

1 **This manuscript is contextually identical with the following published paper:**

2 Bolgovics Á., Ács É., Várбірó G., Görgényi J., Borics G. (2016) Species area
3 relationship (SAR) for benthic diatoms: a study on aquatic islands. HYDROBIOLOGIA
4 764: (1) pp. 91-102. DOI: 10.1007/s10750-015-2278-1

5 **The original published PDF available in this website:**

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

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

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18

19 **Abstract**

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

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

34

35

36 **Keywords:** biogeography, small lake effect, diatom guilds

37

38 **Introduction**

39 The so-called “species-area relationship” (SAR) is one of the most general patterns in ecology
40 (Schoener, 1976; Lomolino, 2000). According to this paradigm the number of species
41 increases with the area surveyed. The relationship was demonstrated for true islands, for
42 habitat fragments and also for segments of a large continuous habitat. The SAR is considered
43 a law in ecology and is applicable to plants, animals and microbes (Woodcock et al., 2006).
44 Several empirical models were developed to describe this relationship mathematically. The
45 most frequently applied are the power (Arrhenius, 1921), the exponential (Gleason, 1922) and
46 the sigmoid (Archibald, 1949) models. Since so far, there is no generally accepted method of
47 curve fitting, it is often depends on the researchers' preconception (Tjørve, 2003; Dengler,
48 2009; Williams et al., 2009, Matthews et al., 2015). However, He & Legendre (1996)
49 demonstrated that the shape of the curve depends on the scale. The exponential model is valid
50 in case of small sampling area, while the power model fits well both at small and intermediate
51 sampling area. If the spatial scale of the sampled area extended over more than three orders of
52 magnitude, the sigmoid model shows the best fit.

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

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

76 Although the SAR has been studied for wide range of taxa and for various spatial scales
77 (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, Várbró 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

103 were supplemented by the planktic guild (Rimet & Bouchez, 2012), thus, four diatom guilds
104 can be distinguished: planktic, low-profile, high-profile and motile guilds. Several papers
105 were published concerning the use of diatom ecological guilds and for predicting various
106 ecological gradients (Berthon et al., 2011; Passy & Larson, 2011; Stenger-Kovács et al.,
107 2013) but size-related questions were not addressed in these studies.

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

117

118

119 **Methods**

120 Differences in climate, trophic, geographic position or other hydromorphological and
121 limnological characteristics of the surveyed areas may bias the results of the SAR analyses;
122 therefore, we selected a study area, where pools and ponds of similar characteristics and of
123 various sizes are found in large numbers (Table 1.). There is an unused shooting range with
124 thousands of bomb crater ponds and other small aquatic pools in the middle of the Hungarian
125 Great Plain (Hungary, 47° 27' 00.36" N and 20° 59' 44.09") which was chosen as sampling
126 area. Thirty seven pools and ponds were sampled at this area in a way that in the range of 10^{-2}
127 -10^2 m² all size categories must be represented at least by five water bodies. To increase the

128 size scale, late summer data of several nearby ponds and oxbows of the Tisza River and larger
129 lakes, pools of the Tisza-tó (Szabó et al., 2005) the Lake Velencei (Ács et al., 2005) and the
130 Lake Balaton (Bolla et al. 2010) were also involved in the analyses. Thus, the total scale
131 covered a range of 10^{-2} to 10^8 m². Altogether, 217 samples were taken from 64 water bodies.
132 Based on the measurements of chemicals (carried out by the official water quality monitoring
133 system of Hungary) all water bodies involved into the study were eutrophic (Krasznai et al.,
134 2010). The exception is the large shallow Lake Balaton, which is a meso-eutrophic system
135 (Borics et al., 2014). By the applied selection of the water bodies only the climatic,
136 biogeographic and trophic characteristics of waters can be standardised. Because of the large
137 size scale the waters are inherently different in terms of their limnological and
138 hydromorphological characteristics (Table 1.). Large, shallow water bodies in the range of
139 area $>10^8$ m² cannot be found in this geographic region, and this means a practical limit of
140 data collection. Larger lakes in the temperate zone are mostly deep and oligotrophic, and
141 because of these limnological and trophic differences their involvement into this analysis
142 would seriously bias our results.

143

144 **Sampling**

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

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

154

155 **Preparation and identification of the diatom taxa**

156 Organic matter of diatoms was removed by digestion using hot H₂O₂. To remove calcium
157 carbonate drops of HCl were added to the samples according to CEN (2003). After digestion
158 the material was washed by repeated sedimentation and permanent slides were made using
159 Cargille Meltmount mounting medium (Refracting index = 1.704). Counting and
160 identification of diatoms were made using oil immersion and DIC contrast at a magnification
161 of 1000×. To equalize the counting effort 400 valves were counted in each sample.
162 Identification of diatoms was performed according to Krammer & Lange-Bertalot (1986 –
163 1991), Krammer (2003) and Hofmann et al. (2011). Diatom species were assigned to the four
164 diatom guilds according to Rimet & Bouchez (2012).

165 **Statistical analyses**

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

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

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

$$189 \text{LogS} = \text{Log}c + z \times \text{LogA}$$

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

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

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

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

206

207 **Results**

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

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

220

221 Diatom guilds

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

226 increasing tendencies with the area (Fig. 3). The diatom guilds 1, 2 and 3 showed similar
227 linear relationships with water body size, while in case of the guild 4 the GAM indicated that
228 the relationship is nonlinear. The relatively large number of species in the motile guild
229 remained nearly unaltered almost in each size category, and it is increased remarkably only at
230 the largest lakes (Fig. 3). This guild was the richest in species because this guild contains the
231 largest *Navicula* sensu lato and *Nitzschia* sensu lato genera. Regarding the number of taxa, the
232 relative contribution of this guild in our dataset was 50 %. This was followed by the low
233 profile (22%), high profile (20%) and planktic guilds (8%). Using these values as bases of the
234 comparisons it can be concluded that the motile guild was characteristic for the small sized
235 water bodies (Fig. 4.). The relative contribution of this guild exceeded the 50 % in the 10^{-2} -
236 10^3 m² size range.

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

250

251 **Discussion**

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

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

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

276 has received much more attention in SAR studies. It has been reported that z values show
277 distinct latitudinal trends; i.e. lower values characterise the SARs in low latitude regions,
278 while in higher latitudes the values of z are higher (Willig & Lyons, 2000). Differences in
279 colonization also influence the value of z . Colonization from mainland results in higher z , than
280 among-island colonisations (Hanski & Gyllenberg, 1997). It is also generally accepted that
281 dispersal limitation results in higher z values. Since the dispersal capabilities of microbes are
282 notoriously good considerably lower z values are obtained when microbial SARs are studied
283 (Whitaker et al., 2003; Bell, 2005). While the z -values fall within the range of 0.1 to 0.5
284 (Lomolino, 2001), z rarely exceeds 0.1 for microbial groups: ciliates: 0.043 (Finlay, 2002);
285 fungi 0.0475, bacteria 0.0626 (Zhou et al., 2008); benthic diatoms 0.066, (Azovksy, 2002),
286 zooplankton 0.17 (Browne, 1981). Comparing our results with the published literature, we
287 found that there were not substantial differences in the z values. Those z values that were
288 given for the whole size range were slightly lower, but those that were calculated for the range
289 above the range of SIE were almost identical with the z values reported for benthic diatoms
290 (Azovksy, 2002). We note that besides differences in the sampling design, comparisons are
291 also hindered by differences in the applied statistical models because besides the ordinary
292 least squares regression occasionally reduced major axis regressions are applied (Azovksy,
293 2002).

294 Shmida and Wilson (1985) defined four biological determinants which affect the species
295 richness at different spatial scales. On the smallest scales niche relations (competition,
296 predation etc.) influence the species diversity. On larger scales habitat diversity and mass
297 effect become more important, while ecological equivalency is the mechanism which shapes
298 the species-area relationships at the largest spatial scales. Following the arguments of Shmida
299 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

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

329

330 **Conclusions**

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

339

340 **Acknowledgements**

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

343

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- 552

554 **Legends for tables and figures**

555 Table 1.

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

	Log Area (m ²)	Depth (m)	Log volume (m ³)	pH	Conductivity (μScm ⁻¹)	Total P (μg Γ 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, Szúcs- 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

560 Table 2.

561 Summary of fitted Generalized Additive Models. (Predictors: log Area) Under the heading
562 “Type” complexity of the model is specified: lin means that a (generalized) linear term was
563 chosen during stepwise selection, while s2 describes a smooth term with complexity value 2
564 measured in degrees of freedom. The best model was selected by Akaike Information
565 Criterion (AIC) values. R² provides a measure of explained variation, F test statistic and
566 following p estimate of type I error rate corresponds to an overall parametric test of the
567 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

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: $\text{Log}S = \text{Log}c + z \times \text{Log}A$; where c
572 is the intercept and z is the slope of the line. R²: Pearson's correlation coefficient

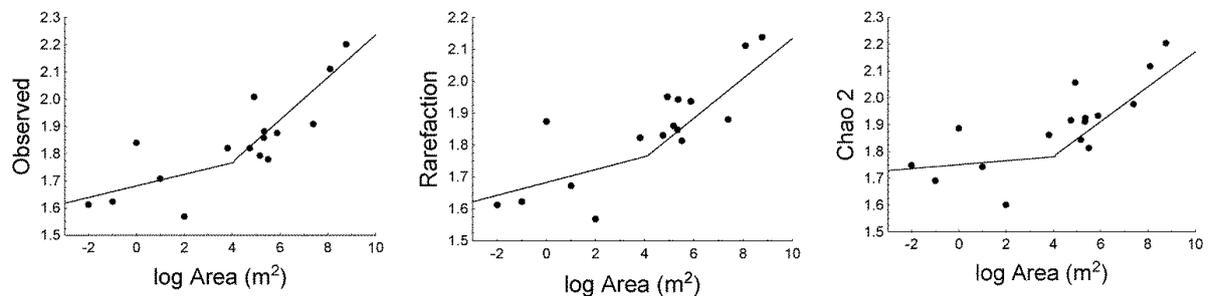
	Complete fit			Fit of larger lakes (log area > 10 ⁴ m ²)			Fit of small ponds (log area < 10 ⁴ m ²)		
	z-value	Intercept (c)	R ²	z-value	Intercept (c)	R ²	z-value	Intercept (c)	R ²
Observed	0.043	1.490	0.65	0.071	1.209	0.630	0.0104	1.557	0.029
Rarefaction	0.042	1.504	0.678	0.059	1.335	0.651	0.0084	1.578	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

573

574 Figure 1.

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

576 Breakpoints indicate the range of Small Island Effect (SIE)



577

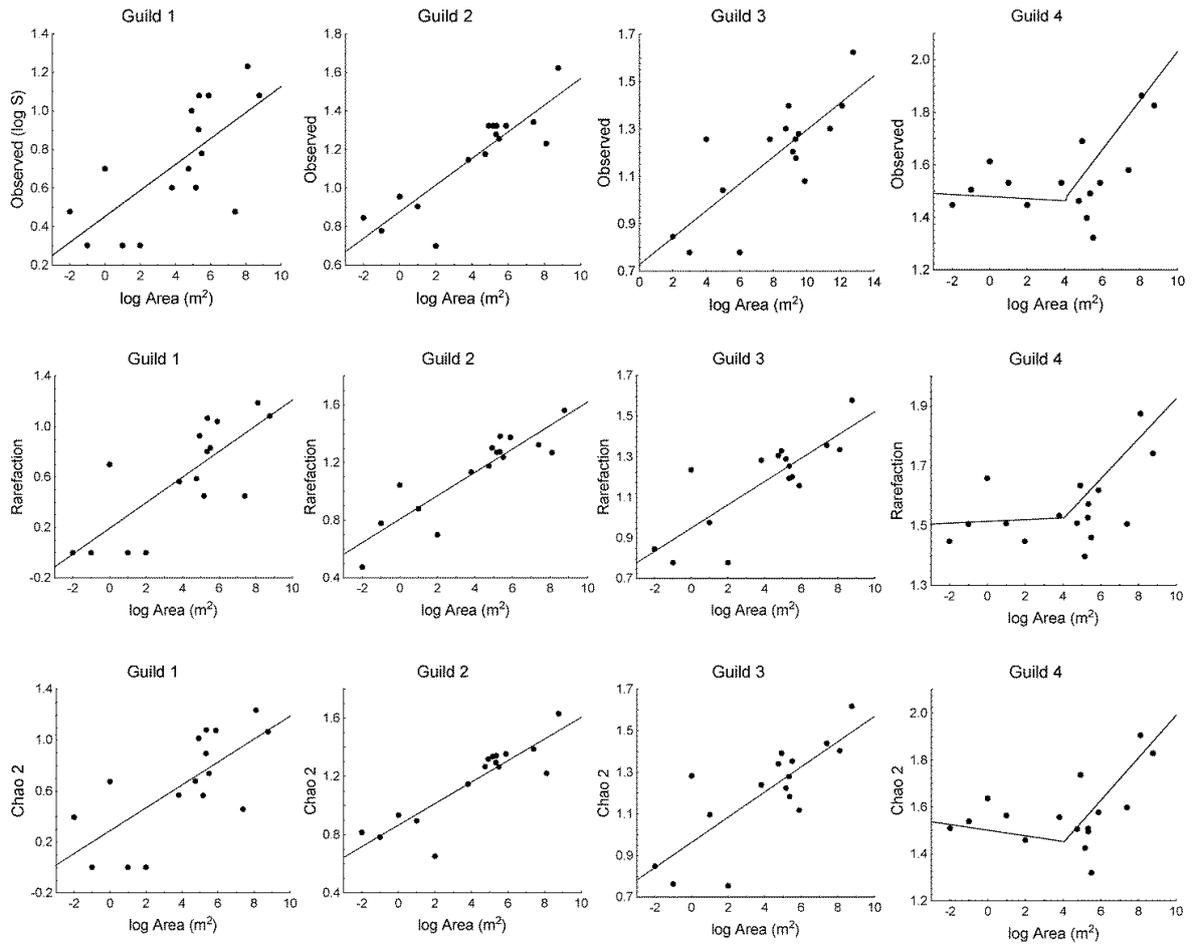
578 Figure 2.

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

580 ecological guilds of diatoms. Breakpoints indicate the range of Small Island Effect (SIE)

581 (Guild 1: planktonic; Guild 2: low-profile; Guild 3: high-profile, Guild 4: motile; for more

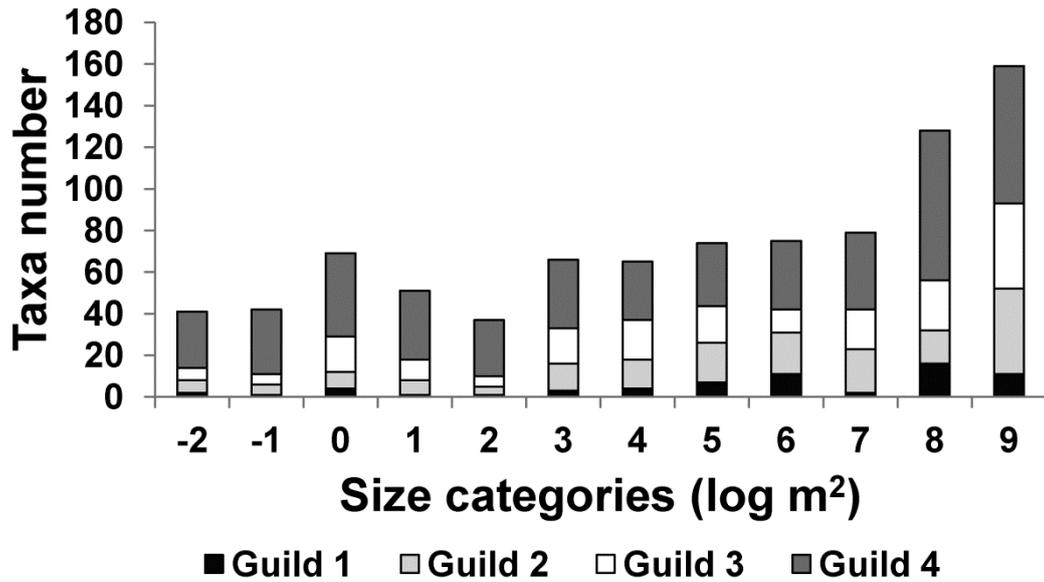
582 information see the text)



583

584 Figure 3.

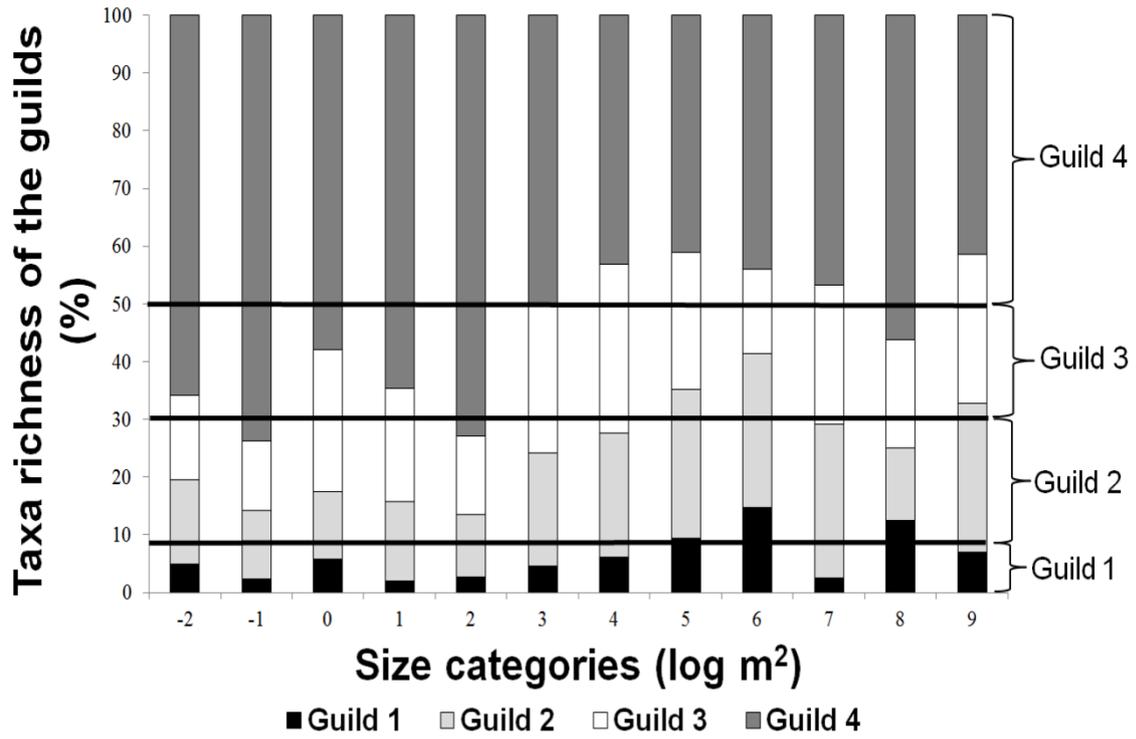
585 Observed number of species in the four ecological diatom guilds in the various size
 586 categories. (meaning of the guilds: Guild 1: planktonic; Guild 2: low-profile; Guild 3: high-
 587 profile, Guild 4: motile)



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