

This manuscript is contextually identical with the following published paper:

Bolgovics Á., Ács É., Várbió G., Görgényi J., Borics G. (2016) Species area relationship (SAR) for benthic diatoms: a study on aquatic islands. HYDROBIOLOGIA 764: (1) pp. 91-102. DOI: 10.1007/s10750-015-2278-1

The original published PDF available in this website:

<http://link.springer.com/article/10.1007%2Fs10750-015-2278-1>

Species area relationship (SAR) for benthic diatoms: A study on aquatic islands

Ágnes Bolgovics¹, Éva Ács³, Gábor Várbió², Judit Görgényi², Gábor Borics²

¹Eötvös Loránd University, Pázmány Péter str. 1/A, H-1117 Budapest, Hungary

²Department of Tisza River Research, Centre of Ecological Research of HAS, Bem sqr 18/C, H-4026 Debrecen, Hungary

³Danube Research Institute, Centre of Ecological Research of HAS, Karolina str. 29. 1113 Budapest, Hungary

Abstract

The question of how species richness depends on the area is one of the most intensively studied subjects in biogeography. Many studies reported this pattern for terrestrial and macroscopic taxa, however microscopic and aquatic communities received much less attention in the literature. The aim of our study was to reveal the relationship between the habitat size and the richness of freshwater benthic diatom assemblages. We hypothesized that if the size of studied water bodies covers wide spatial scales the species-area relationship (SAR) could be described by a sigmoid model. Benthic diatom assemblages were investigated in pools, ponds and lakes of various sizes (10^{-2} - 10^8 m²). We demonstrated that although the

SAR in the log-log space can be described by linear model, the linear breakpoint regression provides better fit to data. Using this technique a characteristic Small Island Effect (SIE) could be distinguished. The SIE fell in the range of 10^{-2} to 10^4 m². We also demonstrated that species richness of the diatom guilds is remarkably different in the various size ranges of the water bodies. We also demonstrated that the slope of the species-area relationship (z value) is similar to those values that have been reported to other microbial organisms.

Keywords: biogeography, small lake effect, diatom guilds

Introduction

The so-called “species-area relationship” (SAR) is one of the most general patterns in ecology (Schoener, 1976; Lomolino, 2000). According to this paradigm the number of species increases with the area surveyed. The relationship was demonstrated for true islands, for habitat fragments and also for segments of a large continuous habitat. The SAR is considered a law in ecology and is applicable to plants, animals and microbes (Woodcock et al., 2006). Several empirical models were developed to describe this relationship mathematically. The most frequently applied are the power (Arrhenius, 1921), the exponential (Gleason, 1922) and the sigmoid (Archibald, 1949) models. Since so far, there is no generally accepted method of curve fitting, it is often depends on the researchers' preconception (Tjørve, 2003; Dengler, 2009; Williams et al., 2009, Matthews et al., 2015). However, He & Legendre (1996) demonstrated that the shape of the curve depends on the scale. The exponential model is valid in case of small sampling area, while the power model fits well both at small and intermediate sampling area. If the spatial scale of the sampled area extended over more than three orders of magnitude, the sigmoid model shows the best fit.

There are several theories that aim to explain the positive relationship between species richness and habitat size (Connor & McCoy, 2001). The most frequent explanations are (1) the habitat diversity hypothesis which argues that within a given area there are many smaller habitats which contain typical species, and larger area contains more habitat patches which can maintain more species. (2) the “area per se hypothesis” which presumes that at larger area-size extinction risk of species is lower than at smaller habitat size, because of the larger possible population size and increasing probability of immigration of new species and (3) the passive sampling hypothesis. The hypothesis assumes that increasing sampling effort in larger area will result in higher species richness (Connor and McCoy, 2001; Bell et al., 2005). Nowadays the SAR is more than a simple theoretical curiosity it became a useful tool in nature conservation issues and in landscape ecology (Lomolino, 2001; Tjørve, 2003). It is used to estimate the species richness of larger, uninspected area, to determine optimum sample size and sample number, to determine the minimum area of a given community, or area requirements of species (Kilburn, 1966; Lomolino, 2001).

When small habitats are involved into the SAR studies the relationships can be characterised at least by two distinct patterns (Lomolino, 2001). It has been demonstrated for several groups of organisms that the positive relationship between area and species richness does not exist below a certain threshold of area size. This phenomenon is called as Small Island Effect (Preston, 1962; MacArthur & Wilson, 1967; Lomolino & Weiser, 2001; Triantis & Sfenthourakis, 2012). Beyond the SIE range, toward larger sized habitats, there is the range of the SAR in the traditional sense of the term, when species number increases with the size of area. The SIE is often a stressful part of SAR, but in most of the studies it does not get enough attention (Lomolino, 2001).

Although the SAR has been studied for wide range of taxa and for various spatial scales (Lomolino & Weiser, 2001; Woodcock et al., 2006), studies on aquatic and especially

78 microscopic systems are deeply under-represented in the literature (Azovsky, 2002; Dolan,
79 2005; Reche et al., 2005; Smith et al., 2005; Barinova & Stenina 2013; Borics et al., 2015).
80 From biogeographical point of view, lakes and ponds are considered as aquatic islands in a
81 terrestrial landscape (Dodson, 1992). The large number of the ponds and the large size
82 differences among them makes these habitats ideal objects for testing the various SAR
83 models. Despite the fact that the aquatic environments provide habitats for various groups of
84 microscopic organisms (bacterio-, phyto and zooplankton, benthic algae, etc.) which play an
85 important role in the functioning of aquatic ecosystems, yet these groups have received little
86 attention in SAR analyses (Horner-Devine et al., 2004; Smith et al., 2005). One reason for this
87 is that concerning the microscopic organisms, definition of individuals and species is highly
88 uncertain (Reche et al., 2005; Peay et al., 2007). The other reason is that in case of
89 microscopic systems complete census of the habitat is not possible; therefore, various
90 sampling strategies and species estimators have to be applied to estimate the richness of the
91 studied systems. The large diversity of methods can lead to high uncertainty of the results
92 (Somerville et al., 1989; Kepner & Pratt, 1994). These uncertainties can be minimized if the
93 selected microscopic organisms can be identified safely and well developed protocols support
94 their samplings. In the microbial world diatoms meet these requirements (Kelly et al., 1998).
95 Besides species richness, functional diversity is also an important component of diversity
96 because it is considered a useful metric which reflects ecosystem complexity and ecosystem
97 processes (Diaz & Cabido, 2001). Similarly to phytoplankton where several functional groups
98 were proposed in the recent years (Reynolds et al., 2002; Salmaso & Padisák, 2007; Borics et
99 al., 2007, Várbiro et al., 2007; Kruk et al., 2010), ecological guilds based on functional
100 differences were also proposed for diatoms (Passy, 2007; Rimet & Bouchez, 2012). Based on
101 their utilization of nutrient resources and their resistance to physical disturbances Passy
102 (2007) identified three diatom guilds (low-profile, high-profile and motile guilds). Later these

were supplemented by the planktic guild (Rimet & Bouchez, 2012), thus, four diatom guilds can be distinguished: planktic, low-profile, high-profile and motile guilds. Several papers were published concerning the use of diatom ecological guilds and for predicting various ecological gradients (Berthon et al., 2011; Passy & Larson, 2011; Stenger-Kovács et al., 2013) but size-related questions were not addressed in these studies.

The aim of our work was to study the SARs for benthic diatoms. Since Mazaris et al. (2010) demonstrated that there is no significant SAR when small range of spatial scale is studied we aimed at investigating the SAR at large spatial scale involving small pools, ponds and lakes into the analysis. It is known that if the size range covers appreciably large spatial scale the SAR takes the form of a sigmoidal curve (Lomolino, 2001). Therefore, we hypothesized that in case of wide range of spatial scale the relationship between the number of diatom species and area can be described by sigmoid model. Our additional hypothesis was that the Small Island Effect can be shown for benthic diatoms. We also hypothesized that the diatom guilds respond in various ways to the increase in size of the water bodies.

Methods

Differences in climate, trophic, geographic position or other hydromorphological and limnological characteristics of the surveyed areas may bias the results of the SAR analyses; therefore, we selected a study area, where pools and ponds of similar characteristics and of various sizes are found in large numbers (Table 1.). There is an unused shooting range with thousands of bomb crater ponds and other small aquatic pools in the middle of the Hungarian Great Plain (Hungary, 47° 27' 00.36" N and 20° 59' 44.09") which was chosen as sampling area. Thirty seven pools and ponds were sampled at this area in a way that in the range of 10^{-2} – 10^2 m² all size categories must be represented at least by five water bodies. To increase the

size scale, late summer data of several nearby ponds and oxbows of the Tisza River and larger lakes, pools of the Tisza-tó (Szabó et al., 2005) the Lake Velencei (Ács et al., 2005) and the Lake Balaton (Bolla et al. 2010) were also involved in the analyses. Thus, the total scale covered a range of 10^{-2} to 10^8 m². Altogether, 217 samples were taken from 64 water bodies. Based on the measurements of chemicals (carried out by the official water quality monitoring system of Hungary) all water bodies involved into the study were eutrophic (Krasznai et al., 2010). The exception is the large shallow Lake Balaton, which is a meso-eutrophic system (Borics et al., 2014). By the applied selection of the water bodies only the climatic, biogeographic and trophic characteristics of waters can be standardised. Because of the large size scale the waters are inherently different in terms of their limnological and hydromorphological characteristics (Table 1.). Large, shallow water bodies in the range of area $>10^8$ m² cannot be found in this geographic region, and this means a practical limit of data collection. Larger lakes in the temperate zone are mostly deep and oligotrophic, and because of these limnological and trophic differences their involvement into this analysis would seriously bias our results.

Sampling

To study the diatoms epipsammon and epipelon samples were collected from the small pools of 10^{-1} - 10^{-2} m². In case of the larger water bodies diatoms were collected from the surface of macrophytes, mostly from reed stems. The samples were preserved with formaldehyde solution (final concentration 4%) and stored in dark bottles at 4°C until analyses. Geographical coordinates of the sampled pools (latitude and longitude) were recorded in the field with handheld Global Positioning System (Garmin TrexH). Diameter of the bomb crater ponds and pools were also measured on the site by tape measure. The samples were

taken in September 2011. The lakes and oxbows involved in the study were also sampled in the late summer period.

Preparation and identification of the diatom taxa

Organic matter of diatoms was removed by digestion using hot H₂O₂. To remove calcium carbonate drops of HCl were added to the samples according to CEN (2003). After digestion the material was washed by repeated sedimentation and permanent slides were made using Cargille Meltmount mounting medium (Refracting index = 1.704). Counting and identification of diatoms were made using oil immersion and DIC contrast at a magnification of 1000×. To equalize the counting effort 400 valves were counted in each sample. Identification of diatoms was performed according to Krammer & Lange-Bertalot (1986 – 1991), Krammer (2003) and Hofmann et al. (2011). Diatom species were assigned to the four diatom guilds according to Rimet & Bouchez (2012).

Statistical analyses

In case of macroscopic organisms the observed number of species gives a good estimate of the species richness. However when microbial communities are studied one has to face the problem of how to determine the exact number of species. This question is usually not crucial when habitat islands are investigated in a contiguous landscape, because in these studies the sampling effort is standardised. However when isolated islands are studied the authors usually use others' data and the efforts in these cases are not standardised (Smith et al., 2005). This implicitly results in high uncertainty of the results. To avoid these uncertainties when microbial diversity is investigated use of species richness estimators is strongly recommended (Ovreas & Curtis, 2010). For this reason, in our analysis the SAR has been given for three datasets: for the observed number of species, for the estimated number of species using Chao2

estimator (Chao, 1987), and for estimated data where the sampling effort was standardised by rarefaction (Gotelli & Colwell, 2011). In the lower size categories (10^2 – 10^3 m²) preparation of the rarefaction curves were based on the five samples that belonged to the same size category. The curves were calculated as the average of 99 curves constructed from random permutations of the sampling order for each water body. In case of the larger water bodies more samples were taken, thus the rarefaction curves could be prepared for each pond and lake respectively. The value of the smallest replicate was five, therefore the species numbers belonging to the fifth replicates were considered later in the analyses. In case of larger lakes more replicates were considered (Lake Velencei: 10; Lake Balaton: 15). The analyses were performed with the PAST software package (Hammer et al., 2001).

Species area relationships were investigated in log-log space. The most frequently applied power model (Arrhenius, 1921) was used to describe the relationship. In log-log space the relationship can be described in linear form:

$$\text{Log}S = \text{Log}c + z \times \text{Log}A$$

where c is the intercept and z is the slope of the line.

General Additive Model (GAM, Hastie & Tibshirani, 1990) as an exploratory tool was used to reveal the general shape of the relationships. The GAM algorithm selects the best shape of given complexity (defined by degree of freedom) using the Akaike information criterion (AIC). In our model the quasi-Poisson distribution and the canonical log link-function were used by the CANOCO 5 package (Ter Braak & Šmilauer, 2012). When the GAM algorithm indicated that the relationship can be better described by nonlinear formula (Table 2), we supposed that nonlinearity is caused by the SIE. The possible occurrence of the SIE and the position of the break point on the shape of the species–area curve were investigated by using linear piecewise (breakpoint) regression (Gentile & Argano, 2005). The method minimizes the sum of square of errors by fitting two lines to the data, and position of the breakpoint is

where one relationship shifts to the other. The software STATISTICA 8.0 (StatSoft, Tulsa, OK, USA) was used to conduct the regression analyses. These analyses were done for the total number of taxa and also for each functional group of diatoms, respectively.

Relative abundance data of diatom guilds in different sized habitats were illustrated in bar-charts.

Results

Total of 517 diatom taxa were identified in the samples from all pools, ponds and lakes. The observed and estimated numbers of species did not differ considerably from each other. The values of the estimated species richness (by Chao 2 estimator) were similar to the observed number of taxa, while based on rarefaction, the species numbers were slightly lower (Fig. 1).

Species numbers were relatively low at the smallest spatial scales (10^{-2} - 10^2 m²), and then, continuously increased with area and reached the highest value at the largest scale. The GAM indicated that the relationships can be described by nonlinear model. Applying the breakpoint regression the relationships could be described by two linear sections with a breakpoint at 10^4 m² water body area. Steepness of the lines in the lake area $< 10^4$ m² size range were considerably lower. Above this point the richness increased remarkably which resulted greater slope of the lines. Asymptotes were not obtained, thus, sigmoid relationships could not be demonstrated. (Fig. 1).

Diatom guilds

Considerable differences in the numbers of taxa of the four diatom guilds were observed (Fig. 2.). Most of the taxa belonged to the motile guild (Guild 4) in all size categories, followed by high profile (Guild 3) and low profile guilds (Guild 2). The planktonic guild (Guild 1) contained the least number of species. Taxa numbers in all functional guilds showed

increasing tendencies with the area (Fig. 3). The diatom guilds 1, 2 and 3 showed similar linear relationships with water body size, while in case of the guild 4 the GAM indicated that the relationship is nonlinear. The relatively large number of species in the motile guild remained nearly unaltered almost in each size category, and it is increased remarkably only at the largest lakes (Fig. 3). This guild was the richest in species because this guild contains the largest *Navicula* sensu lato and *Nitzschia* sensu lato genera. Regarding the number of taxa, the relative contribution of this guild in our dataset was 50 %. This was followed by the low profile (22%), high profile (20%) and planktic guilds (8%). Using these values as bases of the comparisons it can be concluded that the motile guild was characteristic for the small sized water bodies (Fig. 4.). The relative contribution of this guild exceeded the 50 % in the 10^{-2} - 10^3 m² size range.

For the total number of taxa the z and c values (steepness of the linear regression lines, and the intercept) were quite similar in case of all three richness estimations (observed: 0.043; Rarefaction: 0.042; Chao 2: 0.037). Much larger differences were found in these values when the SARs were studied for the guilds (Table 3). Similar values characterised the first three (1-3) diatom guilds, while as to the guild 4, both c and z values were remarkably different from the other three guilds. The intercepts (c values) were high, which means large initial slope (i.e. the number of the species in this guild is high even in the very small water bodies) but the z values were lower, which indicate only a slight increase along the size scale. In case of the total richness and guild 4 the linear regression models were applied for the subsets of data, for the SIE range (10^{-2} m² – 10^4 m²) and for the range above the SIE (Table 3). The low R^2 values of the linear models applied for the small water bodies supported the results of the breakpoint regression, because the low R^2 values indicate that at this range the richness varies independently of size. Above the SIE range the z values were remarkably higher.

Discussion

We hypothesised that SAR would be described by sigmoid model if sufficiently wide range of spatial scale is considered, but our results support that it does not hold true for benthic diatoms. We demonstrated that the relationship can be described best by breakpoint regression applying a single breakpoint at 10^4 m^2 , which means that a considerable increase in species number can be expected in large lakes. The curves did not show asymptotes, as would be expected, thus the slope of the curves didn't decrease at large spatial scale. However, it is reasonable to suppose, that the number of species should not increase indefinitely with further increase of the habitat size.

We found that in small-sized water bodies (10^2 - 10^4 m^2) the species richness did not increase considerably and the variation in the number of taxa was remarkable. Thus, SIE is a characteristic feature of the benthic diatom SARs. Investigation of the SAR for the four guilds revealed that the SIE observed for the total taxa can be attributed to the motile guild (guild 4). Since the SIE could not be observed in case of guild 1, 2 and 3, the guild of motile taxa (guild 4) determined the position of the breakpoint of the SAR (Fig. 1). Although the SIE has received little attention to date in the literature (Triantis & Sfenthourakis, 2012) besides its theoretical importance, the SIE also has practical consequences. The stochastic variation of the species richness observed in the "small island region" is in a great part due to the greater vulnerability of the smaller systems (Triantis & Sfenthourakis, 2012).

In the power model proposed by Arrhenius (1921) the slope of the SARs is influenced by two regression parameters: c measures the initial slope, while z measures the rate of change along the size gradient. These two parameters show considerable variations depending on the groups studied, the latitudinal differences and differences in sampling design. When comparisons are made among studies both parameters should be evaluated, but the c value (mostly because its value shows great variation) is usually neglected in the studies (Lomolino, 2001). The z value

has received much more attention in SAR studies. It has been reported that z values show distinct latitudinal trends; i.e. lower values characterise the SARs in low latitude regions, while in higher latitudes the values of z are higher (Willig & Lyons, 2000). Differences in colonization also influence the value of z . Colonization from mainland results in higher z , than among-island colonisations (Hanski & Gyllenberg, 1997). It is also generally accepted that dispersal limitation results in higher z values. Since the dispersal capabilities of microbes are notoriously good considerably lower z values are obtained when microbial SARs are studied (Whitaker et al., 2003; Bell, 2005). While the z -values fall within the range of 0.1 to 0.5 (Lomolino, 2001), z rarely exceeds 0.1 for microbial groups: ciliates: 0.043 (Finlay, 2002); fungi 0.0475, bacteria 0.0626 (Zhou et al., 2008); benthic diatoms 0.066, (Azovksy, 2002), zooplankton 0.17 (Browne, 1981). Comparing our results with the published literature, we found that there were not substantial differences in the z values. Those z values that were given for the whole size range were slightly lower, but those that were calculated for the range above the range of SIE were almost identical with the z values reported for benthic diatoms (Azovksy, 2002). We note that besides differences in the sampling design, comparisons are also hindered by differences in the applied statistical models because besides the ordinary least squares regression occasionally reduced major axis regressions are applied (Azovksy, 2002).

Shmida and Wilson (1985) defined four biological determinants which affect the species richness at different spatial scales. On the smallest scales niche relations (competition, predation etc.) influence the species diversity. On larger scales habitat diversity and mass effect become more important, while ecological equivalency is the mechanism which shapes the species-area relationships at the largest spatial scales. Following the arguments of Shmida and Wilson (1985) complexity of niche relations could be responsible for maintaining high

300 species richness even in very small (10^{-2} - 10^0 m²) water bodies. Habitat diversity plays a
301 considerable role in the larger lake categories.

302 Our hypothesis that the proportion of diatom guilds varies at different size scales was
303 supported by the results. Although species richness of all guilds increased with the area of the
304 water bodies, ratio of these guilds also showed differences in the various water body size
305 categories. However it is important to note that the species richness of these guilds is
306 different. The high relative and absolute abundance of the motile taxa indicates that motility is
307 a successful adaptation strategy in those water bodies where the algae do not have to cope
308 with the physical disturbances caused by the wind induced turbulences. Several species in the
309 motile guild might occasionally occur in semi-aquatic environments (wet rock surfaces, soil)
310 (van Kerckvoorde et al., 2000). These taxa can tolerate harsh, adverse environmental
311 conditions (freezing, overheating and desiccation) which they are often exposed to in small
312 aquatic environments (Souffreau et al., 2013). At the larger size scale (10^4 - 10^8 m²) increase of
313 the richness of the low and high-profile guilds is partly attributable to their good competitive
314 abilities. Elements of these groups constitute diverse mature assemblages in which light and
315 space competition are the driving forces (Cholnoky, 1927, 1929; Lange et al., 2011).

316 Although slight increase in the richness of the planktic-guild could also been demonstrated,
317 the species numbers showed great variations in all size categories. Perhaps this partly can be
318 explained by the low number of taxa in this guild. It is not surprising because planktic taxa are
319 not characteristic for phytobenthos. However, planktic species frequently occur in benthic
320 diatom samples in standing waters (Szabó et al., 2001), in creeks (Szabó et al., 2004) and in
321 large rivers (Ács et al., 2003; van Dam et al., 2007) as well, mostly because of the way of
322 samplings and hydrological reasons. The occurrence of these taxa in the phytobenthos is
323 probably not just accidental. Istvánovics & Honti (2011) demonstrated that truly planktonic
324 diatoms might occasionally prevail in benthic environments. This phenomenon was also

described for other planktonic groups of algae (Borics et al., 2003). Our results seem to demonstrate the view that contribution of diatom guilds in periphytic communities of lakes depends primarily on the physical constraints of the environment the role of nutrients is of secondary importance (Kahlert et al., 2014).

Conclusions

Several difficulties are associated with the numerical characterisation of SARs. It is especially true for microscopic systems where many uncertainties are involved in the selection of sample sites, or in the sampling and identification of the taxa. Despite these uncertainties, our results clearly demonstrate that the size of water body is a key variable affecting the richness of benthic diatom communities. We demonstrated that the SIE is a characteristic feature of the benthic diatom SAR. As this term has been described for terrestrial systems, in case of aquatic systems it seems a little confusing; therefore the term “Small Lake Effect” (SLE) might be used when aquatic islands, e.g. lakes, ponds are studied.

Acknowledgements

This work was funded by the OTKA Grant K104279 and by the Bolyai János fellowship of the Hungarian Academy of Sciences.

References

- Ács, É., K. Szabó, K. T. Kiss & F. Hindák, 2003. Benthic algal investigations in the Danube river and some of its main tributaries from Germany to Hungary. *Biologia* 58: 545–554.
- Ács, É., M. Reskóné Nagy, K. Szabó, Gy. Taba & K.T. Kiss, 2005. Application of epiphytic diatoms in water quality monitoring of Lake Velence – recommendations and assignments. *Acta Botanica Hungarica* 47: 211–223.
- Archibald, E. E. A., 1949. The specific character of plant communities: II. A quantitative approach. *The Journal of Ecology* 37: 260–274.

352 Arrhenius, O., 1921. Species and area. *Journal of Ecology* 9: 95–99.
 353 Azovsky, A. I., 2002. Size-dependent species-area relationships in benthos: is the world more
 354 diverse for microbes? *Ecography* 25: 273–282.
 355 Barinova, S. & A. Stenina, 2013. Diatom diversity and ecological variables in the Arctic lakes
 356 of the Kostyanoi Nos Cape (Nenetsky Natural Reserve, Russian North), *Plant*
 357 *Biosystems*, 147(2): 397–410,
 358 Bell, T., D. Ager, J.–I. Song, J. A. Newman, I. P. Thompson, A. K. Lilley & C. J. van der
 359 Gast, 2005. Larger islands house more bacterial taxa. *Science* 308: 1884.
 360 Berthon, V., A. Bouchez & F. Rimet, 2011. Using diatom life-forms and ecological guilds to
 361 assess organic pollution and trophic level in rivers: a case study of rivers in south-
 362 eastern France. *Hydrobiologia* 673: 259–271.
 363 Bolla, B., G. Borics, K. T. Kiss, M. Reskóné Nagy, G. Várbíró & É. Ács, 2010.
 364 Recommendations for ecological status assessment of lake Balaton (largest shallow lake
 365 of central Europe), based on benthic diatom communities *Vie et Milieu–Life and*
 366 *Environment* 60: 197–208.
 367 Borics, G., G. Várbíró, I. Grigorszky, E. Krasznai, S. Szabó & K.T. Kiss, 2007. A new
 368 evaluation technique of potamo-plankton for the assessment of the ecological status of
 369 rivers. *Archive für Hydrobiologie Suppl.* 17: 465–486.
 370 Borics, G., B. Tóthmérész, I. Grigorszky, J. Padisák, G. Várbíró & S. Szabó, 2003. Algal
 371 assemblage types of boglakes in Hungary and their relation to water chemistry,
 372 hydrological conditions and habitat diversity. *Hydrobiologia* 502: 145–155.
 373 Borics, G., B. A. Lukács, I. Grigorszky, Z. L. Nagy, L. G–Tóth, Á. Bolgovics, S. Szabó, J.
 374 Görgényi & G. Várbíró, 2014. Phytoplankton-based shallow lake types in the
 375 Carpathian basin: steps towards a bottom-up typology. *Fundamental and Applied*
 376 *Limnology* 184: 23–34.
 377 Borics, G., B. Tóthmérész, G. Várbíró, I. Grigorszky, A. Czébely & J. Görgényi, 2015.
 378 Functional phytoplankton distribution in hypertrophic systems across water body
 379 size DOI : 10. 1007/s10750-015-2268-3.
 380 Brown, J. H. & M. V. Lomolino, 1998. *Biogeography*. Sinauer, Sunderland, MA.
 381 Browne, R. A., 1981: Lakes as islands: biogeographic distribution, turnover rates, and species
 382 composition in the lakes of central New York. *Journal of Biogeography* 8: 75–83.
 383 CEN (2003). Water quality – guidance standard for the routine sampling and pretreatment of
 384 benthic diatoms from rivers. EN 13946: 2003. Comité Européen de Normalisation,
 385 Geneva, 14 p.

386 Chao, A., 1987. Estimating the population size for capture-recapture data with unequal
387 catchability. *Biometrics* 43: 783–791.

388 Cholnoky, B., 1927. Untersuchungen tiber die Okologie der Epiphyten. *Archiv für*
389 *Hydrobiologie* 18: 661–704.

390 Cholnoky, B., 1929. Epiphyten-Untersuchungen im Balatonsee. *Internationale Revue der*
391 *gesamen Hydrobioogie* 22: 313–345.

392 Connor, E. F. & E. D. McCoy, 2001. Species-area relationships. *Encyclopedia of*
393 *Biodiversity* Volume 5.

394 Dengler, J., 2009. Which function describes the species–area relationship best? A review and
395 empirical evaluation. *Journal of Biogeography* 36: 728–744.

396 Díaz, S. & M. Cabido, 2001. Vive la différence: plant functional diversity matters to
397 ecosystem processes. *Trends in Ecology and Evolution* 16: 464–655.

398 Dodson, S. I., 1992. Predicting crustacean zooplankton species richness. *Limnology and*
399 *Oceanography* 37: 848–856.

400 Dolan, J. R., 2005. Biogeography of aquatic microbes. *Aquatic Microbial Ecology* 41: 39–48.

401 Finlay, B. J., 2002. Global dispersal of free-living microbial eukaryote species. *Science* 296:
402 1061–1063.

403 Fahrig, L., 2001. How much habitat is enough? *Biological conservation* 100: 65–74.

404 Gentile, G. & R. Argano, 2005. Island biogeography of the Mediterranean sea: the species
405 relationship for terrestrial isopods. *Journal of Biogeography* 32: 1715–1726.

406 Gleason, H. A., 1922. On the relation between species and area. *Ecology* 3:158–162.

407 Gotelli, N. J. & R. K. Colwell, 2011. Estimating species richness in *Biological Diversity:*
408 *Frontiers in Measurement and Assessment* (Magurran, A.E. & B. J. McGill, eds),
409 Oxford University Press.

410 Hammer, Ø., D. A. T. Harper & P. D. Ryan, 2001. PAST: Paleontological statistics software
411 package for education and data analysis. *Palaeontologia Electron* 4: 9.

412 Hanski, I. & M. Gyllenberg, 1997. Uniting two general patterns in the distribution of species.
413 *Science* 275: 397–400.

414 Hastie, T. & R. Tibshirani, 1990. *Generalized Additive Models*. Chapman and Hall, London.

415 He, F. & P. Legendre, 1996. On species-area relations. *American Naturalist* 148: 719–737.

416 Hofmann, G., M. Wermun & H. Lange-Bertalot, 2011. *Diatomeen in Süßwasser–Benthos*
417 *von Mitteleuropa*. A.R.G. Gantner Verlag/ Koeltz Scientific Books, Königstein,
418 Germany.

- Horner-Devine, M.C., M. Lage, J. B. Hughes & B. J. M. Bohannon, 2004. A taxa–area relationship for bacteria. *Nature* 432: 750–753.
- Istvánovics, V. & M. Honti, 2011. Phytoplankton growth in three rivers: The role of meroplankton and the benthic retention hypothesis. *Limnology and Oceanography* 56: 1439–1452.
- Kelly, M. G., A. Cazaubon, E. Coring, A. Dell’Uomo, L. Ector, B. Goldsmith, H. Guasch, J. Hürlimann, A. Jarlman, B. Kawecka, J. Kwandrans, R. Laugaste, E.-A. Lindstrøm, M. Leitao, P. Marvan, J. Padisák, E. Pipp, J. Prygiel, E. Rott, S. Sabater, H. van Dam & J. Vizinet, 1998. Recommendations for the routine sampling of diatoms for water quality assessments in Europe. *Journal of Applied Phycology* 10: 215–224.
- Kahlert, M. & S. Gottschalk, 2014. Differences in benthic diatom assemblages between streams and lakes in Sweden and implications for ecological assessment. *Freshwater Science* 33: 655–669.
- Reche, I., E. Pulido-Villena, R. Morales-Baquero & E. O. Casamayor, 2005. Does ecosystem size determine aquatic bacterial richness? *Ecology* 86: 1715–1722.
- Kepner, R. L., Jr. & J. R. Pratt, 1994. Use of fluorochromes for direct enumeration of total bacteria in environmental samples: past and present. *Microbiological Reviews* 58: 603–615.
- Kilburn, P. D., 1966. Analysis of the species-area relation. *Ecology* 47: 831–843.
- Krammer, K., 2003. Diatoms of the European Inland Waters and Comparable Habitats, vol. 4, Cymbopleura, Delicata, Navicymbula, Gomphocymbellopsis, Afrocymbella. Edited by H. Lange-Berlot. Ruggell, Liechtenstein: A. R. Gantner Verlag.
- Krammer, H. & H. Lange-Bertalot, 1986–1991. Bacillariophyceae. In Ettl, H., G. Gärtner, J. Gerloff, H., Heynig & D. Mollenhauer (eds): Süßwasserflora von Mitteleuropa 2 (1–4). Gustav Fischer, Stuttgart.
- Krasznai, E., G. Borics, G. Várbíró, A. Abonyi, J. Padisák, Cs. Deák & B. Tóthmérész, 2010. Characteristics of the pelagic phytoplankton in shallow oxbows. *Hydrobiologia* 639: 261–269.
- Kruk, C., V. L. M. Huszar, E. T. H. M. Peeters, S. Bonilla, L. Costa, M. Lüring, C. S. Reynolds & M. Scheffer, 2010. A morphological classification capturing functional variation in phytoplankton. *Freshwater Biology* 55: 614–627.
- Lange, K., A. Liess, J. J. Piggott, C. R. Townsend & C. D. Matthaei, 2011. Light, nutrients and grazing interact to determine stream diatom community composition and functional group structure. *Freshwater Biology* 56: 264–78.

453 Lomolino, M. V., 2000. Ecology's most general, yet protean pattern: the species–area
454 relationship. *Journal of Biogeography* 27: 17–26.

455 Lomolino, M. V., 2001. The species–area relationship: new challenges for an old pattern.
456 *Progress in Physical Geography* 25: 1–21.

457 Lomolino, M. V. & M. D. Weiser, 2001. Towards a more general species–area relationship:
458 diversity on all islands, great and small. *Journal of Biogeography* 28: 431–445.

459 MacArthur, R. H. & E. O. Wilson, 1967. The theory of island biogeography. Princeton
460 University Press, Princeton, NJ.

461 Matthews, T. J., F. Guilhaumon, K. A. Triantis, M. K. Borregaard & R. J. Whittaker, 2015.
462 On the form of species–area relationships in habitat islands and true islands. *Global*
463 *Ecology and Biogeography* doi: 10.1111/geb.12269

464 Mazaris, A. D., M. Moustaka-Gouni, E. Michaloudi & D. C. Bobori, 2010. Biogeographical
465 patterns of freshwater micro- and macroorganisms: a comparison between
466 phytoplankton, zooplankton and fish in the eastern Mediterranean. *Journal of*
467 *Biogeography* 37: 1341–1351.

468 Ovreas, L. & T. P. Curtis, 2011. Microbial diversity and ecology. In *Biological Diversity:*
469 *Frontiers in Measurement and Assessment* (Magurran, A.E. & B. J. McGill, eds),
470 Oxford University Press.

471 Padisák, J., L. O. Crossetti & L. Naselli–Flores, 2009. Use and misuse in the application of
472 the phytoplankton functional classification: a critical review with updates.
473 *Hydrobiologia* 621: 1–19.

474 Padisák, J., G. Vasas & G. Borics, 2015. Phycogeography of freshwater phytoplankton –
475 traditional knowledge and new molecular tools *Hydrobiologia* DOI: 10.1007/s10750-
476 015-2259-4.

477 Passy, S., 2007. Diatom ecological guilds display distinct and predictable behavior along
478 nutrient and disturbance gradients in running waters. *Aquatic Botany* 86: 171–178.

479 Passy, S. I. & C. A. Larson, 2011. Succession in stream biofilms is an environmentally driven
480 gradient of stress tolerance. *Microbial Ecology* 62: 414–424.

481 Peay, K. G., T. D. Bruns, P. G. Kennedy, S. E. Bergemann & M. Garbelotto, 2007. A strong
482 species–are a relationship for eukaryotic soil microbes: island size matters for
483 ectomycorrhizal fungi. *Ecology Letters* 10: 470–480.

484 Preston, F. W., 1962. The canonical distribution of commonness and rarity. Part I. *Ecology*
485 43: 185–215.

486 Reche, I., E. Pulido-Villena, R. Morales-Baquero & E. O. Casamayor, 2005. Does ecosystem
487 size determine aquatic bacterial richness? *Ecology* 86: 1715–1722.

488 Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores & S. Melo, 2002. Towards a
489 functional classification of the freshwater phytoplankton. *Journal of Plankton Research*
490 24: 417–428.

491 Rimet, F. & A. Bouchez, 2012. Life-forms, cell-sizes and ecological guilds of diatoms in
492 European rivers. *Knowledge and Management of Aquatic Ecosystems* 406: 01.

493 Salmaso, N. & J. Padisák, 2007. Morpho-functional groups and phytoplankton development
494 in two deep lakes (Lake Garda, Italy and Lake Stechlin, Germany). *Hydrobiologia* 578:
495 97–112.

496 Schoener, T. W., 1976. The species–area relation within archipelagos: models and evidence
497 from island land birds. *Proceedings of the International Ornithological Congress* 16:
498 628–642.

499 Shmida, A. & M. V. Wilson, 1985. Biological determinants of species diversity. *Journal of*
500 *Biogeography* 12: 1–20.

501 Smith, V. H., B. L. Foster, J. P. Grover, R. D. Holt, M. A. Leibold & F. deNoyelles, Jr., 2005.
502 Phytoplankton species richness scales consistently from laboratory microcosms to the
503 world's oceans. *PNAS* 102: 4393–4396.

504 Souffreau, C., P. Vanormelingen, K. Sabbe & W. Vyverman, 2013. Tolerance of resting cells
505 of freshwater and terrestrial benthic diatoms to experimental desiccation and freezing is
506 habitat-dependent. *Phycologia* 52: 246 –255.

507 Stenger-Kovács, C., E. Lengyel, L. O. Crossetti, V. Üveges & J. Padisák, 2013. Diatom
508 ecological guilds as indicators of temporally changing stressors and disturbances in the
509 small Torna-stream, Hungary. *Ecological Indicators* 24: 138–147.

510 Somerville, C. C., I. T. Knight, W. L. Straube & R. R. Colwell, 1989. Simple, rapid method
511 for direct isolation of nucleic acids from aquatic environments. *Applied and*
512 *Environmental Microbiology* 1989: 548–554.

513 Szabó, K., É. Ács, E. Párista, K. T. Kiss, S. Barreto & J. Makk, 2001. Periphyton and
514 phytoplankton in the Soroksár – Danube in Hungary. I. Periphytic algae on reed stems.
515 *Acta Botanica Hungarica* 43: 13–35.

516 Szabó, K., K. T. Kiss, L. Ector, M. Kecskés & É. Ács, 2004. Benthic diatom flora in a small
517 Hungarian tributary of River Danube (Rákos stream). *Archiv für Hydrobiologie Suppl.*,
518 150 *Algological Studies* 111: 79–94.

- Szabó, K., K. T. Kiss, G. Taba & É. Ács, 2005. Epiphytic diatoms of the Tisza River, Kisköre Reservoir and some oxbows of the Tisza River after the cyanide and heavy metal pollution in 2000. *Acta Botanica Croatica* 64: 1–46.
- Ter Braak, C. J. F. & P. Šmilauer, 2012. Canoco reference manual and user's guide: software ordination, version 5.0. Microcomputer Power, Ithaca, USA, 496.
- Tjørve, E., 2003. Shapes and functions of species–area curves: a review of possible models. *Journal of Biogeography* 30: 827–835.
- Triantis, K. A. & S. Sfenthourakis, 2012. Island biogeography is not a single-variable discipline: the small island effect debate. *Diversity and Distributions* 18: 92–96.
- Triantis, K. A., F. Guilhaumon & R. J. Whittaker, 2012. The island species–area relationship: biology and statistics. *Journal of Biogeography* 39: 215–231.
- van Kerckvoorde, A., K. Trappeniers, I. Nijs & L. Beyens, 2000. Terrestrial soil diatom assemblages from different vegetation types in Zackenberg (Northeast Greenland). *Polar Biology* 23: 392–400.
- van Dam, H., C. Stenger-Kovács, É. Ács, G. Borics, K. Buczkó, É. Hajnal, É. Soróczki-Pintér, G. Várbíró, B. Tóthmérész & J. Padisák, 2007. Implementation of the European Water Framework Directive: Development of a system for water quality assessment of Hungarian running waters with diatoms. *Archiv für Hydrobiologie Suppl. Large Rivers* 17: 339–383.
- Várbíró, G., É. Ács, G. Borics, K. Érces, G. Fehér, I. Grigorszky, T. Japport, G. Kocsis, E. Krasznai, K. Nagy, Zs. Nagy-László, Zs. Pilinszky & K.T. Kiss, 2007. Use of Self-Organising Maps SOM for characterization of riverine phytoplankton associations in Hungary. *Archiv für Hydrobiologie Suppl.* 161: 383–394.
- Whittaker, R. J., D. W. Grogan & J. W. Taylor, 2003. Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science* 301: 976–978.
- Williams, M. R., B. B. Lamont & J. D. Henstridge, 2009. Species–area functions revisited. *Journal of Biogeography* 36: 1994–2004.
- Willig, M. R. & S. K. Lyons, 2000: A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* 80: 248–92.
- Woodcock, S., T. P. Curtis, I. M. Head, M. Lunn & W. T. Sloan, 2006. Taxa–area relationships for microbes: the unsampled and the unseen. *Ecology Letters* 9: 805–812.
- Zhou, J., S. Kang, C. W. Schadt & C. T. Garten, Jr., 2008. Spatial scaling of functional gene diversity across various microbial taxa. *PNAS* 105: 7768–7773.

Legends for tables and figures

Table 1.

Hydro-morphological and chemical variables of the investigated water bodies (pH, Electrical conductivity and TP values are vegetation period means for 2011; * indicate single late summer data)

	Log Area (m ²)	Depth (m)	Log volume (m ³)	pH	Conductivity (μScm ⁻¹)	Total P (μg l ⁻¹)
*Shooting range 10 ⁻² m ²	-2.105	0.1	-3.105	8.65	2100	2410
*Shooting range 10 ⁻¹ m ²	-1.974	0.15	-1.974	8.65	2100	1582
*Shooting range 10 ⁰ m ²	0.337	0.41	-0.097	7.9	2073	1394
*Shooting range 10 ¹ m ²	1.226	1.12	1.258	8.86	2589	1332
*Shooting range 10 ² m ²	1.823	1.4	1.964	9.12	3450	758
Morotvaközi holt meder, Egyek	3.813	1.6	4.017	7.37	723	1838
Egyeki Holt Tisza, Egyek	4.748	1.5	4.924	7.77	671	310
Tiszadobi Holt-Tisza, Darab Tisza	4.924	1.6	5.128	7.72	273	82
Tiszadobi Holt-Tisza, Szűcs- Tisza	5.167	2.5	5.565	8.05	304	134
Tiszadobi Holt-Tisza, Falu-Tisza	5.334	3.6	5.891	8.3	322	369
Holt-Szamos, Géberjén	5.354	2.2	5.696	8.16	674	468
Tiszadobi Holt-Tisza, Malom-Tisza kanyar	5.508	3.2	6.013	8.07	281	180
Holt-Szamos, Tunyogmatolcs	5.886	3.5	6.43	8.31	611	700
Lake Velencei	7.396	1.5	7.572	8.77	3056	64
Kiskörei-tározó	8.104	1.3	8.218	8.44	370	118
Lake Balaton	8.772	3.3	9.292	8.57	690	31

Table 2.

Summary of fitted Generalized Additive Models. (Predictors: log Area) Under the heading “Type” complexity of the model is specified: lin means that a (generalized) linear term was chosen during stepwise selection, while s2 describes a smooth term with complexity value 2 measured in degrees of freedom. The best model was selected by Akaike Information Criterion (AIC) values. R² provides a measure of explained variation, F test statistic and following p estimate of type I error rate corresponds to an overall parametric test of the selected model against the null model

	Type	R ²	F	p
Observed	s2	0.74	18.3	0.00017
Rarefaction	s2	0.74	18.5	0.00009
Chao 2	s2	0.7	15.3	0.00036
Observed, guild 1	lin	0.49	13.2	0.00273
Observed, guild 2	lin	0.76	49.4	<0.00001
Observed, guild3	lin	0.58	19.5	0.00058
Observed, guild 4	s2	0.49	6.4	0.01172
Rarefaction, guild 1	lin	0.59	20.3	0.0005
Rarefaction, guild 2	lin	0.8	57	<0.00001
Rarefaction, guild 3	lin	0.66	27.6	0.00012
Rarefaction, guild 4	s2	0.42	4.8	0.02702
Chao 2, guild 1	lin	0.5	14.1	0.00214
Chao 2, guild 2	lin	0.77	47	<0.00001
Chao 2, guild 3	lin	0.62	23.2	0.00027
Chao 2, guild 4	s2	0.46	5.5	0.01823

568

569 Table 3.

570 Attributes of regression fits between log Area and the log diatom taxon numbers (S). Results
571 are based on the log form of Arrhenius's (1921) equation: $\text{LogS} = \text{Log}c + z \times \text{LogA}$; where c
572 is the intercept and z is the slope of the line. R²: Pearson's correlation coefficient

	Complete fit			Fit of larger lakes (log area > 10 ⁴ m ²)			Fit of small ponds (log area < 10 ⁴ m ²)		
	<i>z</i> -value	Intercept (<i>c</i>)	R ²	<i>z</i> -value	Intercept (<i>c</i>)	R ²	<i>z</i> -value	Intercept (<i>c</i>)	R ²
Observed	0.043	1.490	0.65	0.071	1.209	0.630	0.0104	1.557	0.029
Rarefaction	0.042	1.504	0.678	0.059	1.335	0.651	0.0084	1.578	0.015
Chao 2	0.038	1.586	0.597	0.061	1.353	0.602	-0.0077	1.182	0.016
Observed, guild 1	0.067	0.182	0.485						
Observed, guild 2	0.069	0.599	0.776						
Observed, guild3	0.057	0.727	0.609						
Observed, guild 4	0.019	1.393	0.177	0.077	0.798	0.488	0.0055	1.449	0.019
Rarefaction, guild 1	0.102	-0.215	0.591						
Rarefaction, guild 2	0.081	0.482	0.802						
Rarefaction, guild 3	0.057	0.719	0.663						
Rarefaction, guild 4	0.018	1.417	0.209	0.058	1.005	0.429	0.0049	1.459	0.009
Chao 2, guild 1	0.09	-0.071	0.501						
Chao 2, guild 2	0.074	0.57	0.770						
Chao 2, guild 3	0.06	0.721	0.624						
Chao 2, guild 4	0.017	1.435	0.134	0.075	0.843	0.431	-0.0018	1.56	0.002

Figure 1.

Relationship between the area of water bodies (log m²) and log species richness of diatoms.

Breakpoints indicate the range of Small Island Effect (SIE)

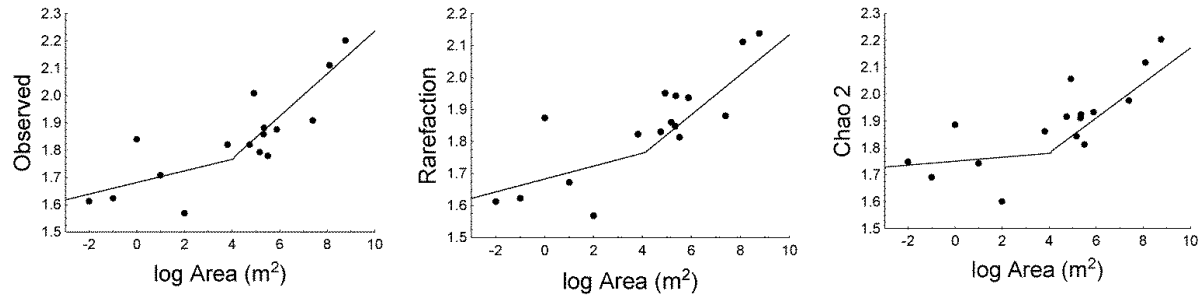
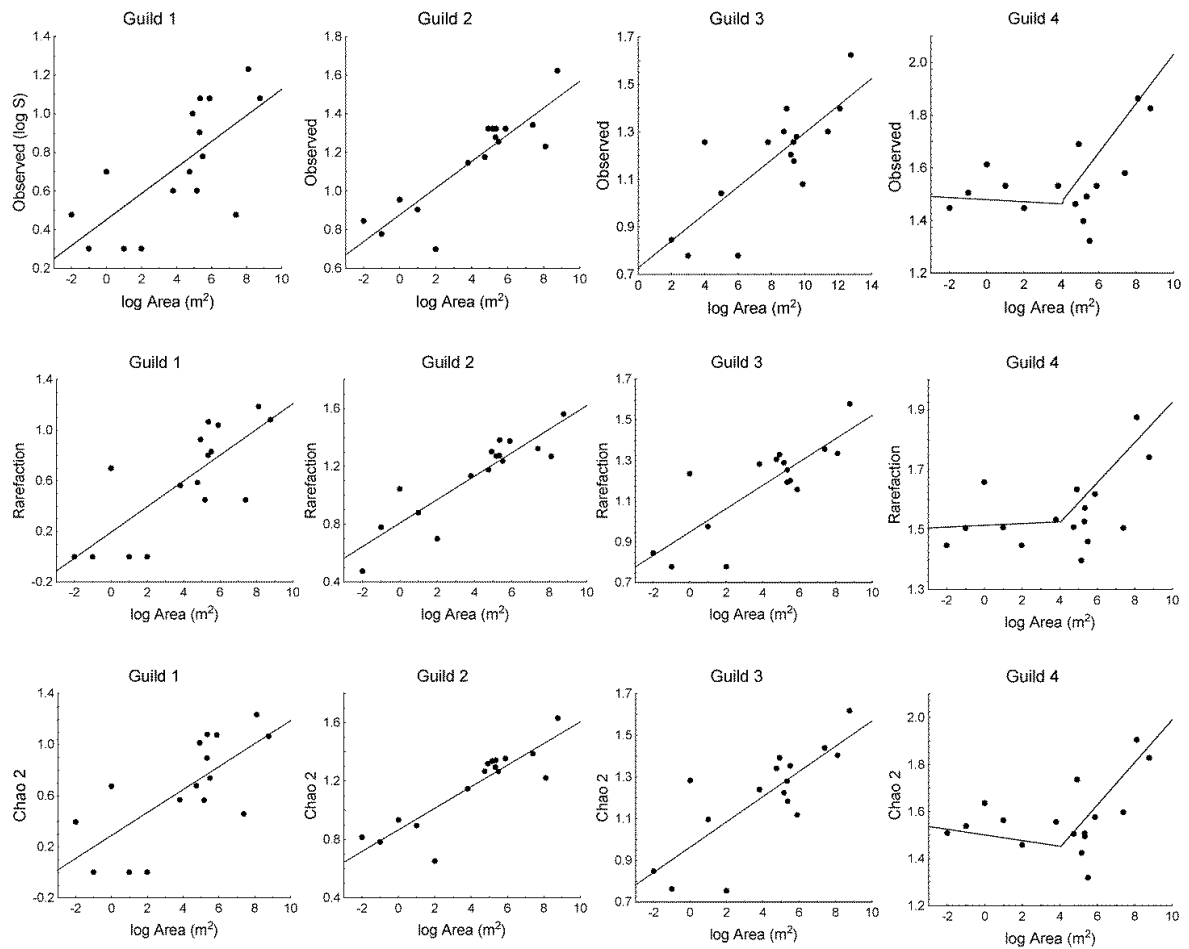


Figure 2.

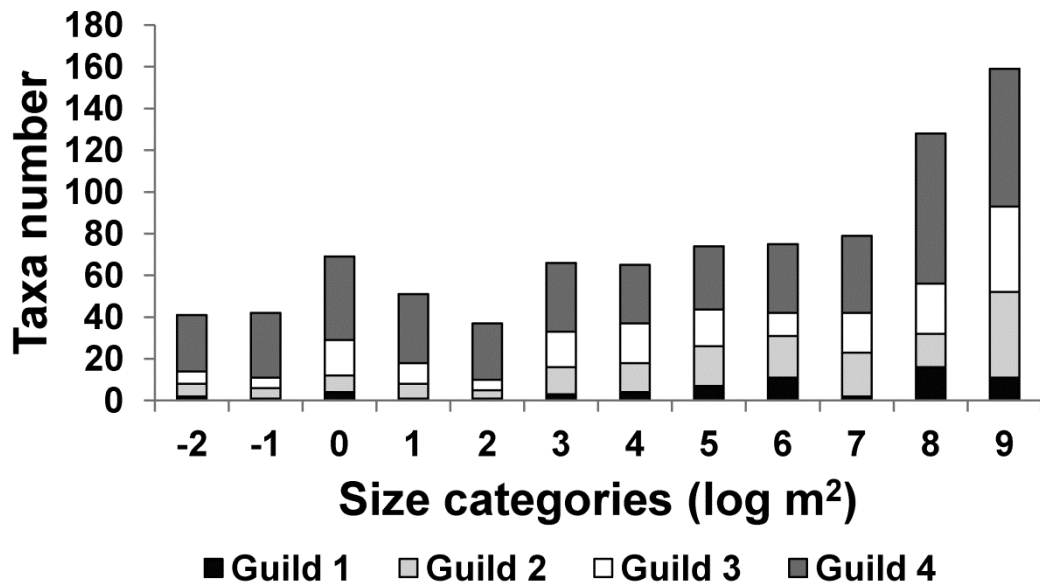
Relationship between the area of water bodies (log m²) and log species richness of the ecological guilds of diatoms. Breakpoints indicate the range of Small Island Effect (SIE) (Guild 1: planktonic; Guild 2: low-profile; Guild 3: high-profile, Guild 4: motile; for more information see the text)



583

584 Figure 3.

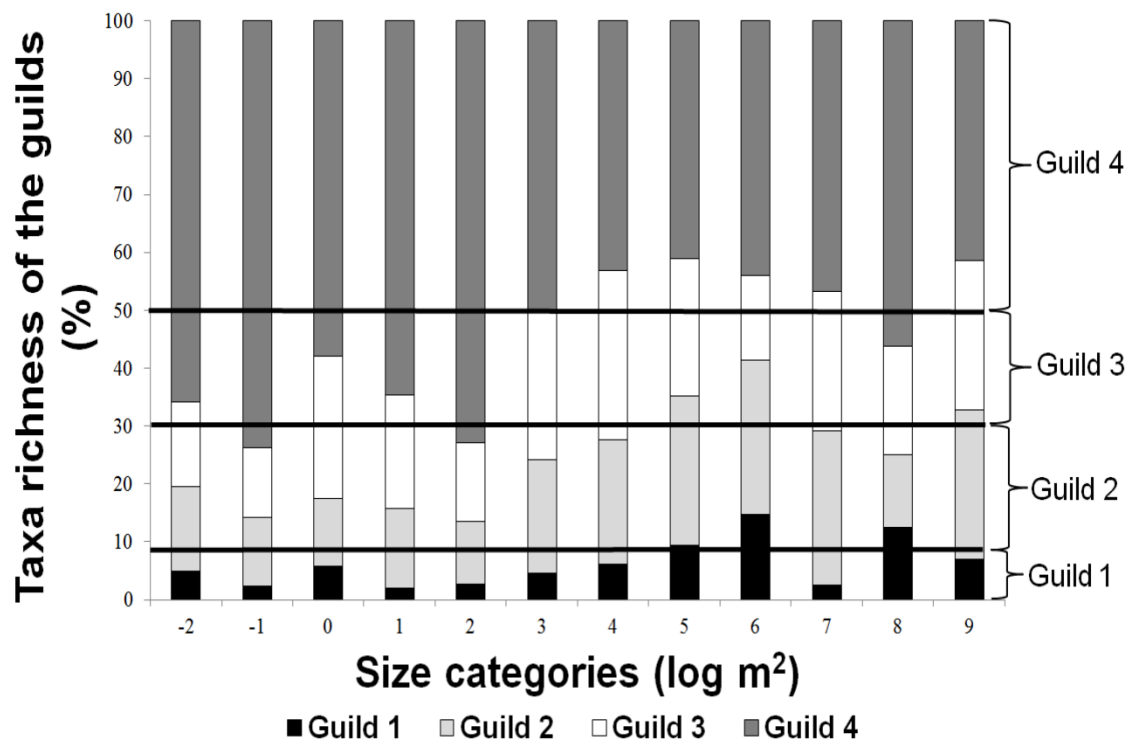
585 Observed number of species in the four ecological diatom guilds in the various size
 586 categories. (meaning of the guilds: Guild 1: planktonic; Guild 2: low-profile; Guild 3: high-
 587 profile, Guild 4: motile)



588

589 Figure 4.

590 Ratio of the four diatom guilds in the various size categories. Species richness ratios are given
 591 in percentage. Black lines indicate the ratio of the guilds based on the entire list of taxa found
 592 in the present study. (Guild 1: 8%; Guild 2: 22%; Guild 3: 20%; Guild 4: 50%; meaning of
 593 the guilds: Guild 1: planktonic; Guild 2: low-profile; Guild 3: high-profile, Guild 4: motile)



594

595