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3 **Niche position drives interspecific variation in occupancy and abundance in a highly-**
4 **connected lake system**

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18 identifications. AV and JH analyzed the data. AV, KT, SK and JH wrote the manuscript.

19 **Abstract**

20 We examined how niche position, niche breadth, biological traits and taxonomic relatedness
21 affect interspecific variation in occupancy and abundance of two commonly-used indicator
22 groups, i.e. diatoms and macroinvertebrates. We studied 327 diatom and 117 macroinvertebrate
23 species that occupied the littoral zones of a large (305 km²) highly-connected freshwater
24 system. We collated information on the biological traits and taxonomic relatedness of each
25 species. Using principal coordinates analysis, we formed biological trait and taxonomic vectors
26 describing distances between species and used the resulting vectors as predictor variables. As
27 environmental data, we had site-specific physico-chemical variables, which were used in
28 outlying mean index analyses to determine the niche position and niche breadth of a species.
29 We used linear models to study if and how these two niche parameters and biological traits as
30 well as taxonomic relatedness affected occupancy and abundance. We observed positive
31 occupancy-abundance relationships for both diatoms and macroinvertebrates. We further found
32 that, for both groups, occupancy was better explained by the predictor variables compared with
33 abundance. We also observed that niche parameters, especially niche position, were the main
34 determinants of variation in occupancy and abundance for both diatoms and
35 macroinvertebrates. Local abundances of diatom and macroinvertebrate species were also, to a
36 small degree, affected by biological traits or taxonomic relatedness. We further saw that the
37 relationship between niche position and occupancy was negative, indicating that the more
38 marginal the niche position, the rarer a species is. Our findings provide support for the use of
39 diatoms and macroinvertebrates as ecological indicators as their occupancies and abundances
40 were affected by niche parameters, which is not necessarily always clear in challenging study
41 systems with high connectivity (i.e. high movement of material and species) among sites. These
42 findings also suggest that indices using information on species' occupancy, abundance and
43 niche requirements are useful in environmental assessment.

44 **Keywords**

45 Diatoms, macroinvertebrates, niche parameters, biological traits, taxonomic relationships

46

47 **1. Introduction**

48 Species occupancy, abundance and their relationships are amongst the most widely-studied
49 topics in macroecology and biogeography (Brown 1984; Gaston et al. 2000), and researchers
50 have described the occupancy-abundance patterns in a variety of ecosystems across the globe
51 (Venier and Fahrig 1996; Soininen and Heino 2005; Foggo et al. 2007; Roney et al. 2015;
52 Tonkin et al. 2016). The message has been relatively consistent: occupancy and abundance
53 tend to be positively and often strongly associated with each other. Species with low local
54 abundances tend to show limited distributions, whereas locally abundant species usually are
55 widespread in a region (Gaston and Blackburn 2000; Gaston et al. 2000). These ideas are
56 important for meaningful biodiversity conservation (Gaston et al. 2000), especially in an era
57 when human impacts are greater than before (Lewis and Maslin 2015; Waters et al. 2016). As
58 freshwaters are one of the most threatened ecosystems in the world (Heino et al. 2009;
59 Vörösmarty et al. 2010; Vilmi et al. 2017), they also deserve special attention in the context of
60 the interspecific occupancy-abundance relationship (Gaston et al. 2000; Heino and Tolonen
61 2018).

62 An increasing number of attempts have been made to detect various factors that account
63 for variation in species occupancy and abundance. In recent years, the niche breadth (Brown
64 1984) and niche position (Hanski et al. 1993; Venier and Fahrig 1996) hypotheses have been
65 employed to investigate how species' niche characteristics (i.e. their relationships to the
66 environment) account for their regional occupancy and local abundance (Tales et al. 2004;
67 Faulks et al. 2015; Tonkin et al. 2016). Ultimately, species optima are located at different parts
68 of a continuum of environmental conditions (Fig. 1). Some species have the same niche

69 positions, while niche positions of other species are located at different parts of the continuum.
70 Some niches may be positioned at the very end of the environmental range, while other niches
71 may be positioned in average environmental conditions. Although species may have similar
72 niche positions, their niche breadths can strongly differ from each other at the same time.
73 Species with large niche breadths can tolerate a wide variety of environmental conditions,
74 while species with small niche breadths are very specialized to certain environmental
75 conditions (Fig. 1, Brown 1984; Venier and Fahrig 1996; Heino and de Mendoza 2016).

76 Previous research has provided strong evidence that the two niche parameters, niche
77 position and niche breadth, strongly affect occupancy and abundance of different types of
78 organisms (Passy 2012; Heino and Tolonen 2018). For instance, when studying stream
79 macroinvertebrates in a tropical region, Tonkin et al. (2016) found that the two niche
80 parameters explained well variation in occupancy, but it was not correlated with mean local
81 abundance. A study on fish species across boreal lakes suggested that intraspecific niche
82 variation and a positive abundance-occupancy relationship are connected to each other (Faulks
83 et al. 2015). Tales et al. (2004) found support for the niche position hypothesis as the largest
84 contributor to regional occupancy and local abundance in temperate river fishes. Recent studies
85 on subarctic stream diatoms and insects (Rocha et al. 2018) as well as boreal lake
86 macroinvertebrates (Heino and Tolonen 2018) have also shown that especially niche position
87 has strong effects on regional occupancy and local abundance.

88 Species characteristics other than niche parameters may also affect occupancy,
89 abundance and their relationships (Tales et al. 2004; Heino and de Mendoza 2016; Heino and
90 Tolonen 2018; Rocha et al. 2018). Body size measures and resource use features are typical
91 examples of species characteristics, i.e. biological traits (e.g. Passy 2012). The importance of
92 biological traits in affecting occupancy, abundance and their relationships has been reported,
93 for instance, for riverine fishes (Tales et al. 2004), for aquatic macroinvertebrates across lentic

94 waterbodies (Verberk et al. 2010) and for diatoms across streams (Rocha et al. 2018). In
95 addition to biological traits of species, also taxonomic relatedness as a proxy for evolutionary
96 aspects has been considered in the same context. Heino and Tolonen (2018) did not find strong
97 influences of taxonomic relatedness nor traits similarity on occupancy and abundance of
98 macroinvertebrates across a set of lakes, while the effects of niche parameters, particularly that
99 of niche position, were clear.

100 Previous research centering on the topic of occupancy and abundance and the factors
101 determining them have covered different types of freshwater ecosystems, ranging from across-
102 streams (Rocha et al. 2018) to across-lakes (Heino and Tolonen 2018) and to across-
103 waterbodies (Verberk et al. 2010) studies. However, there is a knowledge gap for information
104 from systems with high connectivity, such as large lake systems. We previously showed that
105 diatom and macroinvertebrate communities exhibited pure spatial patterns (e.g. dispersal-
106 related processes) and that local environmental conditions only comparatively little affected
107 community structures in such a highly-connected system (Vilmi et al. 2016; Tolonen et al.
108 2017). These findings were not in line with main assumptions of current bioassessment
109 methods that assume a high importance of local environment on species compositions (Heino
110 2013). The high connectivity of a system is thus a characteristic which can enhance the effects
111 of dispersal and other spatial processes (Foggo et al. 2007). Thus, in that sense, it is worth
112 studying how interspecific occupancy and abundance, the building blocks of ecological
113 indicators, are formed in these sorts of open, large freshwater systems.

114 Here, we investigated if and how niche parameters, biological traits and taxonomic
115 relatedness affect occupancy and abundance of freshwater diatoms and macroinvertebrates in
116 a large lake system which contains no apparent barriers for dispersal. For each species, we
117 calculated niche position and niche breadth (based on an extensive dataset of local
118 environmental variables) and determined biological traits and taxonomic relatedness. Using

119 species as data points, we asked the following questions: (1) What are the relationships between
120 occupancy and abundance of freshwater diatom and macroinvertebrate species within a large
121 lake system? (2) Which factors (niche parameters, traits, and taxonomy) best predict
122 occupancy, abundance and their relationship of diatom and macroinvertebrate species in such
123 a study system? (3) Are the findings similar for the two distinct groups of organisms? (4) Are
124 the findings similar to studies examining patterns across waterbodies?

125

126 **2. Material and Methods**

127 *2.1. Field sampling and laboratory analyses*

128 We used data on diatom and macroinvertebrate taxa to explore our research questions. The
129 biological data were collected in early autumn 2013 from a large (305 km²) lake system of
130 Lake Kitkajärvi. The originally oligotrophic lake system is located in north-eastern Finland.
131 Due to land use and inflow of purified municipal waste water, some parts of the lake system
132 have shown signs of eutrophication (e.g. Vilmi et al. 2015). We collected the diatom and
133 macroinvertebrate samples from 81 similar, stony littoral sites around the lake system (see map
134 of study area in Fig. A.1). In the laboratory, for diatoms, we identified approximately 500
135 valves from each site, and for macroinvertebrates, we identified all individuals that were
136 captured in a site-specific kick-net sampling. We identified the diatoms and macroinvertebrates
137 to the lowest taxonomic level possible, which was in most cases species level, although some
138 valves or individuals were assigned to genus level. Thus, from now on, we refer to the studied
139 taxa here as ‘species’.

140 We gathered a broad set of site-specific local environmental variables. In the field, we
141 visually assessed the particle sizes of the benthic substratum and measured the slope of bottom.
142 We also collected water samples, which were analyzed in the laboratory. We used fetch,
143 calculated with the Wind Fetch Model (Rohweder et al. 2008), as a proxy for wave disturbance

144 at each site. Further details on the sampling and laboratory methods are thoroughly presented
145 in our earlier publications on the effects of local environmental variables on diatom and
146 macroinvertebrate community structures (Vilmi et al. 2016; Tolonen et al. 2017).

147 In this study, we used the following variables as local environmental variables: electrical
148 conductivity, saturation of oxygen, suspended solids, slope, fetch, mean particle size, and
149 particle size diversity, as well as concentrations of aluminium, boron, manganese, NH₄-N,
150 NO₂+NO₃-N, oxygen, PO₄-P, silicon, sodium, soluble total nitrogen, soluble total phosphorus,
151 and zinc. These variables were not highly correlated with each other and showed considerable
152 among-site variation within the data.

153

154 *2.2. Niche position and niche breadth*

155 We first determined niche position (OMI values) and niche breadth (Tolerance values; Tales
156 et al. 2004) of each species using the outlying mean index (OMI) analysis (Dolédec et al. 2000).
157 The analysis basically measures the marginality of species habitat distributions by the distances
158 between mean environmental conditions used by a species and average environmental
159 conditions that are available among the study sites. The ecological interpretation of the OMI
160 and Tolerance values, which the analysis produces, is as follows: species with high OMI values
161 have marginal niches and species with low OMI values have non-marginal niches. Species with
162 high Tolerance values occur in a variety of environmental conditions thus having large niche
163 breadths. Species with low Tolerance values are present only in certain environmental
164 conditions and they have smaller niches.

165 For the OMI analysis, a site-by-species abundance data matrix is needed, as well as an
166 environmental variables data matrix. We made logarithmic transformations for the
167 environmental variables and standardized them. Before proceeding to the OMI analyses, we
168 excluded species that were present only at one site. After doing so, we had a set of 327 diatom

169 and 117 macroinvertebrate species to investigate. We log-transformed ($\log x + 1$) the species
170 abundance matrices. We used the R package *ade4* (Dray et al. 2018) for conducting the OMI
171 analyses.

172

173 *2.3. Biological traits*

174 We collated information on biological traits for all 327 diatom and 117 macroinvertebrate
175 species. For diatoms, we followed Rimet and Bouchez's (2012) work and gathered information
176 on sizes, ecological guilds and colonial formation of species. The sizes are reported as
177 biovolume classes: 0-99 μm^3 (class S1), 100-299 μm^3 (S2), 300-599 μm^3 (S3), 600-1499 μm^3
178 (S4), and $> 1500 \mu\text{m}^3$ (S5). Diatom species were assigned to four guilds: low profile, high
179 profile, motile and planktonic guilds. The different ecological guilds differ from each other by,
180 for instance, resource use and motility (Passy 2007). As a third biological trait, we
181 distinguished colonial and single cell species. This aspect is important in terms of, for example,
182 resource use (e.g. light or nutrients) or potential grazing pressure. Although the biological trait
183 information was mainly collected from Rimet and Bouchez (2012), not all of our species were
184 in their list. We hence used OMNIDIA software (Lecointe et al. 1993) and its databases to find
185 out the missing information. In some cases, we made trait assignments based on characteristics
186 of similar species belonging to the same genus.

187 For macroinvertebrates, we also considered a measure of size as a biological trait. Here,
188 the size is actually the dry mass of each species, and it was divided to five classes: 0-0.99 mg
189 (class DM1), 1-3.49 mg (DM2), 3.5-9.99 mg (DM3), 10-34.99 mg (DM4), and > 35 mg (DM5)
190 to facilitate comparisons with the diatom data. Further, we assigned each species to functional
191 feeding groups (FFG), which were shredders, scrapers, predators, piercers, collector-gatherers
192 and filterers. The third biological trait for macroinvertebrates was their substrate-association
193 type. In our data, there were crawlers, swimmers, burrowers, sessiles and semisessiles. The

194 biological trait classifications used here were earlier given in a previous study by Tolonen et
195 al. (2017) using the same macroinvertebrate data. The three trait groups we used are directly
196 related to species' vulnerability to predation and resource acquisition and habitat use (Merritt
197 and Cummins 1996; Tolonen et al. 2003; Schmera et al. 2015).

198 We calculated trait distances between species using function `gowdis` in the R package
199 `FD` (Laliberté et al. 2014). Using the resulting trait distances, we performed principal
200 coordinates analysis (PCoA) with function `pco` from the R package `labdsv` (Roberts 2016) to
201 form trait vectors. Using trait vectors was appropriate, because species are not a manifestation
202 of only one trait, but, instead, a summary of several traits (e.g. Verberk et al. 2013).

203

204 *2.4. Phylogenetic relatedness*

205 Without true phylogenies at hand, we used taxonomic information as proxies for phylogenetic
206 information. For each of the diatom and macroinvertebrate species, we determined multiple
207 taxonomic levels above species. In the diatom dataset, we had genus, family, order, subphylum
208 and phylum levels. These were collected from Rimet and Bouchez (2012), but updated when
209 necessary, using new literature (e.g. Lange-Bertalot et al. 2017) and AlgaeBase
210 (www.algaebase.org). For macroinvertebrates, we had genus, family, suborder, order, class,
211 phylum, superphylum and kingdom levels. This information was collected from Fauna
212 Europaea (www.fauna-eu.org).

213 To account for taxonomic relatedness, we calculated taxonomic distances between
214 species using the function `taxa2dist` from the R package `vegan` (Oksanen et al. 2018). We then
215 formed taxonomic vectors using principal coordinates analysis (PCoA) using the function `pco`
216 from the R package `labdsv` (Roberts 2016).

217

218 *2.5. Statistical methods*

219 First, we explored the relationship between occupancy and abundance of diatom and
220 macroinvertebrate species using linear regression models. In practice, we used logit-
221 transformed proportion of sites occupied as ‘occupancy’. As ‘abundance’, we used log-
222 transformed mean abundance at occupied sites. We performed the linear models and drew the
223 plots with the R packages stats (R Core Team 2018) and ggplot2 (Wickham 2016).

224 We then used linear regression models to study the explanatory power of the two niche
225 parameters (i.e. niche position and niche breadth), biological trait vectors and taxonomic
226 vectors on occupancy, abundance, and their relationship. The relationship of these two original
227 response variables was investigated using variation in residuals of the occupancy-abundance
228 relationship as a third response variable in our linear models. Here, the residual variation
229 actually describes occupancy when the effect of abundance has been removed. Of the
230 explanatory trait and taxonomic vectors, we used the first six vectors in all models. This was
231 because the first six vectors were clearly stronger than the following ones. The directions how
232 to interpret vectors are presented in Appendix B. We again used the R packages stats (R Core
233 Team 2018) and ggplot2 (Wickham 2016) to perform the linear regression models and to draw
234 associated plots.

235 When using linear regression models as the primary statistical method, commonality
236 analysis (Ray-Mukherjee et al. 2014) provides additional information on the effects of the
237 explanatory variables on the response variables. We performed commonality analyses with the
238 R package yhat (Nimon et al. 2013). Doing so, we were able to see the individual, shared and
239 total contributions of each explanatory variable on variation in our response variables.

240

241 **3. Results**

242 We analyzed data on 327 diatom and 117 macroinvertebrate species and found that there were
243 large differences in their occupancies and abundances. The proportion of sites occupied varied

244 from 2.5% to 100% for diatom species, and from 2.5% to 89% for macroinvertebrate species.
245 The mean abundances of species at the sites they occupied varied from one to 133 for diatoms,
246 and from one to 47 for macroinvertebrates. Appendix C presents the list of diatom and
247 macroinvertebrate species studied in order of occupancy.

248

249 *3.1. The relationship between occupancy and abundance*

250 For both groups of organisms, we found rather strong, positive occupancy-abundance
251 relationships. The linear regression models showed that abundance explained over 50% of
252 variation in diatom species occupancy, and almost 40% of variation in macroinvertebrate
253 species occupancy (Table 1). Scatter plots further showed that macroinvertebrate species
254 indeed had more “outliers” than diatom species, when considering a pure linear relationship,
255 which made the explanatory power of the macroinvertebrate model lower compared to the
256 diatom model (Fig. 2).

257

258 *3.2. Factors explaining variation in occupancy*

259 The linear regression models explained approximately 60% of variation in the occupancy of
260 diatom species and 77% of variation in the occupancy of macroinvertebrate species (Table 2).
261 Niche position was, out of our explanatory factors, the strongest predictor of occupancy for
262 both diatoms and macroinvertebrates. For both groups of organisms, niche position was
263 negatively associated with occupancy. The linear regression models indicated that niche
264 breadth was also related to the occupancy of diatom and macroinvertebrate species. For both
265 organism groups, the relationship between niche breadth and occupancy was positive. For
266 diatoms, trait vector 5 was also statistically significantly associated with occupancy.

267 The results of commonality analyses also supported the chief role of niche position on
268 occupancy of diatom and macroinvertebrate species (unique contributions 0.531 and 0.552,

269 respectively; Table 2). In addition, niche breadth had some unique effects on occupancy,
270 having a larger role for the occupancy of macroinvertebrate species (0.152) than for diatom
271 species (0.080).

272

273 *3.3. Factors explaining variation in mean abundance*

274 The linear models explained 32% of variation in mean abundance of diatom species and 34%
275 of variation in mean abundance of macroinvertebrate species (Table 3). Both niche parameters,
276 four trait vectors and two taxonomic vectors were statistically significantly associated with the
277 mean abundances of diatom species. Regarding macroinvertebrates, both niche position and
278 breadth, as well as trait vector 3 and taxonomic vector 2, were associated with mean
279 abundances. Niche position was negatively and niche breadth positively associated with mean
280 abundances in both groups of organisms (Table 3).

281 The commonality analysis indicated that niche position had a clear and comparatively
282 strong effect on mean species abundance of diatoms (unique effect 0.146; Table 3). For
283 diatoms, the other associated explanatory factors had smaller unique roles on mean abundance
284 (unique effects ranging from 0.009 for taxonomic vector 2 to 0.055 for trait vector 5). The
285 commonality analysis results further showed for macroinvertebrates that niche position and
286 niche breadth had similar, but relatively small unique effects on mean abundance (unique
287 effects 0.056 and 0.054, respectively). Trait vector 3 and taxonomic vector 2 also had small
288 unique effects on mean abundance (0.053 and 0.028, respectively). Boxplots in Appendix B
289 imply that diatom trait vector 5 may be a combination of size and colony-forming, while
290 macroinvertebrate vector 3 is not as clearly related to a single trait but instead is probably a
291 combination of all biological trait groups.

292

293 *3.4. Factors explaining the relationship between occupancy and abundance*

294 Modelling the residuals of the occupancy-abundance relationship provided a possibility to
295 model their relationship, which means basically occupancy once the effect of abundance has
296 been removed. The linear models explained 51% of variation in residuals of the occupancy-
297 abundance relationship for diatoms, and 76% of the residual variation for macroinvertebrates
298 (Table 4). Results of the linear regression models showed, regarding both organism groups,
299 that niche position, niche breadth and trait vectors (trait vector 2 for diatoms and trait vector 3
300 for macroinvertebrates) explained the residual variation for both groups of species. For
301 diatoms, taxonomic vectors 1 and 5 were also statistically significantly associated with the
302 residual variation.

303 The commonality analyses showed that niche position, with its large unique
304 contributions, was the main predictor of residual variation for both groups of organisms (Table
305 4). The effects of other factors, although being statistically significantly associated, were
306 minor, with the exception of the unique effect of niche breadth on macroinvertebrates (0.098).
307

308 **4. Discussion**

309 Our results showed relatively strong and positive occupancy-abundance relationships in our
310 diatom and macroinvertebrate data collected from a large highly-connected lake system. These
311 results thus corroborated both classical (e.g. Brown 1984) and more recent (e.g. Passy 2012)
312 ideas that occupancy and abundance are strongly correlated. In addition, we showed that niche
313 features were the chief determinants of interspecific variation in both occupancy and
314 abundance, aligning with recent studies from various systems (Tales et al. 2004; Tonkin et al.
315 2016).

316 Occupancy was well explained by our set of explanatory variables. The linear models
317 explained almost 60% of variation in diatom species occupancy and nearly 80% of variation in
318 macroinvertebrate species occupancy. Thus, the occupancy of a species is closely tied to its

319 ecological characteristics, such as habitat preferences or resource use. It was, however, evident
320 that niche position was the main variable in predicting variation in occupancy of both diatom
321 and macroinvertebrate species. The strong effect of niche position on occupancy of freshwater
322 organisms has previously been noted in across-waterbodies systems (Tales et al. 2004; Heino
323 and Soinen 2006; Rocha et al. 2018). We also found that the relationship between niche
324 position and occupancy was always negative, basically indicating that rare species possess
325 marginal niches. This imposes that conservation actions should be directed to regionally
326 marginal habitats in order to secure the living conditions of regionally rare species (see also
327 Gaston et al. 2000; Heino and Tolonen 2018; Rocha et al. 2018).

328 The strong impact of niche position on occupancy is, in part, surprising here, because the
329 areal extent of our study system was comparatively small (305 km²), the aquatic system was
330 highly-connected (i.e. apparently free movement of organisms), and thus the ranges of
331 environmental conditions (which were used to calculate the niche parameters in our analyses)
332 were relatively subtle. In addition, high rates of dispersal among sites in our highly-connected
333 study system might interfere with species sorting processes, resulting in weakly-determined
334 species-environment relationships (Vilmi et al. 2016; Tolonen et al. 2017). The fact that niche
335 position was also in this kind of a study setting such a strong factor in explaining interspecific
336 variation in occupancy suggests that these patterns are perhaps universal and not strongly
337 affected by the study systems' ecological properties (Tales et al. 2004; Tonkin et al. 2016;
338 Heino and Tolonen 2018; Rocha et al. 2018). Thus, what we observed now from a large lake
339 system, may be also found in similarly highly-connected aquatic systems, such as marine areas.

340 The linear regression models for the mean abundances resulted in lower explanatory
341 powers than the models for occupancy. They explained over 30% of variation in mean
342 abundances of diatom and macroinvertebrate species. This may indicate that mean abundance
343 is a more complex variable than occupancy. The fact that abundance of macroinvertebrate

344 species was not as well explained by the explanatory factors as their occupancy (34% vs. 77%
345 explained) indicates that, for macroinvertebrates, the formation of variation in abundance is a
346 more complex process than formation of variation in occupancy, and could partly be a result
347 of other factors, such as stochasticity or random effects. The complexity was also visible in the
348 scatter plots, where the occupancy-abundance relationship was weaker for macroinvertebrates
349 than for diatoms. Previous research has also shown that abundance of macroinvertebrates
350 cannot be as clearly linked to niche parameters as their occupancy (Tonkin et al. 2016).

351 The importance of niche position, and to a lesser extent that of niche breadth, was evident
352 for explaining variation in our response variables. However, that was generally not the case
353 with biological traits or taxonomic relatedness. There were small effects of the trait or
354 taxonomic vectors, but nothing evident. This basically means that the biological traits studied
355 here were not strongly related to occupancy and abundance. Although previous research on
356 streams has shown that biological traits, such as body size, are connected to species regional
357 occupancy and mean local abundance (Passy 2012; Rocha et al. 2018), we could not detect any
358 clear patterns suggesting the importance of biological traits. Perhaps the characteristics of our
359 study system, i.e. high connectivity, resulted in the lack of a clear relationship. Previous
360 research, however, has shown that biological traits (i.e. organism's dispersal capacity) may
361 affect the elevation of the abundance-occupancy relationship in highly-connected marine
362 systems (Foggo et al. 2007). This finding was reported from a significantly larger area than
363 what we investigated here. Consequently, perhaps we did not detect clear effects of biological
364 traits because of the small spatial scale addressed (Brändle and Brandl 2001) or maybe we used
365 the wrong traits (Heino and Tolonen 2018). In addition, it is possible that niche characteristics
366 are simply just more important than biological traits for the formation of variation in occupancy
367 and abundance of aquatic organisms (e.g. Rocha et al. 2018).

368 Similarly, taxonomic relatedness did not play a role in affecting occupancy, abundance
369 and their relationships for freshwater diatom and invertebrate species. Previous research has
370 neither found support for clear effects of taxonomy to variation in occupancy and abundance
371 of freshwater organisms (Tales et al. 2004; Heino and Tolonen 2018). As biological traits are
372 products of evolution and thus portrayed by phylogeny (Harvey 1996), it is not surprising that
373 taxonomic relatedness neither appeared as a strong predictor of occupancy and abundance. On
374 the other hand, some biological traits have evolved many times and can be characteristic of
375 comparatively distant orders (Rimet and Bouchez 2012), so in that sense, biological traits may
376 not always be as closely related to phylogeny as expected (Harvey 1996). It is also possible
377 that the spatial scale investigated in this study was not sufficient to detect clear effects of
378 taxonomic relatedness on occupancy and abundance. Phylogenetic signals might have been
379 found over larger areas crossing regional species pools (Heino and Tolonen 2018).

380 A possible caveat of this study is that the species' niche parameters were calculated based
381 on environmental variables collected during the same sampling as the biological samples.
382 Because of no other suitable data existed to calculate the species-specific niche parameters, we
383 opted to use the same dataset. There may thus be a possibility that the effects of niche
384 parameters on occupancy and abundance may have been overestimated. Previous research
385 however has shown that irrespective of the underlying data (i.e. same or different dataset) to
386 calculate niche parameters, they arise as important determinants of occupancy and abundance
387 (Heino 2005; Heino & Grönroos 2014; McCreadie and Adler 2014; Teittinen et al. 2018).

388

389 **5. Conclusions**

390 We found that niche position was the strongest predictor of occupancy and abundance of
391 diatoms and macroinvertebrates in a freshwater system with high connectivity. This finding is
392 consistent with previous knowledge from across-waterbody systems with presumably lower

393 connectivity among sites (Tales et al. 2004; Heino and Soininen 2006; Tonkin et al. 2016;
394 Heino and Tolonen 2018; Rocha et al. 2018). The fact that our highly-connected freshwater
395 system showed similar results to comparatively weakly-connected across-waterbody systems
396 implies that these patterns in occupancy and abundance are perhaps universal and are not
397 strongly related to the connectivity of a study system. Furthermore, due to high connectivity,
398 our study setting had fairly subtle environmental ranges, indicating that niche position and, to
399 a smaller extent, niche breadth, can have strong effects on occupancy and abundance also in a
400 situation where environmental variation is comparatively small. Importantly, these findings
401 were evident even when controlling for biological traits and taxonomic relatedness. As species
402 abundances and occupancies are basically the building blocks for a number of ecological
403 indicators, the observed importance of niche parameters is alleviating regarding the use of these
404 sorts of indicators in environmental assessment.

405 The effect of niche position on the response variables was negative, indicating that the
406 more marginal the niche, the rarer the species both in terms of occupancy and abundance. In
407 other words, rare species tended to possess marginal niches within a large lake system. This
408 was evident for two very distinct groups of freshwater organisms, which represent different
409 trophic positions of the food web and contribute differently to the overall functioning of the
410 aquatic ecosystem. Thus, in order to enhance biodiversity conservation, protection of
411 regionally marginal habitats is important for protecting regionally rare species, also in systems
412 of high connectivity.

413

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418

419 **Conflict of Interest:** The authors declare that they have no conflict of interest.

420

421 **Supplementary material**

422 **Appendix A.** A map showing the sampling sites around a large lake system of Lake Kitkajärvi.

423 **Appendix B.** Examples of how to interpret vectors.

424 **Appendix C.** The diatom and macroinvertebrate species studied, in order of occupancy.

425

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546

547 **Tables**

548

549 **Table 1.** Linear regression model statistics presenting the relationship of logit-transformed
 550 occupancy and log-transformed mean abundance at occupied sites for diatom and
 551 macroinvertebrate species. Bolded p values indicate statistically significant results ($p \leq 0.05$).

552 The explanatory power of the linear models, as indicated by R^2 values, were 0.568 for diatoms
 553 ($p < 0.001$) and 0.384 for macroinvertebrates ($p < 0.001$).

		Estimate	SE	t	p
Diatoms	(Intercept)	-4.0807	0.12281	-33.23	<0.001
	Abundance	1.80665	0.08748	20.65	<0.001
Invertebrates	(Intercept)	-3.7342	0.2589	-14.43	<0.001
	Abundance	1.4106	0.1667	8.46	<0.001

554 **Table 2.** Linear regression model statistics for occupancy models for diatoms and
555 macroinvertebrates. Bolded p values indicate statistically significant results ($p \leq 0.05$). The
556 explanatory powers of the linear models, as indicated by multiple R^2 values, were 0.596 ($p <$
557 0.001) for diatoms and 0.773 ($p < 0.001$) for macroinvertebrates. Followed by linear regression
558 model results are the results of commonality analysis, which inform the unique, common and
559 total contributions of each factor on occupancy of diatom and macroinvertebrate species.

		Estimate	SE	t	p	Unique	Common	Total
Diatoms	(Intercept)	-0.574	0.102	-5.614	<0.001			
	Niche position	-1.100	0.054	-20.257	<0.001	0.531	-0.082	0.449
	Niche breadth	0.516	0.066	7.863	<0.001	0.080	-0.078	0.002
	Trait vector 1	-0.304	0.201	-1.508	0.133	0.003	-0.003	0.000
	Trait vector 2	0.092	0.254	0.363	0.717	0.000	0.004	0.004
	Trait vector 3	0.231	0.342	0.674	0.501	0.001	0.009	0.009
	Trait vector 4	0.060	0.258	0.232	0.816	0.000	0.001	0.002
	Trait vector 5	1.132	0.281	4.021	<0.001	0.021	-0.001	0.020
	Trait vector 6	-0.587	0.336	-1.749	0.081	0.004	0.004	0.008
	Tax. vector 1	-0.002	0.003	-0.459	0.646	0.000	0.001	0.001
	Tax. vector 2	-0.002	0.003	-0.517	0.606	0.000	0.023	0.023
	Tax. vector 3	-0.001	0.004	-0.198	0.843	0.000	0.005	0.005
	Tax. vector 4	-0.005	0.005	-1.103	0.271	0.002	0.002	0.004
	Tax. vector 5	0.003	0.004	0.768	0.443	0.001	0.001	0.002
	Tax. vector 6	0.005	0.005	1.173	0.242	0.002	-0.002	0.000
Invertebrates	(Intercept)	-0.694	0.171	-4.062	<0.001			
	Niche position	-1.429	0.091	-15.737	<0.001	0.552	-0.037	0.515
	Niche breadth	0.890	0.108	8.249	<0.001	0.152	-0.111	0.040
	Trait vector 1	-0.185	0.302	-0.613	0.541	0.001	0.003	0.004

Trait vector 2	0.348	0.384	0.907	0.367	0.002	0.017	0.019
Trait vector 3	-0.450	0.371	-1.212	0.228	0.003	-0.003	0.000
Trait vector 4	0.684	0.372	1.842	0.068	0.008	-0.002	0.006
Trait vector 5	-0.070	0.393	-0.179	0.858	0.000	0.008	0.008
Trait vector 6	0.097	0.493	0.198	0.844	0.000	0.034	0.034
Tax. vector 1	0.002	0.003	0.499	0.619	0.001	0.006	0.006
Tax. vector 2	0.005	0.005	1.133	0.260	0.003	0.013	0.016
Tax. vector 3	0.013	0.007	1.763	0.081	0.007	-0.007	0.000
Tax. vector 4	0.004	0.007	0.642	0.522	0.001	0.018	0.019
Tax. vector 5	-0.011	0.009	-1.243	0.217	0.003	0.109	0.112
Tax. vector 6	0.000	0.010	-0.015	0.988	0.000	0.002	0.002

560 **Table 3.** Linear regression model statistics for mean local abundance models for diatoms and
561 macroinvertebrates. Bolded p values indicate statistically significant results ($p \leq 0.05$). The
562 explanatory power of the linear models, as indicated by multiple R^2 values, were 0.322 for
563 diatoms ($p < 0.001$) and 0.339 for macroinvertebrates ($p < 0.001$). Followed by linear
564 regression model results are the results of commonality analysis, which inform the unique,
565 common and total contributions of each factor on abundance of diatom and macroinvertebrate
566 species.

		Estimate	SE	t	p	Unique	Common	Total
Diatoms	(Intercept)	1.505	0.055	27.264	<0.001			
	Niche position	-0.240	0.029	-8.186	<0.001	0.146	-0.027	0.118
	Niche breadth	0.156	0.035	4.396	<0.001	0.042	-0.035	0.007
	Trait vector 1	-0.239	0.109	-2.194	0.029	0.011	-0.010	0.000
	Trait vector 2	0.276	0.137	2.007	0.046	0.009	0.013	0.022
	Trait vector 3	0.219	0.185	1.183	0.238	0.003	0.008	0.011
	Trait vector 4	0.053	0.140	0.377	0.706	0.000	0.000	0.000
	Trait vector 5	0.764	0.152	5.028	<0.001	0.055	0.017	0.072
	Trait vector 6	-0.491	0.181	-2.706	0.007	0.016	0.004	0.020
	Tax. vector 1	0.003	0.002	1.434	0.153	0.005	0.000	0.004
	Tax. vector 2	0.000	0.002	0.076	0.940	0.000	0.016	0.016
	Tax. vector 3	0.002	0.002	0.679	0.498	0.001	0.002	0.003
	Tax. vector 4	-0.005	0.003	-1.875	0.062	0.008	0.005	0.013
	Tax. vector 5	-0.005	0.002	-2.604	0.010	0.015	0.009	0.024
	Tax. vector 6	0.005	0.003	2.145	0.033	0.010	0.001	0.011
Invertebrates	(Intercept)	1.408	0.128	11.016	<0.001			
	Niche position	-0.200	0.068	-2.943	0.004	0.056	-0.026	0.030
	Niche breadth	0.233	0.081	2.888	0.005	0.054	0.034	0.088

Trait vector 1	0.056	0.226	0.248	0.804	0.000	0.043	0.044
Trait vector 2	0.276	0.288	0.960	0.339	0.006	-0.001	0.005
Trait vector 3	-0.795	0.278	-2.862	0.005	0.053	-0.026	0.027
Trait vector 4	0.157	0.278	0.564	0.574	0.002	0.005	0.007
Trait vector 5	-0.111	0.294	-0.377	0.707	0.001	0.017	0.018
Trait vector 6	0.615	0.369	1.667	0.099	0.018	0.030	0.048
Tax. vector 1	0.003	0.002	1.149	0.253	0.009	-0.003	0.006
Tax. vector 2	0.007	0.004	2.065	0.041	0.028	0.051	0.078
Tax. vector 3	0.010	0.005	1.871	0.064	0.023	-0.022	0.000
Tax. vector 4	0.000	0.005	-0.034	0.973	0.000	0.000	0.000
Tax. vector 5	-0.005	0.007	-0.734	0.465	0.004	0.064	0.067
Tax. vector 6	0.010	0.007	1.443	0.152	0.014	0.006	0.019

567 **Table 4.** Linear regression model statistics for occupancy-abundance relationship (i.e.
568 residuals of occupancy-abundance linear model) models for diatoms and macroinvertebrates.
569 Bolded p values indicate statistically significant results ($p \leq 0.05$). The explanatory power of
570 the linear models, as indicated by multiple R^2 values, were 0.514 for diatoms ($p < 0.001$) and
571 0.757 for macroinvertebrates ($p < 0.001$). Followed by linear regression model results are the
572 results of commonality analysis, which inform the unique, common and total contributions of
573 each factor on the occupancy-abundance relationship of diatom and macroinvertebrate species.

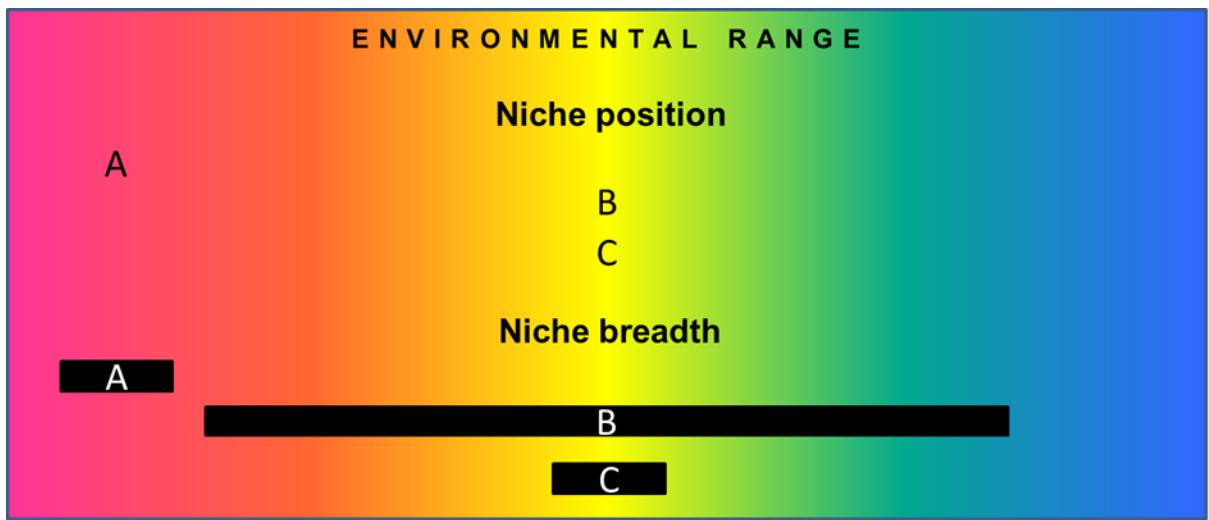
		Estimate	SE	t	p	Unique	Common	Total
Diatoms	(Intercept)	0.788	0.074	10.690	<0.001			
	Niche position	-0.666	0.039	-17.009	<0.001	0.450	-0.059	0.391
	Niche breadth	0.235	0.047	4.954	<0.001	0.038	-0.037	0.001
	Trait vector 1	0.127	0.145	0.878	0.381	0.001	-0.001	0.000
	Trait vector 2	-0.406	0.183	-2.212	0.028	0.008	-0.002	0.006
	Trait vector 3	-0.164	0.247	-0.666	0.506	0.001	0.000	0.001
	Trait vector 4	-0.035	0.186	-0.188	0.851	0.000	0.003	0.003
	Trait vector 5	-0.249	0.203	-1.229	0.220	0.002	0.006	0.008
	Trait vector 6	0.300	0.242	1.238	0.217	0.002	-0.002	0.001
	Tax. vector 1	-0.006	0.002	-2.577	0.010	0.010	-0.010	0.000
	Tax. vector 2	-0.002	0.003	-0.819	0.413	0.001	0.007	0.008
	Tax. vector 3	-0.004	0.003	-1.193	0.234	0.002	0.000	0.002
	Tax. vector 4	0.003	0.003	1.008	0.314	0.002	-0.001	0.001
	Tax. vector 5	0.012	0.003	4.589	<0.001	0.033	-0.019	0.014
	Tax. vector 6	-0.004	0.003	-1.276	0.203	0.003	0.008	0.010
Invertebrates	(Intercept)	1.054	0.139	7.607	<0.001			
	Niche position	-1.146	0.074	-15.558	<0.001	0.576	0.026	0.603
	Niche breadth	0.561	0.088	6.404	<0.001	0.098	-0.097	0.001

Trait vector 1	-0.264	0.245	-1.078	0.283	0.003	0.005	0.007
Trait vector 2	-0.041	0.312	-0.132	0.895	0.000	0.015	0.015
Trait vector 3	0.672	0.301	2.230	0.028	0.012	0.007	0.019
Trait vector 4	0.463	0.302	1.534	0.128	0.006	-0.004	0.001
Trait vector 5	0.086	0.319	0.270	0.788	0.000	0.000	0.000
Trait vector 6	-0.770	0.400	-1.926	0.057	0.009	-0.005	0.004
Tax. vector 1	-0.002	0.002	-0.881	0.381	0.002	0.023	0.025
Tax. vector 2	-0.005	0.004	-1.293	0.199	0.004	-0.001	0.004
Tax. vector 3	-0.002	0.006	-0.262	0.794	0.000	0.000	0.000
Tax. vector 4	0.004	0.005	0.835	0.406	0.002	0.030	0.032
Tax. vector 5	-0.004	0.007	-0.576	0.566	0.001	0.048	0.049
Tax. vector 6	-0.015	0.008	-1.896	0.061	0.009	-0.006	0.003

574 **Figure captions**

575 **Fig. 1.** A schematic figure illustrating three species, A, B and C, and their niche positions and
576 niche breadths across an environmental range. Species A has a marginal niche position, while
577 species B and C have non-marginal niche positions (i.e. their niches are located close to the
578 mean environmental conditions). Species A and C have small niche breadths, while species B
579 has a large niche breadth (i.e. it is able to live in a broader range of environmental conditions
580 compared to species A and C). It is noteworthy that two species can have the same niche
581 position although the niche breadth differs (species B vs. species C). Thus, although niche
582 position of species C is non-marginal, it is still a specialist species for those non-marginal
583 conditions.

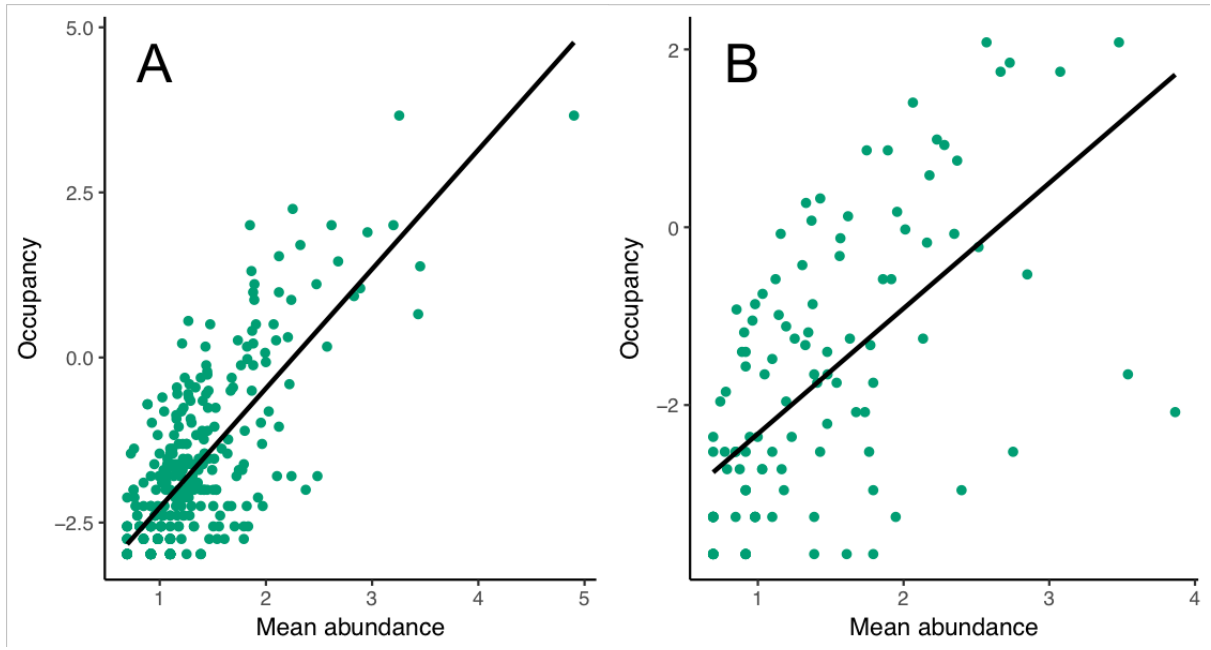
584 **Fig. 2.** Scatter plots describing the relationships between logit-transformed occupancy and log-
585 transformed mean abundance at occupied site of diatoms (A) and macroinvertebrates (B).



587

588 **Fig. 1.**

589



590

591 **Fig. 2.**