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

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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} m^2). 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} m^2. 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 microscopic systems are deeply under-represented in the literature (Azovsky, 2002; Dolan, 2005; Reche et al., 2005; Smith et al., 2005; Barinova & Stenina 2013; Borics et al., 2015). From biogeographical point of view, lakes and ponds are considered as aquatic islands in a terrestrial landscape (Dodson, 1992). The large number of the ponds and the large size differences among them makes these habitats ideal objects for testing the various SAR models. Despite the fact that the aquatic environments provide habitats for various groups of microscopic organisms (bacterio-, phyto and zooplankton, benthic algae, etc.) which play an important role in the functioning of aquatic ecosystems, yet these groups have received little attention in SAR analyses (Horner-Devine et al., 2004; Smith et al., 2005). One reason for this is that concerning the microscopic organisms, definition of individuals and species is highly uncertain (Reche et al., 2005; Peay et al., 2007). The other reason is that in case of microscopic systems complete census of the habitat is not possible; therefore, various sampling strategies and species estimators have to be applied to estimate the richness of the studied systems. The large diversity of methods can lead to high uncertainty of the results (Somerville et al., 1989; Kepner & Pratt, 1994). These uncertainties can be minimized if the selected microscopic organisms can be identified safely and well developed protocols support their samplings. In the microbial world diatoms meet these requirements (Kelly et al., 1998).

Besides species richness, functional diversity is also an important component of diversity because it is considered a useful metric which reflects ecosystem complexity and ecosystem processes (Diaz & Cabido, 2001). Similarly to phytoplankton where several functional groups were proposed in the recent years (Reynolds et al., 2002; Salmaso & Padisák, 2007; Borics et al., 2007, Várbíró et al., 2007; Kruk et al., 2010), ecological guilds based on functional differences were also proposed for diatoms (Passy, 2007; Rimet & Bouchez, 2012). Based on their utilization of nutrient resources and their resistance to physical disturbances Passy (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, trophy, 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} m^2 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} m^2. 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 $>10^{8}$ m^2 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} m^2. 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 (Garmine 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 H_2O_2. 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} m^2) 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 (Arrherius, 1921) was used to describe the relationship. In log-log space the relationship can be described in linear form:

$$LogS = Logc + z \times LogA$$

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} m^2), 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 m^2 water body area. Steepness of the lines in the lake area $< 10^4$ m^2 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} m^2 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} m^2 – 10^{4} m^2) 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 species richness even in very small (10^{-2} - 10^{0} m^2) water bodies. Habitat diversity plays a considerable role in the larger lake categories.

Our hypothesis that the proportion of diatom guilds varies at different size scales was supported by the results. Although species richness of all guilds increased with the area of the water bodies, ratio of these guilds also showed differences in the various water body size categories. However it is important to note that the species richness of these guilds is different. The high relative and absolute abundance of the motile taxa indicates that motility is a successful adaptation strategy in those water bodies where the algae do not have to cope with the physical disturbances caused by the wind induced turbulences. Several species in the motile guild might occasionally occur in semi-aquatic environments (wet rock surfaces, soil) (van Kerckvoorde et al., 2000). These taxa can tolerate harsh, adverse environmental conditions (freezing, overheating and desiccation) which they are often exposed to in small aquatic environments (Souffreau et al., 2013). At the larger size scale (10^4-10^8 m^2) increase of the richness of the low and high-profile guilds is partly attributable to their good competitive abilities. Elements of these groups constitute divers mature assemblages in which light and space competition are the driving forces (Cholnoky, 1927, 1929; Lange et al., 2011).

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

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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. R^2 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

Table 3.

Attributes of regression fits between log Area and the log diatom taxon numbers (S). Results are based on the log form of Arrhenius's (1921) equation: $\text{LogS} = \text{Log}c + z \times \text{LogA}$; where c is the intercept and z is the slope of the line. R^2: 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)		
	z-value	Intercept (*c*)	R^2	*z*-value	Intercept (*c*)	R^2	*z*-value	Intercept (*c*)	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 m^2) and log species richness of diatoms. Breakpoints indicate the range of Small Island Effect (SIE)

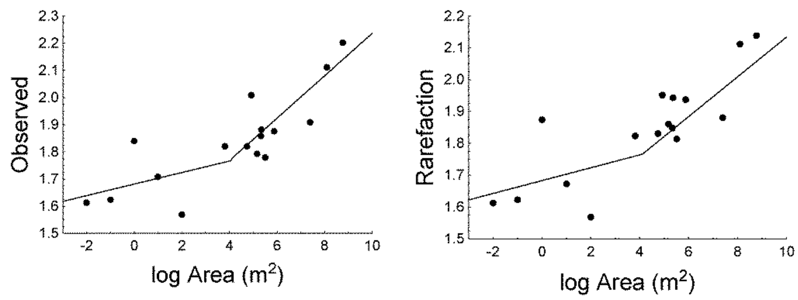


Figure 2.

Relationship between the area of water bodies (log m^2) 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)

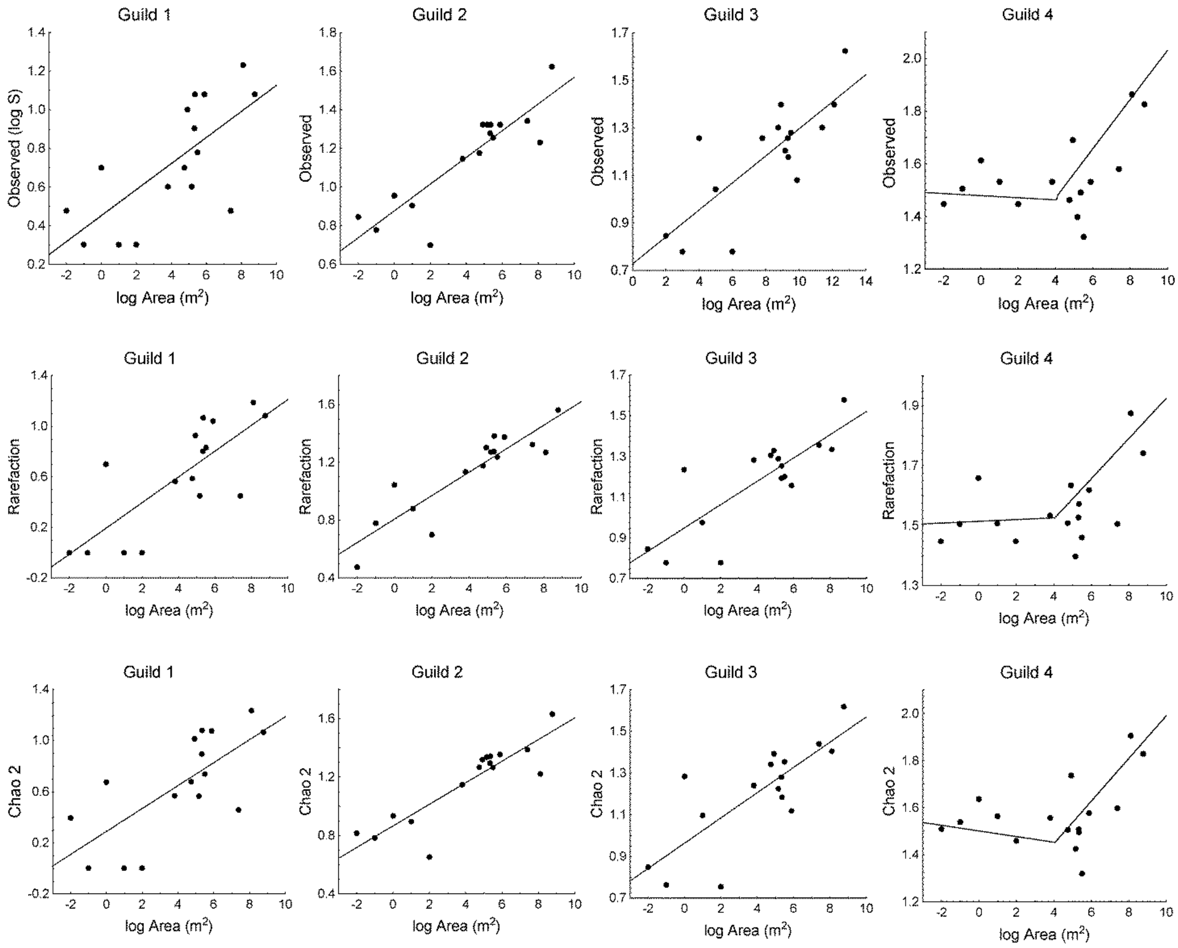


Figure 3.

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

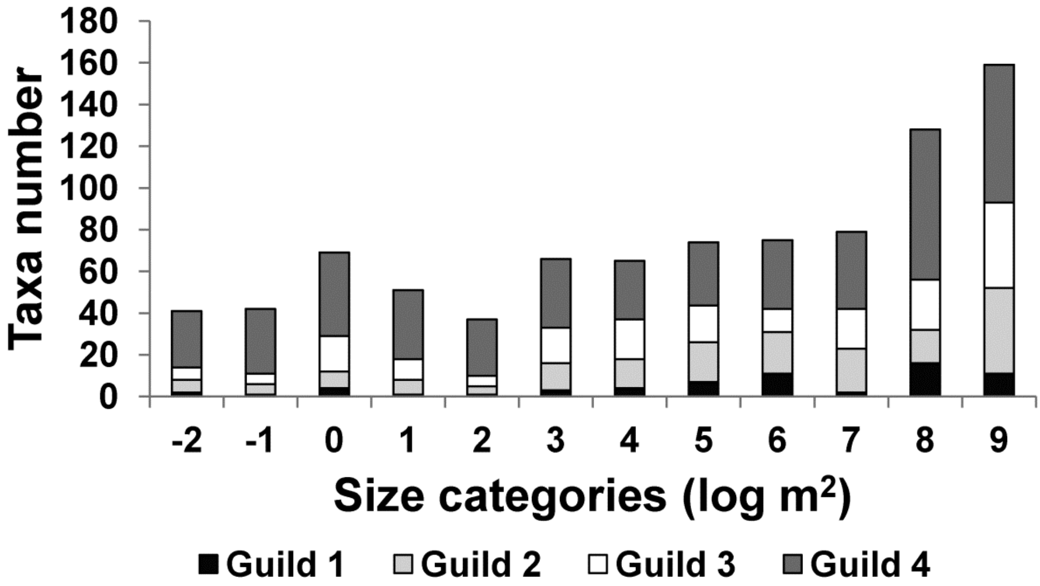
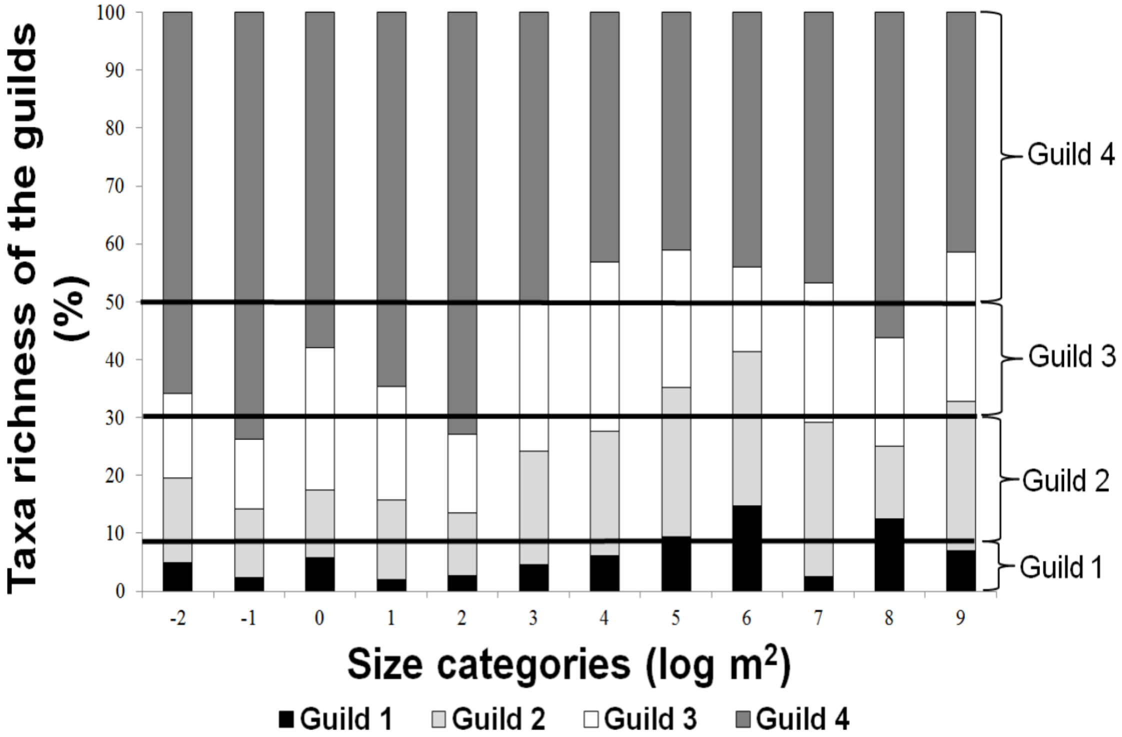


Figure 4.

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


Taxa richness of the guilds (%)
100
90
80
70
60
50
40
30
20
10
0
-2
-1
0
1
2
3
4
5
6
7
8
9
Size categories (log m²)
Guild 1
Guild 2
Guild 3
Guild 4
Guild 4
Guild 3
Guild 2
Guild 1