintain greater phytoplankton and benthic diatom species richness than single large ones; thus the results did not corroborate our first hypothesis. Considering that the aggregated areas of the several small water bodies were smaller in almost each case of comparisons (Fig. 2), the results are even more convincing.

In line with our second hypothesis the ESR_{SL}/ESR_{SS} values did not show any trends in the case of small water bodies. Species numbers were lower and changed randomly in the smaller size categories (10^{-2}-10^{2} m^{2}) resulting in hectic changes in the ESR_{SL}/ESR_{SS} values. An interesting interpretation of these results can be made in the context of the species-area relationship (SAR). At large spatial scale, the SARs follow a power model (Arrhenius, 1921). In contrast, the richness values change independently from the area in very small habitats, resulting in unpredictable diversity patterns in these small habitats. This stochastic pattern has been described as small island effect (SIE) in the literature of island biogeography (Lomolino and Weiser, 2001; Triantis and Sfenthourakis, 2011). We think, that this phenomenon can explain the large variations in the ESR_{SL}/ESR_{SS} ratio experienced in the case of small water bodies.

Several empirical studies demonstrated that the exponent of the Arrhenius's power-law formula falls within the range of 0.1–0.5 (Lomolino, 2001), which gives a slightly asymptotic character to the fitted curve. Practically, it means that drastic increase in species numbers cannot be expected with increasing habitat size. Our findings are in line with this phenomenon, because despite cumulative areas of SS lakes were smaller than that of the single large ones, richness of SS lakes was higher than that of SL lakes. However, one exception occurred both in case of phytoplankton and benthic diatoms. This can be partly explained by the above mentioned methodological limitations, but other explanations should also be considered. Using a large dataset, Várbíró et al. (2017) demonstrated that the shape of the SAR for phytoplankton is hump shaped, having a maximum in richness about 10^{5} -10^{6} m^{2} range. Water bodies at this size range are exposed to moderate wind action and have an extensive macrophyte belt; conditions which help the development of various microhabitats for the phytoplankters. In large lakes, the wind induced turbulences homogenize the water both horizontally and vertically creating a quasi uniform aquatic habitat. This phenomenon was called the Large Lake Effect (LLE), and this seems to explain our findings that the lowest values appeared in the largest size category.

Although dispersion ability of benthic taxa is lower than that of the planktic ones (Wetzel et al., 2012), comparing to those groups where because of the obligate sexual reproduction mate limitation exists (Havel and Shurin, 2004) both groups of microalgae are very good dispersers (Padisák et al., 2016). Therefore, dispersal limitation is not a crucial factor affecting diversity in microalgal meta-communities, instead, environmental filtering and demographic stochasticity are those processes that determine the fate of colonizers in the habitats (Leibold and Chase, 2017). Theoretically, the large area would benefit the colonization of habitats, but size is a relative "notion" for algae, and very small habitats can satisfy the spatial needs of various groups (Borics et al., 2016). The fact that ESR_{SS} was higher than ESR_{SL} clearly highlighted that the species pool of the SS lakes cannot be considered as a subset of the SL lake. Based on the logic proposed by Baselga (2010), in these situations the high species turnover and the local heterogeneities maintain the compositional differences among the small habitats, and contribute to the larger cumulative species and functional richness both in case of phytoplankton and benthic diatoms.

The large within group diversity of the phytoplankton and the benthic diatoms, and the good dispersal capabilities of taxa might occasionally result in species rich, but functionally redundant assemblages. Therefore it is necessary to interpret the background of the SLOSS dilemma at functional level. Functional richness can be a useful measure of ecosystem complexity, which is determined by system attributes like amount of available resources, isolation, habitat size, position of the system on the successional sequence, or random processes e.g. colonization history and disturbances (Persson et al., 1996; Kitching, 2001; Post 2002). These attributes has pronounced influence on the food-chain length, which in this case can be considered as a top-down effect on the primary producers. Several field and laboratory studies demonstrated that both planktic and benthic grazers prefer certain group of algae (Parsons et al., 1967; Pimm and Kitching, 1987; Gresens and Lowe, 1994; Sommer, 1999; Kagami et al., 2002), and this preferential grazing contributes to maintain higher complexity. Although an increasing complexity of water bodies could be demonstrated along the size gradient (Fig. 8 A and Fig. 8 B), the functional composition of both algal groups indicates, that this increasing complexity exists at the level of the whole size range (10^{-2} –10^{7} m^{2}). The results supported our third hypothesis, however, differences in habitat complexity (number of FGs) between the adjacent size groups were not considerable, especially in the case of benthic algal assemblages. An exception to this rule was the 10^{2} –10^{3} m^{2} size range, where considerably higher FG richness was found in 10^{3} m^{2} water bodies than in the smaller ones both for benthic diatoms and phytoplankters. Typically, planktic diatoms were missing from the bomb crater ponds and from the small pools, resulting in a slightly decreasing complexity here. In contrast, FGs tolerating the drying up of waters (e.g. motile diatoms, or codon T) (Holzinger et al., 2010; Lukács et al., 2018; B-Béres et al., 2019), were characteristics in these small sized ponds and pools. The fact however, that the number of FGs was almost equal in the adjacent size categories (both in the case of phytoplankton and benthic diatoms) strongly implies that higher ESR_{SS} values can be explained by the non-nested nature of the species pool in the smaller water bodies, that is, identical FGs were represented by different species in these waters.

The SLOSS debate inevitably attracted many theoretical approaches and explanations, and the roots of this dilemma are deeply embedded in conservation management and landscape planning. Although a popular view is, that protection of larger sized areas is better

(Tscharntke et al., 2002) investigations of different sized habitats and different animal and plant groups revealed that there are arguments on “both sides of the SLOSS-debate” (Tscharntke et al., 2002; Moussaoui and Auger, 2015). There is no doubt, fragmented landscape is a common phenomenon worldwide, and creation of large, contiguous protected areas is only rarely feasible (Gaz and Garcia-Boyero, 1996). However, as it was shown by a number of studies (Tscharntke et al., 2002; Hokkanen et al., 2009; Rösch et al., 2015), in certain cases, small habitats can be as valuable as larger sized areas. It is especially true for small bodied organisms such as insects, snails or birds (Tscharntke et al., 2002). The results of our study are not only in line with these previous findings, but demonstrate that for two important microscopic aquatic groups, the higher conservational value of SS water bodies is valid through the whole range of the area gradient. It is evitable, that from a practical point of view, the conservation relevance of the water bodies of less than a few square meters is negligible, thus, in respect to the 10^{-2}-10^{0} m^2 size range, our results could be considered theoretical curiosities. However, in Hungary, after the large river regulations of the 19th century, the formerly extended bogs and marshlands disappeared almost entirely, and the biota of these ecosystems now survives in the remaining small bog-pools, that mostly are not larger than 10^{2}-10^{3} m^2 (Borics et al., 1998, 2003). While the Water Framework Directive (2000) requires the achievement of good ecological status for all natural standing water bodies larger than 50 hectares in Europe, smaller aquatic habitats do not belong under the umbrella of this legislative approach. Therefore those small water bodies that are not parts of Natura 2000 sites are especially threatened, and need special consideration.

5. Conclusions

Results of the present study supported the view that microalgal species richness of several small water bodies exceeds that of a single large one. These results are valid almost for the entire scale of the area gradient, and for both phytoplankton and benthic diatoms.

Practical importance of these results is, that it draws attention to the fact that from a nature conservation point of view, water bodies with very small areas might have relevant conservational values.

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7. Author contributions

ÁB wrote the manuscript. GV and EÁKK carried out the statistical analyses. VBB, ÉÁKK and KTK provided data. GB raised the topic, and helped the first author during the whole course of research and writing of the manuscript. All authors gave final approval for publication.

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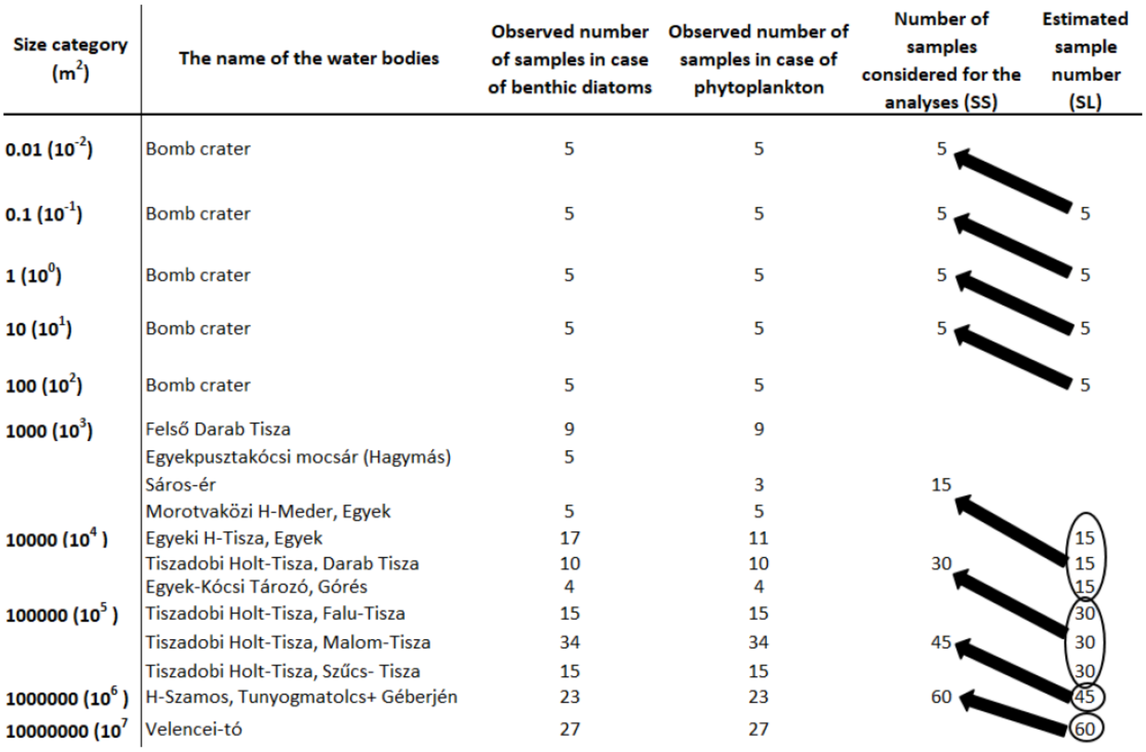
9. Captions

Table 1 Sample numbers (original and estimated) considered in a given sample site. Black arrows indicate how we divided the species richness of SL lakes with species richness of SS lakes in the one smaller size category.



Size category (m^2)	The name of the water bodies	Observed number of samples in case of benthic diatoms	Observed number of samples in case of phytoplankton	Number of samples considered for the analyses (SS)	Estimated sample number (SL)
0.01 (10^{-2})	Bomb crater	5	5	5	
0.1 (10^{-1})	Bomb crater	5	5	5	5
1 (10^{0})	Bomb crater	5	5	5	5
10 (10^{1})	Bomb crater	5	5	5	5
100 (10^{2})	Bomb crater	5	5		5
1000 (10^{3})	Felső Darab Tisza	9	9		
	Egyekpusztakócsi mocsár (Hagymás)	5			
	Sáros-ér		3	15	
	Morotvaközi H-Meder, Egyek	5	5		
10000 (10^{4})	Egyeki H-Tisza, Egyek	17	11		15
	Tiszadobi Holt-Tisza, Darab Tisza	10	10	30	15
	Egyek-Kócsi Tározó, Górés	4	4		15
100000 (10^{5})	Tiszadobi Holt-Tisza, Falu-Tisza	15	15		30
	Tiszadobi Holt-Tisza, Malom-Tisza	34	34	45	30
	Tiszadobi Holt-Tisza, Szűcs- Tisza	15	15		30
1000000 (10^{6})	H-Szamos, Tunyogmatolcs+ Géberjén	23	23	60	45
10000000 (10^{7}	Velencei-tó	27	27		60

Table A.1 Limnological characteristics of studied lakes. Characterisation of lakes' trophic level was based on the OECD proposal (1982) (hypertrophic: TP > 100 mg/l).

Table A.2 Codes of the combined eco-morphological functional groups of diatoms

Table A.3 Characteristics of the observed phytoplankton functional groups

Fig. 1 Illustration of the applied study design. Circles represent the area of the water bodies.

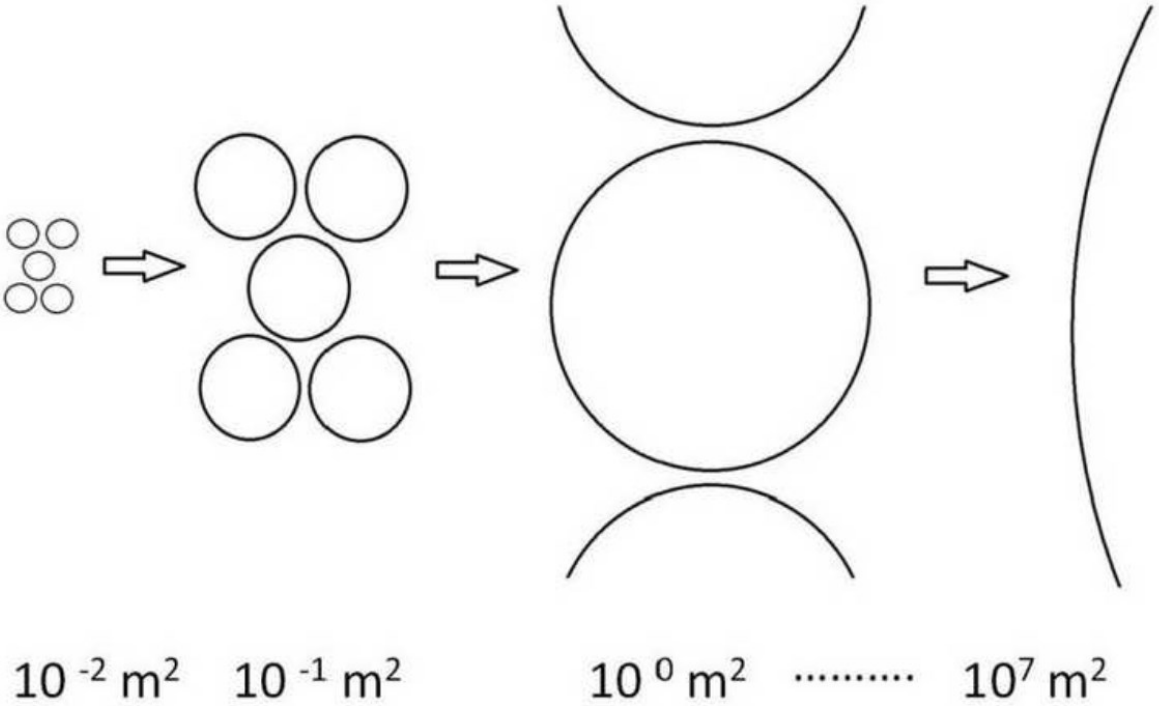


Fig. 2 Area covered by the SS lakes comparing to that of SL lakes. The dark grey part of the pie charts with 100 % represents the size of the SL lakes. The white parts of the pie charts show the size of the SS lakes expressed as the percentage of the area of the SL lake. Area of the SL lake was considered as the mean area of the lakes in the given size category. Numbers in the pie charts indicate the percentages covered by the small lakes. The light grey parts show the ratio of uncovered area.

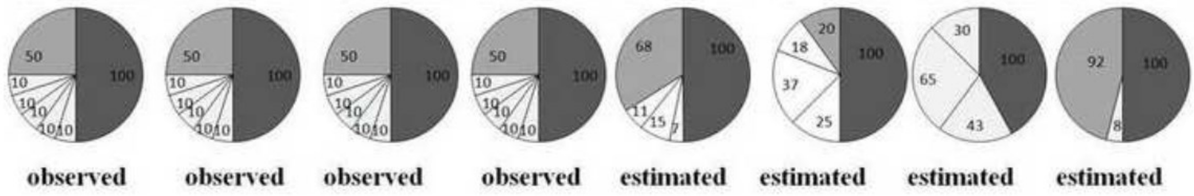


Fig. 3 Calculation of the species richness for the single large (SL) lakes (SL: 10^3-10^7 m^2) within a given size category. Abbreviations: A, B, C – water bodies; n (A, B, C) – sample number; t – taxa; ni – number of individuals; ESR – estimated species richness; Ns – number

of samples considered during richness estimations; SL – single large; SS – several small lakes.

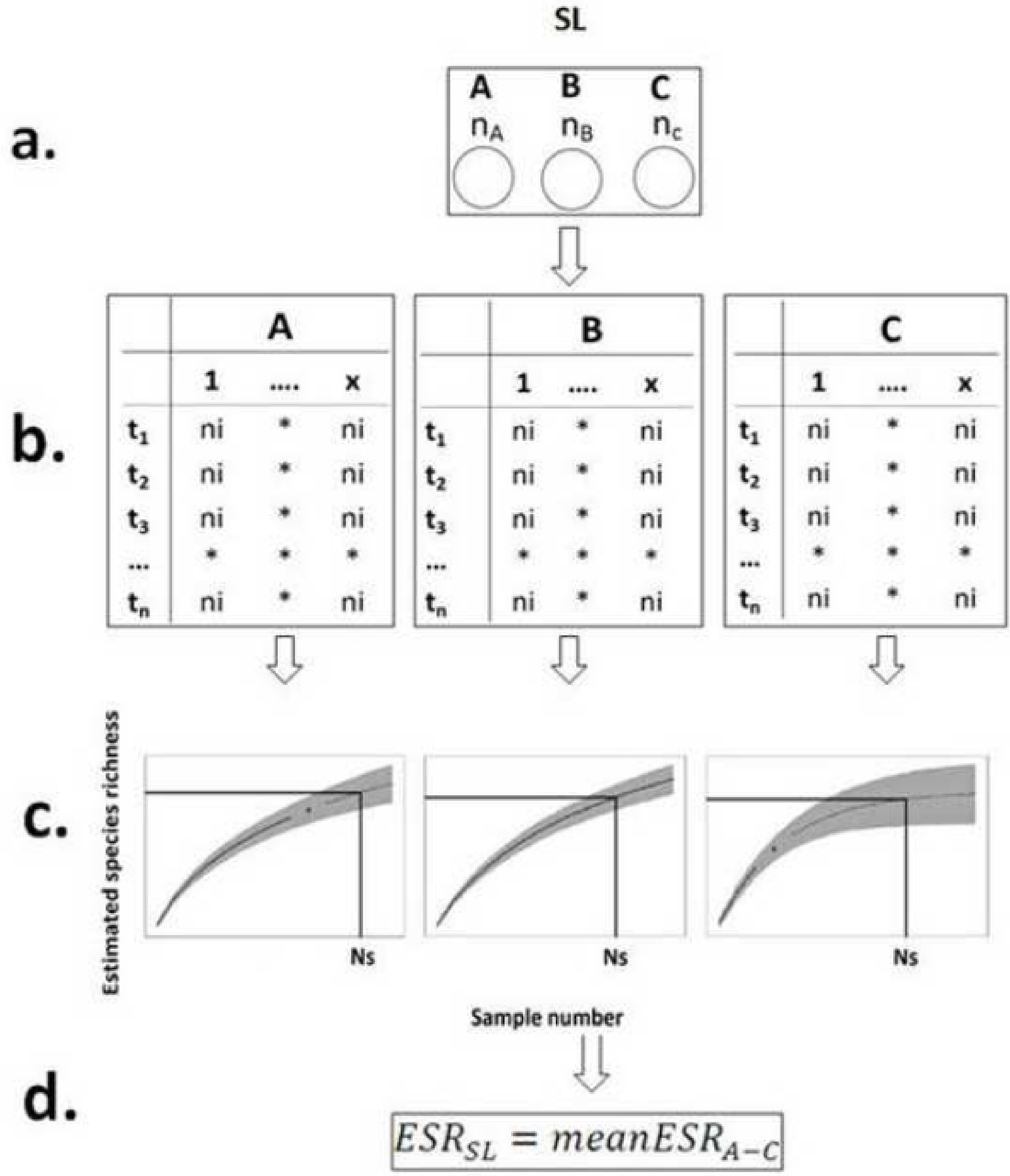


Fig. 4 Calculation of the species richness for the several small (SS) lakes (SL: 10^3-10^7 m^2) within a given size category. Abbreviations: A, B, C – water bodies; n (A, B, C) – sample number; t – taxa; ni – number of individuals; ESR – estimated species richness; Ns – number

of samples considered during richness estimations; SL – single large; SS – several small lakes.

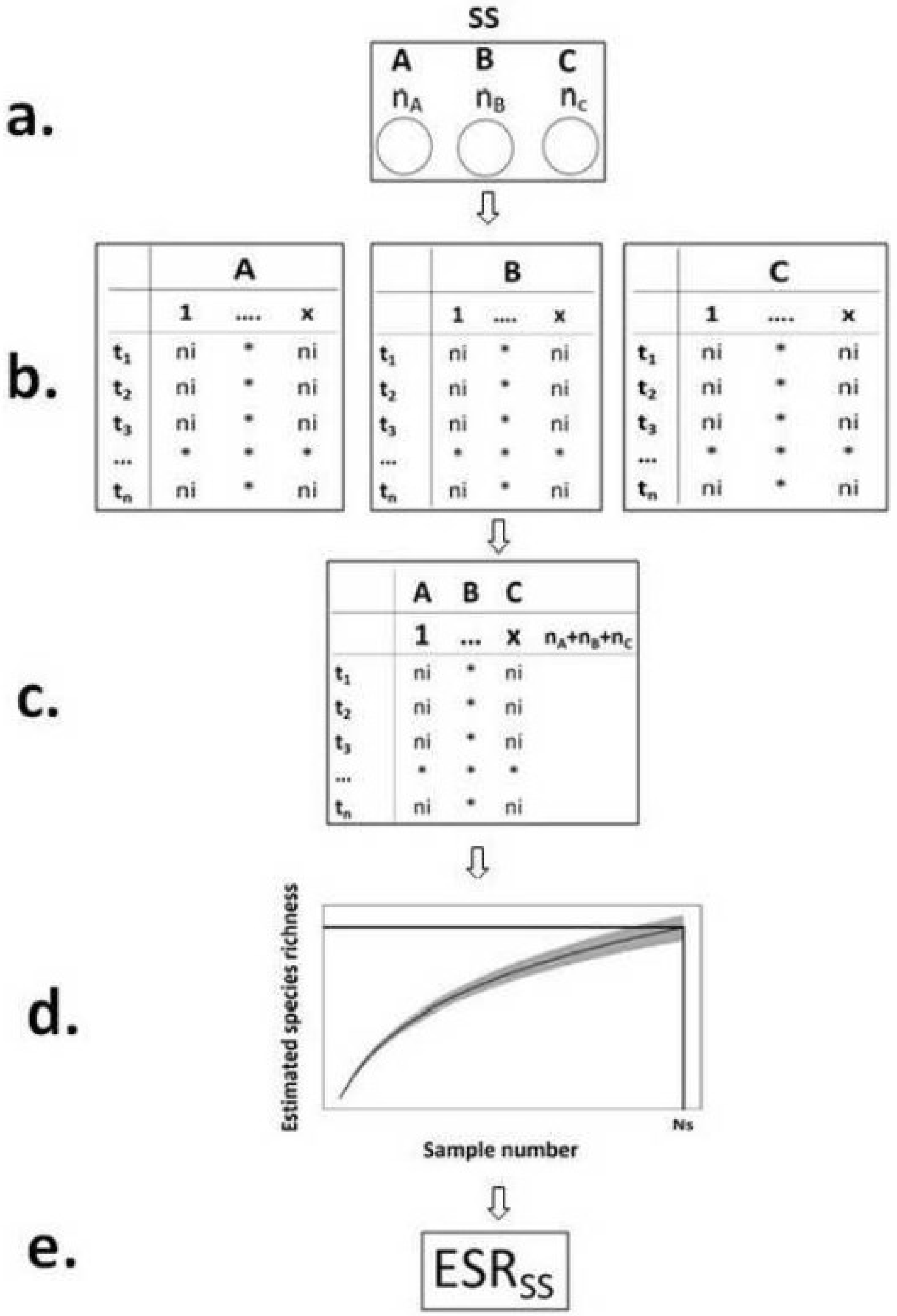


Fig. 5 Numerical characterisation of the SLOSS debate and its presentation in the compared water body size categories. ESR_{SL}: estimated species richness in single large lake, ESR_{SS}: estimated species richness for several small lakes.

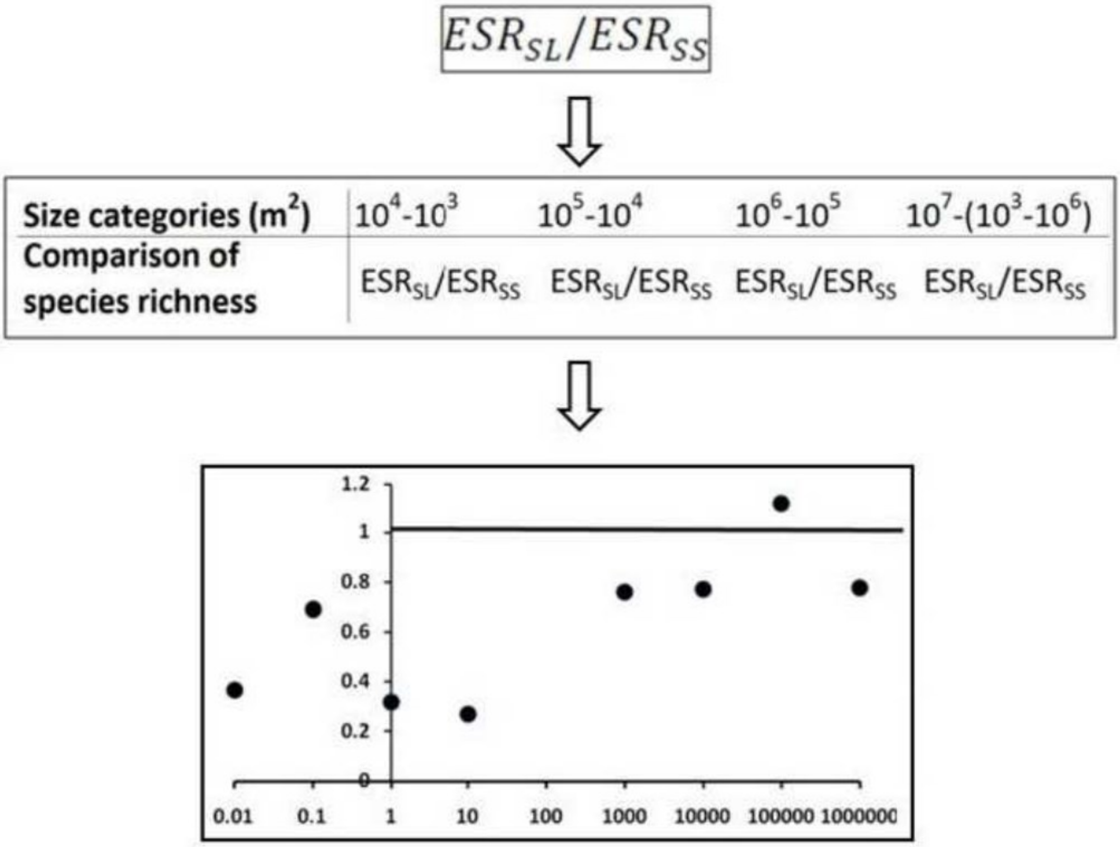
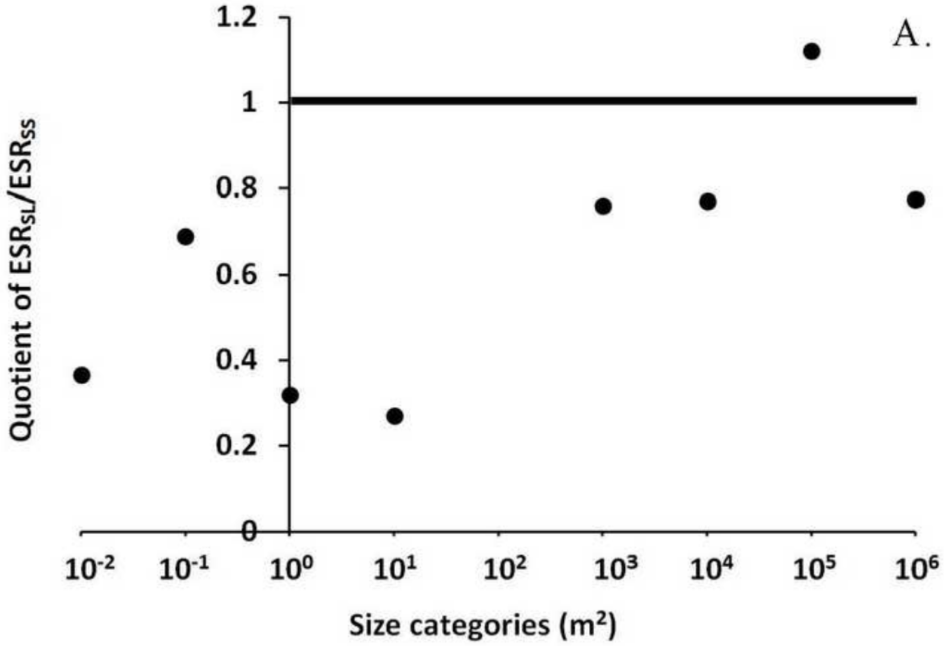


Fig. 6 A-B Benthic diatom and phytoplankton ESR_{SL}/ESR_{SS} values in the compared water body size categories. Values under black line show when the species richness of SS lakes were higher than in case of SL lakes, while the values above the black line mark higher species richness of SL lakes than in SS ones.



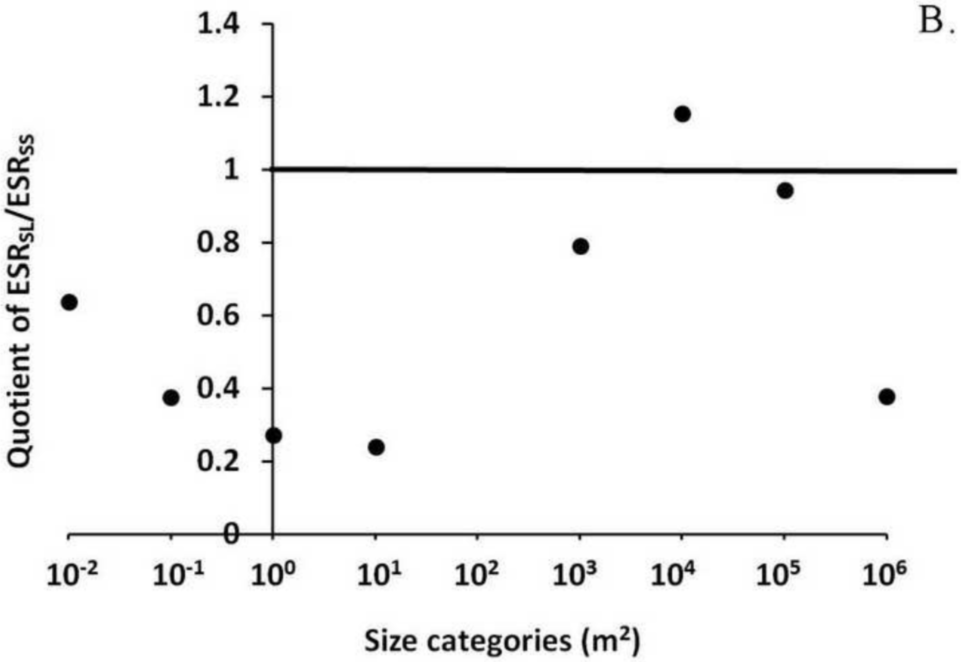


Fig. 7 A-B. Cumulative number of benthic diatom and phytoplankton FGs in the water body size categories.

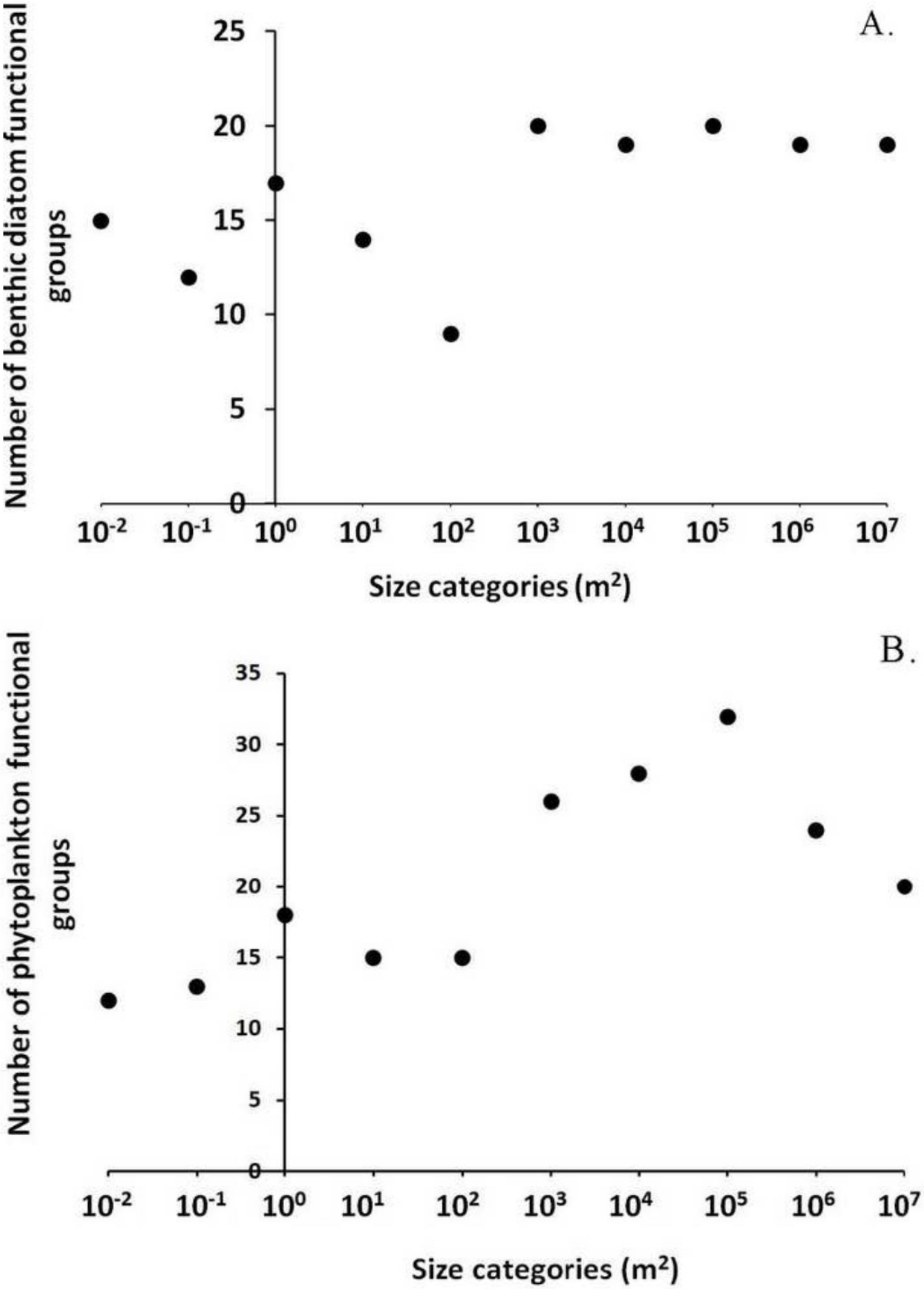
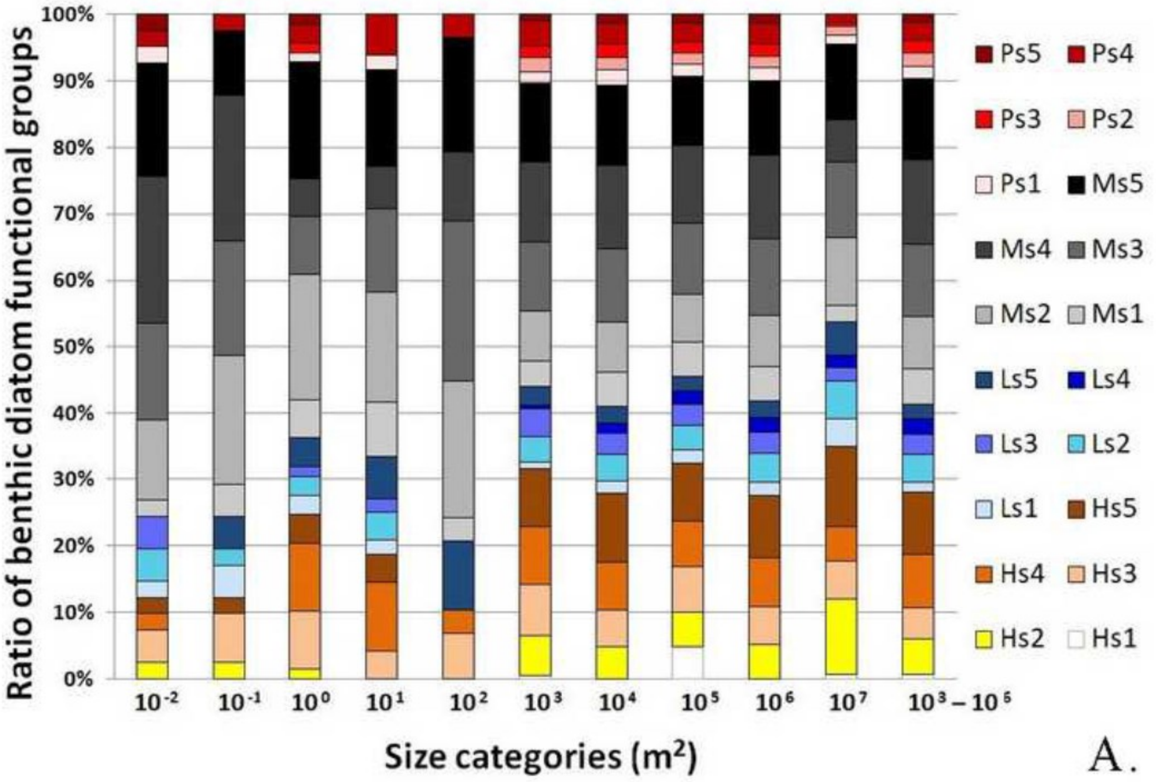
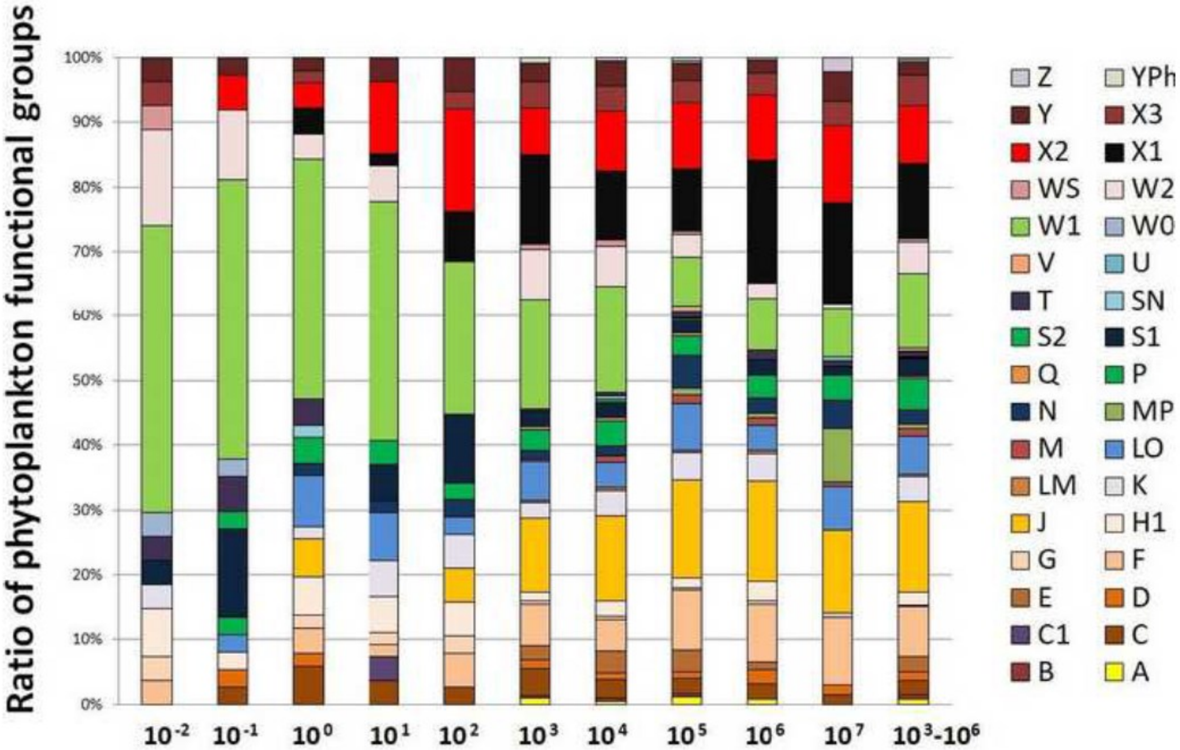


Fig. 8 A-B Relative species abundances in the functional groups of benthic diatoms and phytoplankton in the different size categories. See abbr. in Table A.1 and Table A.3


Ratio of benthic diatom functional groups
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
10^{4}
10^{5}
10^{6}
10^{7}
$10^{3}-10^{6}$
Size categories (m²)
Ps5
Ps4
Ps3
Ps2
Ps1
Ms5
Ms4
Ms3
Ms2
Ms1
Ls5
Ls4
Ls3
Ls2
Ls1
Hs5
Hs4
Hs3
Hs2
Hs1
A.


Ratio of phytoplankton functional groups
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
10^{4}
10^{5}
10^{6}
10^{7}
10^{3}-10^{6}
Size categories (m²)
Z
YPh
Y
X3
X2
X1
WS
W2
W1
W0
V
U
T
SN
S2
S1
Q
P
N
MP
M
LO
LM
K
J
H1
G
F
E
D
C1
C
B
A
B.