



Realized ecological niche-based occupancy–abundance patterns of benthic diatom traits

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Abstract Nowadays, when aquatic habitats are threatened by human and climatic disturbances leading to reductions in biodiversity and ecosystem functions, the study of the abundance–occupancy relationships of species traits and their underlying mechanisms is of great importance to future conservation management. To study the distribution patterns of benthic diatom traits, lakes were sampled during the summer and early autumn. Niche breadth, niche position (NP), regional occupancy and local abundances (LAs) of benthic diatom traits and their combinations were determined along different environmental gradients. Benthic diatom traits were identified in all possible niche types (14% non-marginal–narrow, 37% non-marginal–broad, 8% marginal–narrow and 41% marginal–broad niche). On the basis of increased niche differentiation, it is possible to achieve an improved and more effective utilization of the eco-morphological concept of diatom traits. The relationships between the occupancy, abundance and niche characteristics suggest that the broader the

niche, the wider the distribution and the greater the LA; the more marginal the NP, the more restricted spatially the distribution and the lower the LA. With regard to the key factors driving the occupancy of benthic diatom traits in lentic ecosystems, the NP hypothesis proves to be the best predictor of its variation.

Keywords Niche breadth · Niche position · Lentic ecosystem · Distribution

Introduction

In recent years, the acceleration of ecosystem degradation, together with a rapid and continuous decline in the Earth's biodiversity, may be observed. These phenomena are caused by anthropogenic disturbances and climate change (Butchart et al., 2010), and by the fragmentation and homogenization of habitats (Balvanera et al., 2006; Cardinale et al., 2012), both of which exercise considerable influence on species distribution. Generally speaking, species distribution depends on an array of different factors, such as local environmental conditions, species dispersal and species interactions (Leibold et al., 2004). The success of a particular species is closely related to and dependent on its traits and tolerance (e.g. phenotypic plasticity by widening the ecological niche; Nicotra et al., 2010);

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these are also recognized as key features in the spread of invasive species (Stachowicz et al., 1999; Gurvich et al., 2005). An understanding of the mechanisms underlying and driving distribution patterns is a key question in a situation, where the maintenance of ecosystem functions and services is the primary and urgent task of the day.

At the species level, a positive relationship between local mean abundance and regional distribution has been identified and recognized as the main macroecological pattern in the case of a variety of organisms (e.g. Gaston et al., 2000; Gaston, 2003; Tales et al., 2004; Soininen & Heino, 2005; Heino & Virtanen, 2006; Frisk et al., 2011; Heino & Grönroos, 2014); a number of ecological hypotheses (including both sampling artefacts and real ecological-based ones) have been devised to account (summarized by Heino 2005). Among them, metapopulation dynamics and niche differentiation [niche breadth (NB) and position hypothesis] have come to be regarded as among the most powerful ecological notions concerning the influence of species distribution (e.g. Soininen & Heino, 2005; Rocha et al., 2018; Teittinen et al., 2018; Vilmi et al., 2019). On the basis of the NB hypothesis (Brown, 1984), species with a wider tolerance range are regarded as generalist, and assumed to be more widespread. According to the niche position (NP) hypothesis (Hanski, 1993; Venier & Fahrig, 1996), species can be found in average (non-marginal position, meaning high habitat availability) or extreme (marginal position, meaning low habitat availability) environmental conditions, and this, in turn, results in different distributions of species: the higher the habitat availability, the wider the distribution. Metapopulation dynamics (Hanski, 1993, 1994) assumes that locally abundant species will have wider distribution due to their ability to colonize empty habitats and consequently, rescue their other populations.

Most of the research in aquatic sciences has focused on the distribution–occupancy relationships of species (e.g. Tales et al., 2004; Heino, 2005; Soininen & Heino, 2005; Heino & Soininen, 2006; Siqueira et al., 2009; Tonkin et al., 2016; Rocha et al., 2018), while trait-based functional studies are relatively rare, having begun only relatively recently (such as Heino & Grönroos, 2014; Heino & de Mendoza, 2016; Heino & Tolonen, 2018; Teittinen et al., 2018; Soininen et al., 2019; Vilmi et al., 2019). Functional approaches are very important, since a species' contribution to

ecosystem functions is closely related to its functional traits (e.g. de Bello et al., 2010; Villnäs et al., 2018). The maintenance of ecosystem stability, functions and consequent services can be achieved by balancing compensatory processes of traits against some level of species loss (Walker, 1992; Walker, 1995). In addition, most of the niche-based researches related to lotic rather than lentic ecosystems generating further lack in this field. In turn, the process forming occupancy–abundance relationship in lentic ecosystem is less complex than in lotic systems which could result in clearer patterns (Dent et al., 2002; Vilmi et al., 2019).

Diatoms are the key organisms in recent research focusing on the occupancy–abundance relationship in aquatic ecosystems (e.g. Soininen & Heino, 2005; Heino & Soininen, 2006; Rocha et al., 2018; Teittinen et al., 2018; Vilmi et al., 2019). Diatoms form a major algal group in both lotic and lentic environments, and are commonly the key organisms of phytobenthos in ecological status assessments (Stevenson & Pan, 1999). Additionally, diatoms have numerous advantages which make them good target organisms: they present a widespread and diverse group; they play a key role in food webs, primary production and the biogeochemical cycle; they are good bioindicators; and they are also relatively easy to examine (e.g. Stevenson & Pan, 1999). Finally, diatoms are affected directly and indirectly by an array of environmental factors, such as pH, conductivity, nutrients (nitrogen and phosphorous), silica, temperature and habitat size (e.g. Stenger-Kovács et al., 2014; Lengyel et al., 2016; Bolgovic et al., 2019).

The primary aim of the present study is to recognize the distribution patterns of a major aquatic group in the hope of overcoming the previously mentioned shortcomings in this field. Therefore, to investigate the drivers of regional occupancy (RO) of functional diatom traits in lentic ecosystems, (i) niche characteristics (NP and NB) were determined along the main environmental gradients, and (ii) the local abundance (LA) of each trait was also specified. On the basis of recent and applied trait categories, some general assumptions were made. These were as follows:

- (i) Higher niche differentiation (in terms of NB, as well as position) will be found in the case of combined traits than in that of the simple trait categories;

- (ii) As in species-based studies, positive relationships may be predicted between RO and local mean abundances of traits;
- (iii) Diatom traits will be clearly distinguishable into generalist/specialist and marginal/non-marginal traits on the basis of their niche.

Material and methods

Altogether, 200 samples were collected from different lentic ecosystems between 2006 and 2017: 99 samples from soda pans, and 101 samples from freshwater lakes in Hungary and Germany. Sampling was restricted to the summer and early autumn period to eliminate the effects of seasonality. The lakes can be characterized by a broad range of their salinity (from freshwater to hyposaline), their trophic state (from oligo- to hypertrophic), their pH (from neutral to highly alkaline) and water body size (from shallow to deep with differing extents, Table 1).

Water temperature ($^{\circ}\text{C}$), pH, conductivity ($\mu\text{S cm}^{-1}$), and dissolved oxygen (mg l^{-1}) were measured in situ using a portable multimeter. In order to study the effect of lake size, the area–depth ratio (SDR) was used, obtained on the basis of OVF (General Directorate of Water Management, 2015; <http://www.ovf.hu/en/>) and Szabó et al. (2017). In the laboratory, the concentrations of dissolved inorganic nitrogen (DIN, as the sum of nitrite, nitrate and ammonium, mg l^{-1}), total phosphorus (TP, $\mu\text{g l}^{-1}$) and soluble reactive silica (SRSi, mg l^{-1}) were determined using spectrophotometric methods, according to APHA (1998).

Benthic diatom communities were collected from the most characteristic substrates (mud in soda pans, stone in Lake Stechlin and reed in other lakes). Samples were preserved in ethanol and prepared using

the hot hydrogen-peroxide method (Comité Européen de Normalisation, CEN, 2003); the diatom valves were then embedded in a mounting resin. At least 400 diatom valves were identified at species level under a light microscope ($1,000\times$ magnification, plan-apochromat lens with DIC, Zeiss Axiovert 1) and the use of up-to-date taxonomic books. Each species was classified by trait, employing diatom ecological guilds (Passy, 2007; Rimet & Bouchez, 2012b). Diatoms were classified further according to their morphological traits (Rimet & Bouchez, 2012a) on the basis of their biovolume (S) and length/width ratio (LW). Besides the basic traits, the various combinations of the traits were also investigated, following the ecomorphological concept found in B-Béres et al. (2016). The traits used in the present study are detailed in Table 2.

RO (% sample number, in where the given trait is presented) and mean LA (% average relative abundances of a given trait counted within a sample) were calculated for each diatom trait. NP (the distance between the average habitat conditions used by a species and the average habitat conditions of the studied region) and NB (index of tolerance to environmental conditions) for each trait and their combinations were determined by outlying mean index (OMI) analyses (Dolédéc et al., 2000). To distinguish the niches (non-marginal/marginal and narrow/broad niches), a corresponding percentage of variability set at 15% was employed, as in Dolédéc et al. (2000). Monte-Carlo test using 1,000 random permutation was implemented for statistical significance comparing the observed species' marginality and the simulated values. Before the analyses, in order to obtain a normal distribution, the transformation of the data was carried out: Hellinger transformation for diatoms, and further transformations (see Table 1) for environmental variables. For the principal component analyses

Table 1 Main limnological parameters of the studied lakes and their applied transformations in the statistical analyses

Parameter	Unit	Min.	Max.	Mean	Transformation
TP	$\mu\text{g l}^{-1}$	3	14,720	1446	$\ln(Y + 1)$
DIN	mg l^{-1}	0.01	199	10	$Y^{1/3}$
SRSi	mg l^{-1}	0.01	57	8	$Y^{1/4}$
Conductivity	$\mu\text{S cm}^{-1}$	91	37,700	3173	$Y^{1/7}$
DO	mg l^{-1}	0.4	24	8	$Y^{1/3}$
pH		7.4	10.4	8.8	–
SDR	km	1	716,667	13,773	$\ln(Y + 1)$

Table 2 Detailed features of the studied benthic diatom traits (code, cat.: trait category to where the traits belong, description: meaning of the applied traits), the results of OMI analyses (NP outlying mean index, NB tolerance index, P significance values of Monte-Carlo test [significant values are in bold italic]), regional occupancy (RO, %), mean local abundance (LA, %), ecological niche type (niche) and dominance (dom., W widespread, C common, R rare) of each trait

Applied traits		NP	NB	P	LA	RO	Niche	Dom.
Code	Cat.	Description						
H	Guilds	0.41	2.12	0.001	9.7	81	Non-marginal–Broad	W
L		0.85	2.95	0.001	29.7	91	Non-marginal–Broad	W
M		0.18	3.05	0.001	58.2	100	Non-marginal–Broad	W
P		0.45	0.92	0.002	10.7	69	Non-marginal–Broad	C
LW1	Morphological traits (length:width ratio)	0.29	2.45	0.001	15.0	87	Non-marginal–Broad	W
LW2		0.27	3.19	0.001	24.7	97	Non-marginal–Broad	W
LW3		0.02	2.78	0.001	41.9	99	Non-marginal–Broad	W
LW4		0.13	3.84	0.001	17.1	98	Non-marginal–Broad	W
LW5		0.10	0.87	0.134	1.8	56	Non-marginal–narrow	C
LW6		0.13	0.51	0.030	7.1	56	Non-marginal–narrow	C
S1	Morphological traits (biotolume)	0.08	3.80	0.002	32.4	98	Non-marginal–Broad	W
S2		0.06	2.91	0.001	28.6	99	Non-marginal–Broad	W
S3		0.01	2.37	0.261	16.7	96	Non-marginal–Broad	W
S4		0.15	2.07	0.001	10.9	89	Non-marginal–Broad	W
S5		0.04	1.52	0.001	15.1	97	Non-marginal–Broad	W
HS1LW1	Eco-morphological traits (combinations of the morphological traits and guilds)	7.04	0.00	0.412	1.0	1	Marginal –narrow	R
HS1LW2		3.25	1.26	0.047	3.1	3	Marginal–narrow	R
HS1LW3		0.25	0.93	0.269	3.3	27	Non-marginal–Broad	C
HS1LW4		1.67	3.86	0.003	3.8	13	Marginal–Broad	R
HS2LW1		4.19	0.97	0.007	1.6	5	Marginal–narrow	R
HS2LW2		0.80	1.18	0.122	1.6	12	Marginal–Broad	R
HS2LW3		0.03	1.42	0.699	5.5	68	Non-marginal–Broad	C
HS2LW4		2.42	3.45	0.001	15.0	62	Marginal–Broad	C
HS2LW5		0.77	0.88	0.203	0.9	8	Non-marginal–Broad	R

Table 2 continued

Applied traits		NP	NB	P	LA	RO	Niche	Dom.
Code	Cat.							
HS2LW6	High, 100–300 μm^3 , 20 < L/W	1.09	0.62	0.535	0.3	3	Marginal–Broad	R
HS3LW2	High, 300–600 μm^3 , 2–4 L/W	1.30	1.02	0.001	1.9	40	Marginal–Broad	C
HS3LW3	High, 300–600 μm^3 , 4–6 L/W	0.40	0.50	0.028	2.2	31	Non-marginal–narrow	C
HS3LW4	High, 300–600 μm^3 , 6–12 L/W	0.50	0.89	0.017	1.0	27	Non-marginal–narrow	C
HS4LW1	High, 600–1,500 μm^3 , < 2 L/W	2.77	1.16	0.049	0.5	4	Marginal–Broad	R
HS4LW2	High, 600–1,500 μm^3 , 2–4 L/W	2.13	2.37	0.001	1.2	29	Marginal–Broad	C
HS4LW3	High, 600–1,500 μm^3 , 4–6 L/W	0.67	1.31	0.001	9.1	57	Non-marginal–Broad	C
HS4LW4	High, 600–1,500 μm^3 , 6–12 L/W	0.83	0.35	0.076	2.5	17	Marginal–narrow	R
HS4LW5	High, 600–1,500 μm^3 , 12–20 L/W	6.04	2.41	0.036	1.3	3	Marginal–Broad	R
HS5LW2	High, 1,500 μm^3 <, 2–4 L/W	0.85	1.49	0.003	4.2	36	Marginal–Broad	C
HS5LW3	High, 1,500 μm^3 <, 4–6 L/W	0.53	0.52	0.008	2.6	31	Non-marginal–narrow	C
HS5LW4	High, 1,500 μm^3 <, 6–12 L/W	0.41	2.98	0.008	1.1	30	Non-marginal–Broad	C
HS5LW5	High, 1,500 μm^3 <, 12–20 L/W	0.19	0.59	0.317	2.1	28	Non-marginal–narrow	C
HS5LW6	High, 1,500 μm^3 <, 20 < L/W	1.09	0.88	0.003	2.2	27	Marginal–Broad	C
LS1LW1	Low, < 100 μm^3 , < 2 L/W	10.96	1.13	0.001	3.6	15	Marginal –narrow	R
LS1LW2	Low, < 100 μm^3 , 2–4 L/W	2.77	3.42	0.001	11.1	49	Marginal–Broad	C
LS1LW3	Low, < 100 μm^3 , 4–6 L/W	3.06	2.54	0.001	14.9	48	Marginal–Broad	C
LS2LW1	Low, 100–300 μm^3 , < 2 L/W	1.65	0.12	0.353	4.6	9	Marginal–narrow	R
LS2LW2	Low, 100–300 μm^3 , 2–4 L/W	0.15	1.26	0.049	2.8	61	Non-marginal–Broad	C
LS2LW3	Low, 100–300 μm^3 , 4–6 L/W	1.15	0.95	0.001	4.1	28	Marginal–Broad	C
LS2LW4	Low, 100–300 μm^3 , 6–12 L/W	1.40	0.38	0.779	1.7	2	Marginal–narrow	R
LS3LW1	Low, 300–600 μm^3 , < 2 L/W	1.19	0.95	0.019	2.5	15	Marginal–Broad	R
LS3LW2	Low, 300–600 μm^3 , 2–4 L/W	1.39	3.82	0.001	2.8	51	Marginal–Broad	C
LS3LW3	Low, 300–600 μm^3 , 4–6 L/W	0.59	0.83	0.004	1.8	31	Non-marginal–narrow	C
LS3LW4	Low, 300–600 μm^3 , 6–12 L/W	3.82	1.71	0.001	1.6	26	Marginal–Broad	C
LS4LW1	Low, 600–1,500 μm^3 , < 2 L/W	8.03	2.94	0.001	1.0	7	Marginal–Broad	R
LS4LW2	Low, 600–1,500 μm^3 , 2–4 L/W	0.44	0.72	0.010	2.0	35	Non-marginal–Broad	C
LS4LW3	Low, 600–1,500 μm^3 , 4–6 L/W	1.31	1.02	0.046	3.3	13	Marginal–Broad	R
LS5LW1	Low, 1,500 μm^3 <, < 2 L/W	2.51	1.53	0.001	6.2	41	Marginal–Broad	C
LS5LW2	Low, 1,500 μm^3 <, 2–4 L/W	0.69	0.88	0.002	2.6	38	Non-marginal–narrow	C
LS5LW3	Low, 1,500 μm^3 <, 4–6 L/W	1.49	1.10	0.040	0.8	9	Marginal–Broad	R

Table 2 continued

Applied traits		NP	NB	P	LA	RO	Niche	Dom.
Code	Cat.							
MS1LW1	Motile, < 100 μm ³ , < 2 L/W	0.84	0.34	0.189	2.6	10	Marginal–narrow	R
MS1LW2	Motile, < 100 μm ³ , 2–4 L/W	0.17	1.08	0.172	3.1	40	Non-marginal–Broad	C
MS1LW3	Motile, < 100 μm ³ , 4–6 L/W	3.23	3.24	0.001	1.8	31	Marginal–Broad	C
MS1LW5	Motile, < 100 μm ³ , 12–20 L/W	1.07	1.35	0.065	0.8	9	Marginal–Broad	R
MS2LW1	Motile, 100–300 μm ³ , < 2 L/W	1.39	0.71	0.010	4.4	9	Marginal–narrow	R
MS2LW2	Motile, 100–300 μm ³ , 2–4 L/W	3.78	3.25	0.001	4.7	42	Marginal–Broad	C
MS2LW3	Motile, 100–300 μm ³ , 4–6 L/W	1.91	1.20	0.001	5.0	38	Marginal–Broad	C
MS2LW4	Motile, 100–300 μm ³ , 6–12 L/W	0.34	0.46	0.018	4.8	46	Non-marginal–narrow	C
MS2LW5	Motile, 100–300 μm ³ , 12–20 L/W	1.43	1.78	0.008	0.8	13	Marginal–Broad	R
MS2LW6	Motile, 100–300 μm ³ , 20 < L/W	2.25	0.21	0.262	0.9	2	Marginal–narrow	R
MS3LW1	Motile, 300–600 μm ³ , < 2 L/W	2.97	0.00	0.826	1.8	1	Marginal–narrow	R
MS3LW2	Motile, 300–600 μm ³ , 2–4 L/W	0.10	0.72	0.243	2.9	57	Non-marginal–narrow	C
MS3LW3	Motile, 300–600 μm ³ , 4–6 L/W	0.31	2.35	0.001	11.9	89	Non-marginal–Broad	W
MS3LW4	Motile, 300–600 μm ³ , 6–12 L/W	1.79	0.88	0.001	3.0	24	Marginal–narrow	R
MS3LW5	Motile, 300–600 μm ³ , 12–20 L/W	0.77	3.06	0.259	0.3	6	Non-marginal–Broad	R
MS4LW1	Motile, 600–1,500 μm ³ , < 2 L/W	0.62	0.66	0.532	0.9	5	Non-marginal–narrow	R
MS4LW2	Motile, 600–1,500 μm ³ , 2–4 L/W	0.17	1.06	0.033	3.0	54	Non-marginal–Broad	C
MS4LW3	Motile, 600–1,500 μm ³ , 4–6 L/W	0.28	3.01	0.001	6.0	83	Non-marginal–Broad	W
MS4LW4	Motile, 600–1,500 μm ³ , 6–12 L/W	2.81	3.47	0.001	1.6	42	Marginal–Broad	C
MS4LW5	Motile, 600–1,500 μm ³ , 12–20 L/W	1.56	2.71	0.020	0.7	7	Marginal–Broad	R
MS4LW6	Motile, 600–1,500 μm ³ , 20 < L/W	0.51	0.51	0.009	4.6	27	Non-marginal–narrow	C
MS5LW1	Motile, 1,500 μm ³ , < 2 L/W	0.77	1.00	0.050	9.5	14	Non-marginal–Broad	R
MS5LW2	Motile, 1,500 μm ³ , 2–4 L/W	0.04	1.20	0.433	5.7	77	Non-marginal–Broad	W
MS5LW3	Motile, 1,500 μm ³ , 4–6 L/W	0.35	2.10	0.002	4.6	61	Non-marginal–Broad	C
MS5LW4	Motile, 1,500 μm ³ , 6–12 L/W	0.22	1.02	0.019	3.7	52	Non-marginal–Broad	C
MS5LW5	Motile, 1,500 μm ³ , 12–20 L/W	1.36	2.16	0.119	0.9	8	Marginal–Broad	R
MS5LW6	Motile, 1,500 μm ³ , 20 < L/W	0.60	0.41	0.027	4.5	22	Non-marginal–narrow	R
PS1LW1	Planktic, < 100 μm ³ , < 2 L/W	0.63	0.37	0.223	1.1	9	Non-marginal–narrow	R
PS1LW4	Planktic, < 100 μm ³ , 6–12 L/W	2.77	0.14	0.518	0.6	1	Marginal–narrow	R
PS2LW1	Planktic, 100–300 μm ³ , < 2 L/W	1.64	1.88	0.008	2.2	13	Marginal–Broad	R
PS2LW4	Planktic, 100–300 μm ³ , 6–12 L/W	1.69	1.52	0.424	1.5	2	Marginal–Broad	R

Table 2 continued

Applied traits		Description	NP	NB	P	LA	RO	Niche	Dom.
Code	Cat.								
PS2LW6		Planktic, 100–300 μm ³ , 20 < L/W	0.31	0.59	0.190	3.9	25	Non-marginal–narrow	R
PS3LW1		Planktic, 300–600 μm ³ , < 2 L/W	3.12	1.86	0.001	1.6	29	Marginal–Broad	C
PS3LW4		Planktic, 300–600 μm ³ , 6–12 L/W	1.00	0.81	0.216	0.5	5	Marginal–narrow	R
PS3LW5		Planktic, 300–600 μm ³ , 12–20 L/W	4.88	1.40	0.095	0.4	2	Marginal–Broad	R
PS3LW6		Planktic, 300–600 μm ³ , 20 < L/W	1.88	0.39	0.098	2.3	6	Marginal–narrow	R
PS4LW1		Planktic, 600–1,500 μm ³ , < 2 L/W	0.14	1.10	0.043	8.5	70	Non-marginal–Broad	C
PS4LW6		Planktic, 600–1,500 μm ³ , 20 < L/W	6.51	1.61	0.067	0.7	2	Marginal –narrow	R
PS5LW1		Planktic, 1,500 μm ³ , < 2 L/W	0.53	0.79	0.112	1.6	19	Non-marginal–Broad	R

(PCA), the environmental parameters were standardized. Linear regression models were run to examine the relation between the niche parameters (NB and NP), the distributions and the mean LA of traits. Prior to the analyses, log transformation ($\log(x + 1)$) was used to improve the degree of normality. Variation partitioning was employed to reveal the importance of individual and shared effects of the three explanatory variables (such as NP, NB and mean LA) on the regional distribution of the different traits. All statistical analyses were performed in the 3.4.3 version of R statistical software (Team, 2010) using the vegan (Oksanen et al., 2012), ade4 (Bougeard & Dray, 2018), adegraphics (Dray & Siberchicot, 2018) and subniche packages (Karasiewicz et al., 2017).

Results

In the total of 200 samples, altogether 463 diatom species were identified belonging to 4 ecological guilds, 5 size traits, 6 LW traits and their 79 combined groups. On the basis of the OMI analysis, axis 1 and axis 2 were the most important axes, together explaining 68.84% of the variance in the abundance of the traits. The major variables were conductivity, TP, DIN for axis 1, while these for axis 2 were pH and SRSi (Fig. 1).

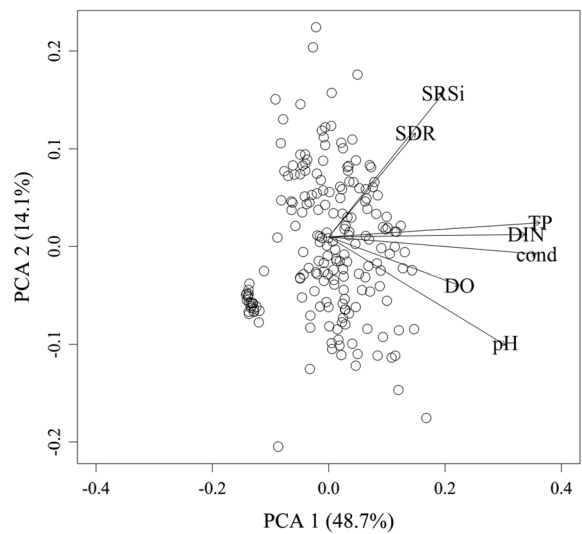


Fig. 1 Principal component analysis (PCA) of the measured environmental parameters (*cond* conductivity, *DIN* dissolved inorganic nitrogen, *DO* dissolved oxygen, *SDR* surface:depth ratio, *SRSi* soluble reactive silica, *TP* total phosphorus)

The NP and NB of each trait, as well as their RO and mean LA are summarized in Table 2. The inertia of the traits varied from 2.9 to 12.6. Among the 94 diatom traits only 63 (= 67%) traits proved to be having significant OMI values, to which the further analysis of niche parameters was restricted. Almost the half of the diatom traits (51%) can be characterized as occupying a non-marginal position (e.g. H, LW1, S1, MS3LW3), while 49% were found to be in a marginal position (e.g. LS3LW1, PS2LW1). On the basis of the NB values, 22% of the traits occupied a narrow niche (e.g. HS3LW4, MS4LW6, LS1LW1), and 78% a broad one (e.g. M, LW1, MS4LW5). Considering the combinations of NP and NB, it was found that 14% of the traits had a non-marginal position and narrow niche, 37% a non-marginal position and broad niche (Fig. 2). A further 5 diatom traits (8%) occupied niches which were both marginal and narrow, and 26 traits (41%) niches which were marginal and broad (Fig. 2).

The RO of the traits ranged from 1% (e.g. HS1LW1) to 100% (M), 40 traits were rare (MS3LW4, PS3LW4), 39 common (P, LW5, LW6) and 15 widespread (e.g. H, L, M, LW1–4, S1–5) (Table 2). The mean LA varied between 0.3% (such as HS2LW6, MS3LW5) and 58.2% (M). With regard to

the relationship between these parameters (LA, RO), the RO proved to be positively and significantly related to mean LA (Fig. 3). NP was strongly and negatively related to occupancy ($R^2 = 0.42$ and $P < 0.0001$), and to the LA ($R^2 = 0.21$ and $P < 0.0001$) of

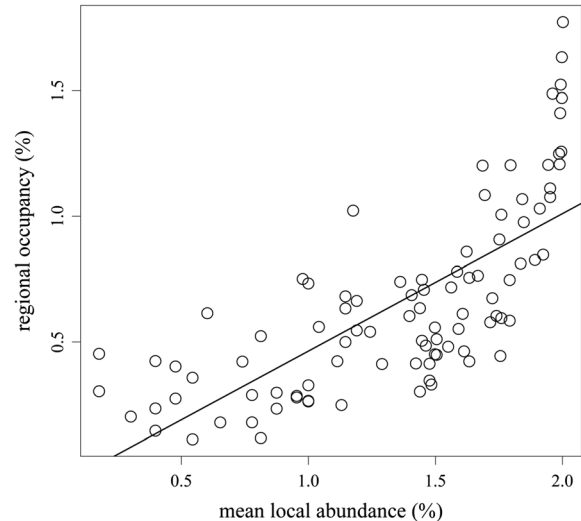


Fig. 3 Relationship between the proportion of regional occupancy and mean local abundance of benthic diatom traits ($R^2 = 0.53$ and $P < 0.0001$) (axes are on logarithmic scales)

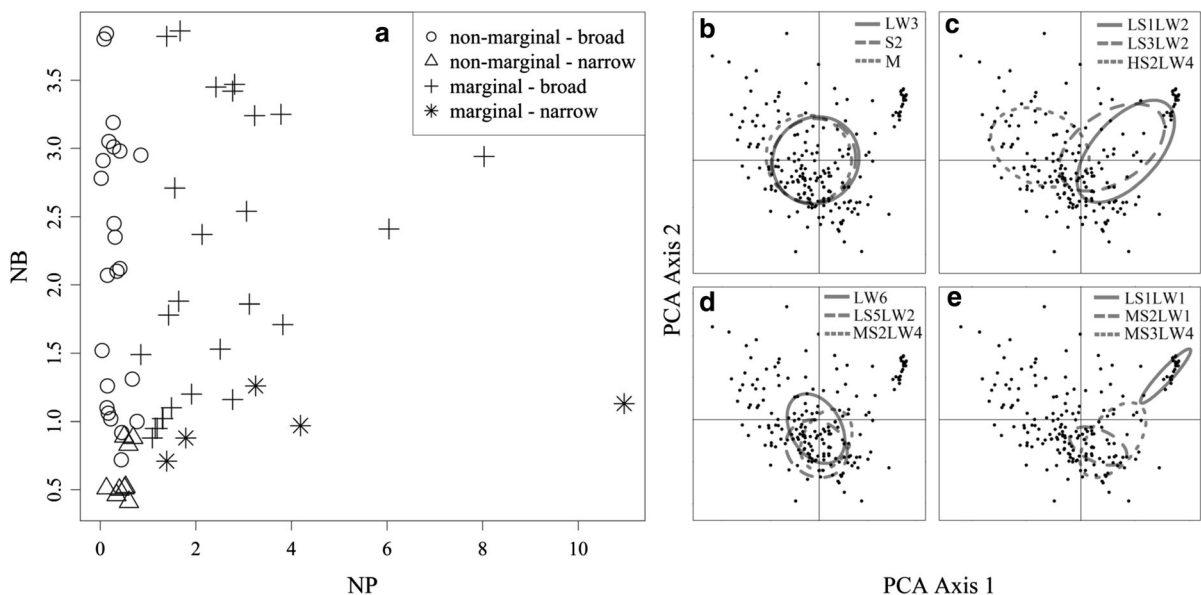


Fig. 2 Distribution of benthic diatom traits on the basis of their ecological niche types (a) and the ecological niches of the three most widespread diatom traits (for trait codes see Table 2) found

in each niche type (b non-marginal/broad, c marginal/broad, d non-marginal/narrow, e marginal/narrow)

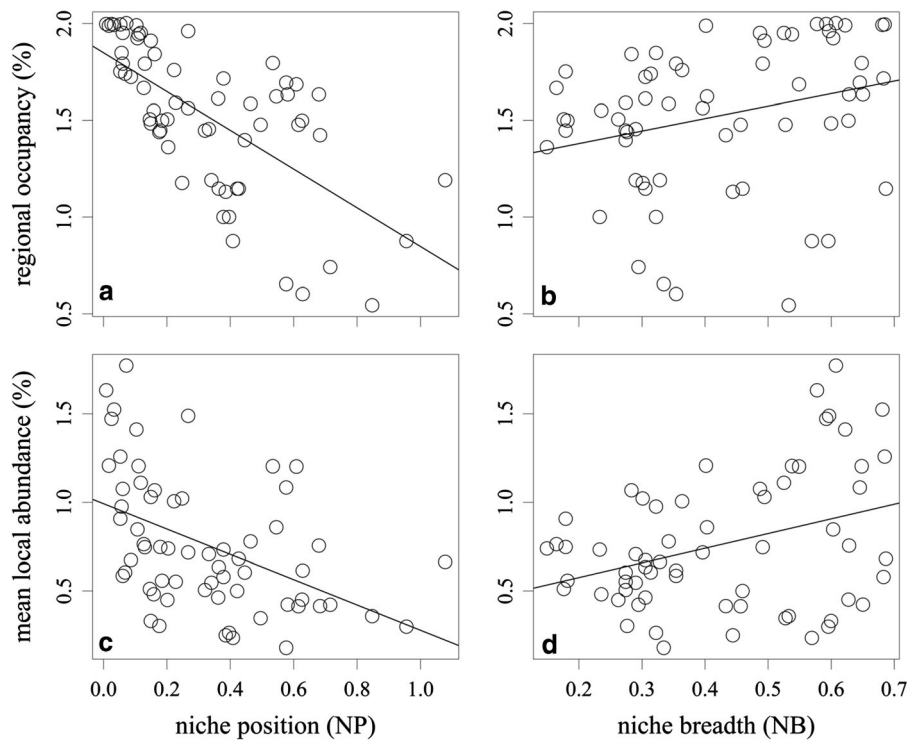


Fig. 4 Relationships between niche parameters and regional occupancy (a, b) and mean local abundance (c, d) of benthic diatom traits (axes are on logarithmic scales)

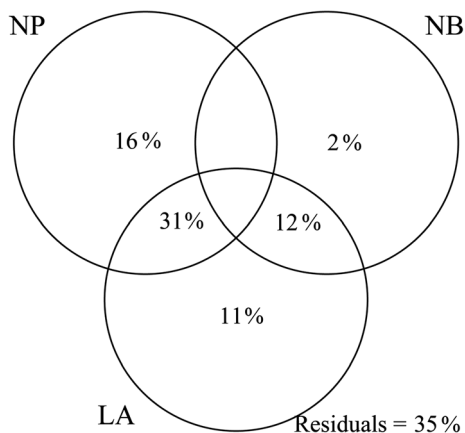


Fig. 5 Partitioning of variation in the occupancy of benthic diatom traits between the three explanatory variables (*NP* niche position, *NB* niche breadth, *LA* mean local abundance). Individual and shared fractions are shown as percentages of total variation on the basis of adjusted R^2 values

the traits (Fig. 4). *NB* showed a significant but weak-positive relationship to the occupancy ($R^2 = 0.06$ and $P = 0.03$) and *LA* ($R^2 = 0.11$ and $P = 0.005$) of the traits (Fig. 4).

As a result of the variation partitioning, *NP* was the most important variable accounting for variation in occupancy (individual effect: 16%), followed by mean *LA* (individual effect: 11%), whilst *NB* only had minor effects on it (individual effect: 2%) (Fig. 5). The greater part of the variation was shared between these explanatory variables, particularly between *NP* and mean *LA* (their shared effect: 31%), as well as between *NB* and mean *LA* (their shared effect: 12%). Nevertheless, 35% of variation in occupancy remained unexplained by the variables studied here.

Discussion

Similarly to other organisms, diatoms living in every type of aquatic environment are facing climatic changes, variations in environmental conditions, increases in environmental stress and vanishing habitat (e.g. Dokulil et al., 2010; Mitsch, 2013; Lengyel et al., 2020). Since the success of the various species is closely related to their traits, the investigation of their abundance–occupancy relationship and the underlying

mechanism are very important in the making of future projections and the formulation of suitable conservation plans to maintain biodiversity and ecosystem functions. This study provides fresh information about the distribution patterns of the diatom traits in lake ecosystems on the basis of the most typical determinant environmental parameters.

The few existing examples of research focusing on trait-based approaches have concluded that biological traits—mainly size and life-forms—can affect occupancy and/or abundance (Verberk et al., 2010; Passy, 2012; Heino & Grönroos, 2014; Rocha et al., 2018): colonial and attached species tended to be more abundant and widespread than non-colonial and non-attached species (Heino & Soininen, 2006; Passy, 2016). Additionally, species of similar size and displaying similar life forms tend to display similar occupancies and abundance (Rocha et al., 2018; Vilmi et al., 2019). As far as organisms with a passive dispersal ability (such as diatoms) are concerned, cell size is generally negatively related to distribution due to the ability of small species to maintain larger populations, to produce more propagules, to achieve more effective dispersion, to be better competitors for all nutrients and to have better resource utilization (Kristiansen, 1996; Soininen & Heino, 2005; Heino & Soininen, 2006; Edwards et al., 2011; Passy, 2012). The results of the present study show up a disparate niche differentiation between the different trait categories. The simple, non-combined trait categories (such as guilds, biovolume and length/width ratio) have a great degree of overlap in their niches (inertia varied between 5.1 and 7.8), implying their decreased niche differentiation. Although the categorization of the main traits was based on clear and significant features, such as differences in nutrient uptake ability or resistance to physical disturbances due to the growth form of guilds (e.g. Passy, 2007), these separations do not appear to be sufficient to be reflected in their degree of niche differentiation. Almost all categories can be characterized as occupying a niche which is both central and broad, with high abundance leading to negligible effects on the different distributions (all of them are widespread or common) found in present study. Similar results have been arrived at by other researchers: the distribution of subarctic diatom species differed only slightly between life-forms (like motile, adnate, pedunculate and colonial forms), and not at all between guilds

(Teittinen et al., 2018); furthermore, the biological traits of stream insects also seemed to be unimportant in the degree of predictability of species distribution (Heino & de Mendoza, 2016; Heino & Tolonen, 2018). Instead of the main trait categories, the better and more effective utilization of the eco-morphological concept of diatom traits (B-Béres et al., 2016) is presented in a way similar to that found in some recent research (e.g. B-Béres et al., 2016; Stenger-Kovács et al., 2018), since smaller amount of overlap in their niches was found (inertia varied from 2.9 to 12.6), implying an increased niche differentiation between them.

With regard to the driving factors of the distribution patterns of functional traits, as has been the case in other species-based studies focusing on a variety of organisms (e.g. Soininen & Heino, 2005; Rocha et al., 2018; Teittinen et al., 2018; Vilmi et al., 2019) the results presented here show that (i) the relationship between occupancy and abundance is significantly positive, and (ii) the regional occurrence of the functional traits of diatoms is related to niche characteristics (such as NP and NB) and LA s, respectively. A positive relation with NB suggests that generalist functional traits (that is, those having a broad tolerance range) had wider distribution and were locally more abundant than specialist traits (those having a narrow tolerance range). A negative relationship with NP implies that traits characterized by a marginal NP tend to be less widely distributed and less locally abundant than traits in non-marginal positions. As has been previously reported, the findings of the present study generally agree on the importance of niche characteristics in distribution and LA (e.g. Heino, 2005; Heino & Soininen, 2006; Heino & Grönroos, 2014; Rocha et al., 2018; Teittinen et al., 2018). Only a few researchers have concluded that niche characteristics are not suitable predictors of LA, due to their more stochastic nature and proneness to error than is the case with occupancy (e.g. Heino & Grönroos, 2014; Tonkin et al., 2016; Rocha et al., 2018). Also as in the present study, it has been found that niche-based mechanisms can dominate and be significant in a positive occupancy–abundance relationship in cases where multiple-drainage environments with steep environmental gradients (Passy, 2012) are examined on the regional scale (Brändle & Brandl, 2001). Nevertheless, in the case of diatom traits, besides niche characteristics, LA is also a key factor in driving

their occupancy in lentic ecosystems. The possibility of time-dependent dispersal in relatively isolated habitats such as lakes situated in different drainage basins, together with the passive propagation of diatoms leads to an assumption of the negligible effects of metapopulation dynamics on the basis of the conclusions of Heino & Grönroos (2014). In contrast to this, the results arrived at here using the trait-based approach reinforce the conclusions of earlier studies, including those conducted in the same region and focusing on benthic diatom species, in which meta-community dynamics were recognized in the form of a mass-effect concept (Szabó et al., 2019) and species-sorting (Szabó et al., 2018).

On the basis of the individual contributions of the ecological theories studied here, the NP hypothesis is the best predictor of variation in occupancy of diatom traits, followed by metapopulation dynamics and finally the NB hypothesis. The occupancy patterns observed here—that the NP hypothesis overrode the NB—are in accordance with general ecological findings (e.g. Tales et al., 2004; Heino, 2005; Heino & Soininen, 2006; Rocha et al., 2018) and are likely to be dependent on spatial extents. Sites belonging to different catchments allow the presence of more non-marginal niches, and therefore lead to the justification of the NP hypothesis, while within one catchment NB is usually more important than NP, due to the possibility of the real separation of generalist and specialist characteristics (Heino, 2005; Siqueira et al., 2009; Heino & Grönroos, 2014). Therefore, the greater predictive power of NB over NP has rarely been encountered in studies focusing on distribution patterns, such as in the case of diatom species in subarctic ponds (Teittinen et al., 2018).

The results of the present study carry important ecological significance from the point of view of conservation. On the basis of recent trait-based research, some diatom traits can indeed be used as indicators of environmental changes: motile, small sized diatom traits with lower LW categories for higher conductivity (Stenger-Kovács et al., 2018), and low-profile diatom traits with small cell size and lower LW categories for a healthy ecological status in streams (Stenger-Kovács et al., 2020). These trait combinations are usually characterized by a marginal NP, and their distribution is limited due to the key driving role of NP in the occupancy patterns of diatom traits. A marginal position is often associated with

rarity, and therefore, these traits are more vulnerable to human- or climate-induced environmental changes (as well as being potential victims of extension) than widespread or non-marginal traits. The preservation of these diatom traits is very important for the future, and may be achieved by, for instance, the extension of protected status to a wide range of habitat conditions, since aside from their importance in ecological status assessments, less common traits may have significant effects on invasion events, or on the maintenance of ecosystem function and stability, as has already been concluded to be the case in terrestrial and marine ecosystems (Lyons & Schwartz, 2001; Ellingsen et al., 2007).

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