**Temporal beta diversity of lake plants is determined by concomitant changes in
environmental factors across decades**

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19 **Acknowledgments**

20

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24

25 **Authors' contributions**

26

27 JH, ML and JA designed the study. ML did the statistical analyses, gathered the land use data and
28 wrote the first version of manuscript. ML also participated in the most recent aquatic plant sampling.
29 HT provided the aquatic plant data from 1940s to 2000s and contributed to interpretation. All authors
30 contributed to writing of the manuscript.

31

32 **Data availability**

33

34 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.t1g1jwsxv>
35 (Lindholm et al. 2020a).

36

37 **Abstract**

38

39 1. To comprehensively understand the impact of anthropogenic activities on biodiversity, we must
40 understand how biodiversity has changed over time and what are the underlying processes. A growing
41 body of evidence has shown that beta diversity reveals more about temporal changes in biodiversity
42 compared with alpha diversity. Temporal beta diversity indicates, for example, degrees of change in
43 species composition at single locations through time.

44 2. We examined if freshwater plant communities showed different patterns in temporal beta diversity
45 in relation to concomitant changes in environmental conditions across decades. In order to do this,
46 we used presence-absence data of lake plants for five decades (1940s to 2010s) from southern Finland
47 and calculated temporal beta diversity indices (TBI) for each lake between pairs of decades to the
48 whole community, hydrophytes and helophytes. To get insights into possible processes behind the
49 observed trends, we decomposed TBIs into beta diversity contributed by either temporal losses or
50 temporal gains of species. We related TBIs and their loss and gain components to lake landscape
51 position and changes in environmental variables.

52 3. Based on comparisons of TBIs between the survey decade pairs, the temporal change in aquatic
53 plant communities was modest through decades. Hydrophyte assemblages have changed more than
54 helophyte assemblages. The main changes in temporal beta diversity occurred from the 1940s to the
55 1970s, when the gain of new species was the dominant process in the lakes throughout the landscape.
56 Following that period, there was only modest changes, but from the 2000s to the 2010s, the dominant
57 process was the loss of species. Temporal changes in environmental conditions played a key role in
58 explaining the TBI.

59 4. Our results showed that relying on only two survey points in time can result in limited knowledge
60 of the ecological phenomenon under study and, for example, an exceptional year in terms of weather
61 conditions can hinder detecting overall long-term trends in compositional changes. Therefore, future

62 studies should try to combine data from several decades to overcome the typical limitations of
63 temporal information.

64

65 **Keywords:** Anthropogenic impacts; Aquatic macrophytes; Beta diversity; Lakes; Land use; TBI;
66 Temporal beta diversity; Temporal patterns

67

68 **Introduction**

69

70 In the era of the Anthropocene (Crutzen 2002), human activities have seriously impacted ecosystems,
71 leading to a decline of biodiversity globally (IPBES 2019). At landscape and local levels, findings
72 related to biodiversity change have been controversial, as alpha diversity has been shown to decline,
73 increase or remain stable over time (Vellend et al. 2013, Dornelas et al. 2014, Newbold et al. 2015).
74 However, there is a growing body of evidence of considerable shifts in community compositions at
75 landscape and local scales through time (McGill et al. 2015). Specifically, studies have shown that
76 even when alpha diversity is increasing or remains stable over time, community composition may be
77 continuously changing (Magurran et al. 2018, Larsen et al. 2018, Blowes et al. 2019, Finderup Nielsen
78 et al. 2019, Hendershot et al. 2020). In this context, Hillebrand et al. (2018) recommended researchers
79 to focus on compositional shifts when local biodiversity change is the target of a study. Also, Gotelli
80 et al. (2017) highlighted the need for community-level assessments of biodiversity trends.
81 Understanding these trends has huge implications for biodiversity conservation, and, therefore,
82 community composition should be taken into account especially in the protection of landscape-level
83 and local biodiversity (Socolar et al. 2016, Hillebrand et al. 2018).

84

85 At landscape and local scales, compositional change is caused by losses and gains of species, i.e.
86 changes in species occupancy (Sax and Gaines 2008). Both temporal species losses and species gains
87 at local sites can be the result of gradual or abrupt changes in environmental conditions, including
88 anthropogenic impacts such as land use changes (Legendre 2019). Also, biotic interactions and
89 stochastic processes can cause temporal variation in species composition. The change in community
90 composition over time in one location can be called temporal beta diversity (Legendre and Gauthier
91 2014, Shimadzu et al. 2015). There are several methods and indices that can be used to measure
92 temporal beta diversity (Magurran et al. 2019), and one novel index is the Temporal Beta diversity

93 Index (TBI; Legendre 2019). Several studies have identified changes in temporal beta diversity
94 patterns (e.g. Cook et al. 2018), but the TBI can go further and help to identify the potential
95 mechanisms behind these changes (Legendre 2019). TBI can be decomposed into losses and gains of
96 species, thus giving information on which process is dominant at each site (Legendre 2019). One of
97 the advantages of TBI is also that it can help to identify the sites that have changed in community
98 composition in exceptional ways, thereby leading to explorations of these sites in more detail
99 (Legendre 2019). In addition, TBI may be useful in helping to guide conservation and management
100 actions by pointing out locations with temporally stable communities and, on the other hand, locations
101 where loss of species is causing a decline in biodiversity. This index has proven its usefulness in
102 detecting patterns in beta diversity through time in different environments, answering different
103 ecological questions and focussing on distinct organism groups (Legendre and Salvat 2015,
104 Winegardner et al. 2017, Kuczynski et al. 2018, Brice et al. 2019, Legendre and Condit 2019).

105

106 A well-known problem when studying biodiversity change through time is the lack of appropriate,
107 high-quality and comprehensive spatio-temporally replicated datasets. This is especially true when
108 temporal beta diversity patterns are of major interest (Magurran et al. 2019). One approach to study
109 temporal patterns is to rely on palaeoecological data (e.g. Tomašových and Kidwell 2009). However,
110 palaeoecological datasets are usually available only for well-preserved organisms (Dornelas et al.
111 2013), and the accuracy of data with the fragmented nature of fossil data (Magurran et al. 2019) is
112 usually not suitable for studies of ecological time scales. Long time series of replicated sampling are
113 quite rare (Magurran 2011), and monitoring data with frequent sampling do not usually cover long
114 time periods (Dornelas et al. 2013). Resurveying historical datasets has gained plenty of attention
115 recently (Hédl et al. 2017), but the limitation of this approach is that these datasets are usually based
116 on only two or three points in time, even though the temporal scale can be quite broad in terms of
117 ecological time scales. There might also be temporal decay of quality of historical data sets; for

118 example, there might be missing metadata (Tessarolo et al. 2017). Due to these issues, existing
119 combinations of historical and contemporary datasets that cover several decades and several sampling
120 points are very valuable when biodiversity change is studied, especially for less-investigated
121 ecosystems, such as inland waters.

122

123 Freshwaters hold a very large proportion of total global biodiversity in relation to their small areal
124 extent (Strayer and Dudgeon 2010). Recently, scientists have warned that these environments are
125 facing a severe biodiversity crisis and are thus losing much of their biodiversity (Albert et al. 2020).
126 This decline of biodiversity is more rapid in freshwaters than in terrestrial or marine ecosystems
127 (WWF 2016, Albert et al. 2020). Therefore, it is important to advance our understanding of temporal
128 shifts in community composition in these environments. There is also a reported loss of aquatic
129 vegetation in lakes, and freshwater plants are globally threatened for multiple reasons, such as land-
130 use change, eutrophication and invasive species (Zhang et al. 2017). This is a concerning trend, as
131 aquatic plants possess essential ecological roles in lakes. For example, they generate three-
132 dimensional habitat structures for other lake-dwelling organisms, are one group of the key primary
133 producers and are part of cycles of substances, like nutrients and sediments (Jeppesen et al. 1998,
134 Sand-Jensen 1998). In addition, aquatic plants can be used as good surrogates for wider biodiversity
135 in lake environments (Law et al. 2019). Therefore, they constitute a good model group for examining
136 long-term changes in lake communities and ecosystems.

137

138 Our main aim was to examine if freshwater plant communities showed different patterns in temporal
139 beta diversity in relation to changes in lake environmental and landscape conditions across decades.
140 We used presence-absence data of vascular aquatic plants in small boreal lakes from five decades
141 (1940s to 2010s). To see if there would be differences in lake plant functional groups, we performed
142 analyses for all taxa, hydrophytes (i.e. true aquatic plants) and helophytes (i.e. emergent species). We

143 obtained temporal beta diversity indices for each lake by comparing the aquatic plant data of all lakes
144 between the time points. To get an insight into possible mechanisms behind the observed trends, we
145 decomposed TBIs into beta diversity contributed by either temporal losses or gains of species. We
146 further related TBIs and their components to the ‘lake landscape position’ variable, which is stable
147 between the time points, and temporal changes in non-stable environmental variables, which have
148 changed between time points, like pH and land use variables. We tested three hypotheses: 1)
149 Temporal beta diversity in each lake will show increasing degrees of change through time. 2)
150 Temporal beta diversity in each lake is strongly related to lake landscape position and temporal
151 changes in pH. 3) There has been variation in temporal losses and gains of species across the
152 landscape. The first hypothesis is based on the review by McGill et al. (2015), where they identified
153 an increasing trend in temporal beta diversity. The second hypothesis is based on our earlier finding
154 that the most important factors affecting spatial beta diversity were pH and lake landscape position
155 in the same study area (Lindholm et al. 2020b). We based the third hypothesis on a previous finding
156 by Winegardner et al. (2017) and the assumption that in the areas where urbanisation has prevailed
157 through time, the dominant process would be the loss of species and, in areas where the agricultural
158 field area has decreased, the dominant process would be the gain of species (Socolar et al. 2016).

159

160 **Material and Methods**

161

162 *Study area*

163 We studied 27 lakes located in the river Kokemäenjoki drainage basin in the southern boreal climate
164 zone (Ahti et al. 1968) in Finland. The study lakes are near the city of Tampere, in the area between
165 the two large lakes, Roine and Pyhäjärvi (Fig. S1). Many of these lakes are situated in small chains
166 of lakes and streams and have brown, humic waters. Naturally more eutrophic lakes are located at
167 lower elevations and are mainly surrounded by agricultural land or settlements, while smaller and

168 more oligotrophic lakes at higher elevations in the landscape are less affected by human activity and
169 are surrounded by coniferous forest and peatland. This is mainly due to glacial and postglacial
170 processes, whereby fine-grained sediments with nutrients have been washed along the elevational
171 gradient in the landscape (Seppälä 2005). Therefore, changes in lake environmental conditions occur
172 along a relatively small elevation gradient (77 to 131 m a.s.l.). More information on the study area
173 can be found in table S1 and Lindholm et al. (2020b).

174

175 *Species data*

176 We used aquatic plant data from five different decades (Lindholm et al. 2020a; Table S2; Fig. S2–
177 S6). The first plant survey was conducted in 1947–1951 (Perttula 1954 unpublished) and
178 reinvestigated using similar methods in 1975–1978 (Toivonen and Huttunen 1995), 1991–1993,
179 2005–2008 and in 2017. For clarity, we refer to these surveys as 1940s, 1970s, 1990s, 2000s and
180 2010s. In this study, we concentrated on species classified traditionally as aquatic vascular plants in
181 Finland according to Linkola (1933) and, in addition, seven tall species from the sedge genus *Carex*
182 growing in the water. In total, 66 vascular plant taxa were included. We focused on presence-absence
183 data, as with historical datasets focusing on the whole lake area, presence-absence data are more
184 reliable source of information compared to coverage information representing abundance. We did not
185 include hybrids (e.g. *Typha* x *glauca*) and taxa identified to genus level (e.g. *Isoëtes* sp.) in the
186 analysis. We combined some species to species complexes due to identification differences between
187 the five decades. In addition, we divided the species into helophytes (including also some species
188 from the genus *Carex*) and hydrophytes (including ceratophyllids, elodeids, isoetids, lemnids and
189 nymphaeids), following Toivonen & Huttunen (1995).

190

191

192

193 *Environmental data*

194 We used the following environmental variables: elevation (m), pH, water transparency (m), field area
195 (%), urban area (%) and ditches. From the 1970s onward, we also have specific conductivity (mS/m)
196 available. We used elevation to represent the lake landscape position. Water transparency (m) was
197 measured using a Secchi disk simultaneously with the aquatic plant sampling. Land use variables
198 from 200 m buffer zones (Pedersen et al. 2006) were derived from the base maps for each decade
199 (National land survey of Finland 2017, 2018). We calculated field area (%) and urban area (%) as a
200 proportion of buffer areas as well as ditches, which thus is an index variable representing the amount
201 of ditches. More information about the environmental variables can be found in table S1 and
202 Lindholm et al. (2020b).

203

204 *Data analysis*

205 We conducted the following analyses for the whole community and, to see if there would be
206 differences between major lake plant functional groups, we performed the analyses also for
207 helophytes and hydrophytes separately following the same procedure as for the whole community.
208 First, we calculated temporal beta diversity indices (TBI; Legendre 2019) for each lake. TBIs are
209 dissimilarity indices that measure temporal beta differentiation, i.e. the change in community
210 composition from one time point to a subsequent time point (Legendre 2019). This index varies from
211 zero (community compositions at two time points are exactly the same) to one (communities have no
212 shared species). As this method is limited to measure only two survey time points, we measured
213 changes between separate survey pairs: the 1940s and 1970s, the 1970s and the 1990s, the 1990s and
214 the 2000s, and the 2000s and 2010s. We also measured changes from the oldest survey (1940s) to the
215 most recent survey (2010s) to observe the long-term trend in the study period. To obtain the index
216 values, we used the *TBI* function with Sørensen dissimilarity indices available in the *adespatial* R

217 package (Dray et al. 2019). The p-values (based on 9 999 random permutations) were corrected for
218 multiple testing, as several lakes were tested simultaneously (Legendre 2019).

219

220 Second, we decomposed the TBIs into beta diversity explained by either species temporal losses or
221 temporal gains. These components describe the contribution of species losses and gains to the total
222 dissimilarity, thus giving insight into the relative importance of these phenomena (Legendre 2019).
223 We tested these indices for significance using parametric and permutational paired t-tests. The TBIs
224 and which process (gains or losses) dominates were visualized on maps, as we aimed to identify sites
225 that have changed in exceptional ways because the patterns of temporal variation may differ from one
226 lake to another in a landscape. We also divided the lakes into two groups according to whether they
227 were above or below 100 meters above sea level. We visualised the loss and the gain components to
228 the B-C-plots (Legendre 2019) to see if the loss and the gain components follow this elevation
229 division.

230

231 Third, to explain the possible changes in TBIs, we related the TBIs to changes in the environment.
232 We calculated the temporal change in pH units, water transparency, field area, urban area and ditches
233 between previously mentioned survey decade pairs, and used these metrics of change in the
234 subsequent analysis. We calculated the change by subtracting the earlier decade's values from the
235 later decade's values (i.e. 1970-1940). Measurements of pH were done in the summertime for the
236 1940s data. Thus, we used summertime pH values from the 1970s when we calculated the changes in
237 pH units between these two decades. In other decades, measurements were conducted during the fall
238 overturn. Thus, we used fall pH values from the 1970s when we calculated the changes in pH units
239 between the 1970s and 1990s. However, we had to use summertime pH values from the 1940s and
240 fall pH values from the 2010s, thus limiting the strict comparability between these decades. In
241 addition, we used elevation values, which represent the lake landscape position, from earlier decade's

242 values, i.e., in the survey decade pair 1940s–1970s, we used values from the 1940s. There are slight
243 changes in elevation values between decades due to changes in measuring techniques and post-glacial
244 rebound, but the relative position of the lakes has remained unchanged. From the 1970s onwards, we
245 also calculated the change in specific conductivity (mS/m) and included it in our models in order to
246 gain more insight into the environment-TBI-relationship. However, to ensure the comparability
247 between the decades, we also did the analyses without specific conductivity, as we do not have this
248 information from the 1940s.

249

250 To model variation in TBI values across lakes, we conducted beta regression (Ferrari and Cribari-
251 Neto 2004) with a log link function using the *betareg* function available in the *betareg* R package
252 (Cribari-Neto and Zeileis 2010). We used previously obtained TBIs as the dependent variables that
253 were explained by the changes in the environment and lake landscape position. We used the same set
254 of variables to enable comparison between the survey decade pairs. Beta regression is suitable when
255 the response variable is constrained between 0 and 1. However, as the TBI also had some values that
256 were exactly zero, we added the constant value 0.00000001 to the TBIs and their components. As the
257 *betareg* function produces a pseudo R-squared value for the model, we tested the model using the
258 *lrtest* function in the *lmtest* R package (Zeileis and Hothorn 2002). We also checked the residuals to
259 see if there is spatial autocorrelation in model residuals by calculating Moran’s I coefficients based
260 on lake centres’ geographical coordinates. We used five distance classes and the *correlog* function
261 available in the *pgirmess* package (Giraudoux 2018).

262

263 Fourth, we focused on the overall dissimilarity in community composition between survey decades.
264 We formed a dissimilarity matrix based on Sørensen dissimilarity index (Legendre and Legendre
265 2012), using the function *beta* in the *BAT* R package (Cardoso et al. 2015, 2020), and an aquatic plant
266 matrix including all sites. To euclidify the dissimilarities, we used a square-root transformation. Then,

267 we conducted the distance-based redundancy analysis (dbRDA; Legendre and Andersson 1999) using
268 the function *capscale* available in the *vegan* R package (Oksanen et al. 2019) and constrained sites
269 by a factor representing the five survey decades.

270

271 Fifth, we aimed to identify lakes where the changes in environmental conditions had been most
272 important. We used the same approach as with the community data and used the TBI for
273 environmental variables to identify the lakes, where the changes in the environment had been
274 exceptional between separate survey decade pairs. We transformed the environmental variable data
275 into non-negative and standardized environmental variables using the function *scale.for.TBI*
276 (Legendre 2019, Appendix S2). We used the *TBI* function with the standardized Euclidean distances
277 available in the *adespatial* R package (Dray et al. 2019) and conducted a test of significance using 9
278 999 permutations. We related aquatic plant TBIs to environmental TBIs by conducting beta
279 regression (Ferrari and Cribari-Neto 2004) with a log link function using the *betareg* function
280 available in the *betareg* R package (Cribari-Neto and Zeileis 2010). All statistical analyses were
281 conducted in R version 3.6.2 (R Core Team 2019).

282

283 **Results**

284

285 *TBI between the survey pairs of decades*

286 The TBI dissimilarities showed that there were no drastic changes, on average, in the vascular aquatic
287 plant composition between the survey decade pairs (Fig. 1; Table S6). Significant between-decade
288 changes in community composition occurred only in a few lakes (Table S3). The changes in
289 community composition had been the highest between the 1940s and the 1970s, when the gain of
290 species had been the prevailing process throughout the landscape (Fig. 1; Fig. 2). From the 1970s to
291 the 1990s and from the 1990s to the 2000s, the losses and gains of species were almost equally

292 common. From the 2000s to 2010s, the dominant process in the landscape was the loss of species
293 (Fig. 1; Fig. 2). There was no clear pattern with elevation, when the lakes were divided into two
294 groups according to whether they were above or below 100 meter above sea level (Fig 3). In some
295 lakes, hydrophytes showed much larger changes in community composition than helophytes (Table
296 S4; Table S5), and the mean TBI was also slightly higher for hydrophytes than helophytes between
297 each decade pair (Table S6). On average, changes in helophyte and hydrophyte assemblages'
298 compositional dissimilarities and their gain and loss components between the pairs of survey decades
299 followed similar patterns as the whole community, but there was, on average, more intensive loss of
300 hydrophytes than helophytes (Table S6).

301

302 We were unable to conduct beta regression analyses to all survey-decade-pairs for helophytes due to
303 low TBI values. Therefore, we focussed only on the results based on the whole community. Based on
304 the beta regression results, aquatic plant communities showed different patterns in TBI in relation to
305 changes in environmental conditions across decades (Table 1). None of the variables explained the
306 TBI from the 1940s to the 1970s. From the 1970s to the 1990s, all changes in environmental
307 conditions included in the model were important. In contrast, from the 1990s to 2000s, only the stable
308 elevation variable, which represents the lake landscape position, was important in explaining
309 variation in the TBI (Table 1). There was little spatial autocorrelation in the residuals of the TBI
310 models between the survey pair decades (Fig. S7). When changes in specific conductivity were added
311 to the models from the 1970s onward, the results followed similar patterns as without it. Changes in
312 specific conductivity were important only between the 1990s and the 2000s in relation to TBI (Table
313 S8).

314

315

316

317 *TBI between the 1940s and the 2010s*

318 The mean temporal beta diversity was 0.25 over all sites in the study area (Table S6). During this
319 period, there were slightly more species gains than species losses, but the overall process at all the
320 sites (the mean change over all sites) in relation to changes of community composition was not clear
321 (Fig. 3; C/den $P > 0.05$). Temporal changes in pH units and water transparency were the most
322 important variables in explaining variation in the TBI (Table 1). The mean TBI was 0.30 for the
323 hydrophytes and 0.20 for the helophytes (Table S6).

324

325 *Community composition*

326 The overall similarity in community composition between survey decades can be seen in a dbRDA
327 biplot, where the centroid of each survey decade is shown surrounded by the 27 lake observations of
328 that decade (Fig. 4). The lakes in the 1940s and 2010s have slightly different species compositions
329 from the surveys that were done in the 1970s, 1990s and 2000s. In those three decades, lakes had
330 relatively similar species compositions (Fig. 4). Sites followed mainly the same patterns for
331 hydrophytes and helophytes as for the whole community (Fig. S9).

332

333 *Environmental TBI*

334 Based on the TBI values for environmental variables between the survey pair decades, there were no
335 significant changes in the environmental conditions between decades. Only in the few lakes
336 surrounded by urban area, changes in the environmental conditions had been exceptional (Table S7).

337 Based on the beta regression results, the environmental TBI was important in explaining the TBI of
338 aquatic plant communities in 1970-1990, 1990-2000 and 2000-2010 (Table S9). There was not much
339 spatial autocorrelation in the model's residuals between the survey pair decades (Figure S8). The
340 overall dissimilarity in environmental variables between survey decades can be seen in a dbRDA
341 biplot, where the centroid of each survey decade is shown surrounded by the 27 lake observations of

342 that decade (Fig. S10). Based on the dbRDA biplot, the lakes in all decades have quite similar
343 environmental conditions (Fig. S10).

344

345 **Discussion**

346

347 In this landscape-scale and long-term observational study, we examined whether the species
348 compositions of aquatic plant communities have changed through time under predominately modest
349 anthropogenic impacts. Based on the comparisons of the TBIs between adjacent sampling periods,
350 the temporal change in aquatic plant communities has also been modest through decades. Therefore,
351 our hypothesis that temporal beta diversity in each lake will show increasing degrees of change
352 through time (McGill et al. 2015) did not receive support. Nevertheless, temporal beta diversity was
353 determined by concomitant changes in environmental conditions across decades. TBIs were related
354 to temporal changes in pH units and water transparency, but also to land use changes, thereby only
355 partly supporting our second hypothesis (Lindholm et al. 2020b). Main changes in temporal beta
356 diversity have occurred from the 1940s to the 1970s, when the gain of new species has been the
357 dominant process in the lakes throughout the landscape. Following that period, there have been only
358 very modest changes in the species composition of communities, and the temporal loss and gain of
359 species have been quite stable. However, from the 2000s to the 2010s, the dominating process was
360 the loss of species in lakes across the landscape. Nevertheless, there was variation in temporal losses
361 and gains of species at the lake level across the landscape, thus supporting our third hypothesis.

362

363 *Patterns in temporal beta diversity*

364 McGill et al. (2015) stated that local temporal beta diversity patterns have not been empirically
365 measured often enough to facilitate the certain identification of the direction of the global trend.
366 However, they stated that there is growing evidence that variation in temporal beta diversity is

367 unexpectedly high at local scales (Dornelas et al. 2014), a phenomenon which later studies have also
368 confirmed (Gotelli et al. 2017, Blowes et al. 2019). Based on our results, the temporal changes in
369 aquatic plant community compositions have been modest through decades, and we did not find signals
370 of an increasing trend in temporal beta diversity patterns. Nevertheless, it seems that during the study
371 period, hydrophyte assemblages have changed more than helophyte assemblages. This finding was
372 expected, as these two macrophyte groups partly respond differently to environment gradients (e.g.
373 Alahuhta and Heino 2013).

374

375 There are only a limited number of studies that have used the TBI approach (Legendre and Salvat
376 2015, Winegardner et al. 2017, Kuczynski et al. 2018, Brice et al. 2019, Legendre and Condit 2019).
377 It is important to notice that our study is mainly based on comparing adjacent sampling periods, while
378 these previous studies are based on reference to a single baseline time period. In addition, there are
379 only a few studies focusing on temporal beta diversity of aquatic plants covering several decades and
380 several sites, and these studies have found changes in community composition through time using
381 other methods and indices (Virola et al. 1999, 2001, Hilli et al. 2007, Baastrup-Spohr et al. 2017). In
382 addition, studies that have concentrated on one lake only have found shifts from submergent-
383 dominated to emergent-dominated floras (e.g. Egertson et al. 2004). This shift has also been detected
384 in a few of our study lakes (e.g. Ranta and Toivonen 2008) affected more strongly by humans and
385 can also be seen in a slightly higher loss of hydrophyte species. In stream environments, studies have
386 also found declining trends in temporal beta diversity of fish and macroinvertebrate communities
387 (Cook et al. 2018, Kuczynski et al. 2018, Larsen et al. 2018). As these studies have focused on stream-
388 dwelling animals, it is possible that these organism groups are more vulnerable to anthropogenic
389 pressure compared to lake plants (Korhonen et al. 2010). Lake plants do not have to rely on only
390 spatial dispersal to re-colonise sites, which is generally the case for fish and most macroinvertebrates.
391 Rather, lake plants can restore their occupancy by re-growth from belowground root and rhizomes or

392 by germination from a seed bank (Harwell and Havens 2003), which could be called “dispersal in
393 time” (Buoro and Carlson, 2014).

394

395 *Relationship of changes in the environment to species temporal losses and gains*

396 From the 1940s to the 1970s, gain of species has been the dominant process in the lakes throughout
397 the landscape. Following that period, temporal loss and gain of species have been quite stable, until
398 the 2000s to the 2010s, when the dominating process was, in contrast, the loss of species. Other
399 studies that have utilised TBI have found inconsistent patterns related to gains and losses. Kuczynski
400 et al. (2018) observed that temporal changes in community composition were mainly due to losses of
401 fish species in France. Brice et al. (2019) found that temporal changes in composition were slightly
402 more due to gains than losses with tree community abundance in the temperate–boreal ecotone of
403 Québec. Also, studies that have used different indices have found distinct patterns: species gains
404 overriding species losses at regional scale in Denmark (Finderup Nielsen et al. 2019) and roughly
405 balanced extinctions and colonisations in 158 assemblages across the globe (Dornelas et al. 2019). It
406 seems that the temporal losses and gains of species are highly context dependent, probably depending
407 on both temporal and spatial scale, the type of organism, as well as the intensity of anthropogenic
408 disturbance.

409

410 Temporal changes in water transparency, pH units and land use played key roles in explaining the
411 TBI. The only exception was from the 1990s to the 2000s, which was the only period when elevation,
412 representing stable lake landscape position, was the only one from our set of variables that explained
413 significant variation in TBI. This is an interesting finding, as there was no clear pattern with elevation
414 (i.e. lake landscape position) in temporal gains or losses of species, when the lakes were divided into
415 two groups according to whether they are above or below 100 meters above sea level (Fig. 3). It
416 seems that during the period between 1990s and 2000s, the changes in the environment did not

417 influence the TBI. In our previous study of spatial beta diversity patterns across these lakes, we found
418 that lake landscape position was important especially in the 1940s, and after that, pH was clearly
419 more important than lake landscape position. However, lake landscape position was still the second-
420 most important variable influencing spatial beta diversity of lake plants (Lindholm et al. 2020b).
421
422 Human-caused nutrient input is a crucial process causing temporal changes in aquatic plant
423 communities (Sand-Jensen et al. 2008, 2017, Salgado et al. 2018). Unfortunately, as we do not have
424 systematic nutrient information available, we have to rely on other factors that are closely related to
425 increasing nutrient input, such as water transparency, pH (Wetzel 2001) and land use variables
426 (Soranno et al. 2015). For example, usually when the amount of nutrients increases, water
427 transparency decreases (Wetzel 2001), and water transparency is related to colonization depth and
428 minimum light requirements of aquatic plants (Middelboe and Markager 1997). In most of our study
429 lakes, water transparency has decreased from the 1940s to the 1970s, when temporal gains have been
430 dominant, and after this period changes have been more sporadic. It is highly likely that between the
431 1940s and the 1970s, the amount of nutrients have increased in these lakes. The increase of nutrients
432 in this period is also supported by the fact that the species that have increased in the study lakes are
433 benefitting from eutrophication (Toivonen 1985, Toivonen and Huttunen 1995). Some of those
434 species (*Typha latifolia*, *Elodea canadense* and *Potamogeton crispus*) have become dominating
435 macrophytes forming large stands in some lakes (Toivonen 2009). Hydrophytes are expected to
436 respond more directly to eutrophication than helophytes, and they are sensitive to anthropogenic
437 impacts (Sand-Jensen et al. 2000). As the changes in the hydrophyte assemblage composition and the
438 loss of hydrophytes were higher than those of the helophytes, these findings further support our
439 interpretation of nutrient increases.
440

441 Increase in pH is also often associated with enhanced nutrient status in lakes (Wetzel 2001). Several
442 studies have shown that pH has a strong influence on aquatic plant communities (reviewed by Lacoul
443 and Freedman 2006). In acid and neutral lakes, increasing pH is related to increasing levels of
444 bicarbonate and the availability of carbon for many submerged plants, particularly for elodeids
445 (Vestergaard and Sand-Jensen 2000, Iversen et al. 2019). Therefore, increasing pH might first enable
446 the occurrence of different kinds of species, resulting in gains of species. Usually photosynthetic
447 actions of algae cause the increase in pH values, thus indicating increasing nutrient concentrations.
448 However, in our study lakes, pH has both decreased and increased when the gain of species has been
449 the prevailing process (i.e. between the 1940s and the 1970s). Therefore, it is difficult to say with
450 certainty what the relationship of decreasing pH and the gains of species could be in our study lakes.
451 Additionally, summer pH values are sensitive to variation in primary production of phytoplankton
452 and submerged plants during the growing season.

453

454 If we only look at the survey decade pair from the 1940s and the 2010s, when the TBI was best
455 explained by changes in water transparency and pH, water transparency has increased in the lakes
456 near urban areas. Even though the built area has also increased during the whole study period,
457 phosphorus removal from industrial and municipal wastewaters was started in the mid-1970s in
458 Finland (Räike et al. 2003). Also, studies conducted in Denmark have found that improved treatment
459 of domestic sewage has reduced the annual phosphorus input to freshwaters substantially from the
460 1970s, bringing input close to the pre-eutrophication level (Sand-Jensen et al. 2008, 2017). However,
461 our study lakes have not gained many new species during the whole study period. On the other hand,
462 of the lakes where water transparency has declined, most are located at higher elevations in the
463 landscape, are less affected by human activity, and are surrounded by coniferous forest and peatlands.
464 Decreasing water transparency can be due to long-term increases in dissolved organic carbon and the
465 brownification it can cause (Evans et al. 2005, Kritzberg et al. 2020).

466 Changes in land use were especially important between the 1970s and the 1990s, when slightly more
467 of the lakes across the landscape gained new species than lost them. During that time, agricultural
468 area (i.e. fields and pasture) decreased adjacent to lakes. Agricultural land within a watershed is
469 strongly related to total phosphorus, but the pattern is opposite to water transparency (e.g. Taranu and
470 Gregory-Eaves 2008). Also, Hilli et al. (2007) found that species turnover was related to changes in
471 agriculture in central Finland between the 1930s and 1996. The number of new aquatic plant species
472 increased in the same areas where agricultural areas decreased (Hilli et al. 2007). In our study lakes,
473 changes in agricultural area were also important between the 2000s and the 2010s. During that period,
474 agricultural area continued to decrease, but changes were smaller than in earlier decades. It seems
475 that some aquatic plant species, especially hydrophytes, can benefit from the decrease in agricultural
476 area with declining nutrient input in small boreal lakes (e.g. Hilli et al. 2007). Also, Winegardner et
477 al. (2017) found that the TBIs were significantly related to land cover in the watershed over c. 150
478 years, and they found both gains and losses of lake diatoms across the United States. They also found
479 higher temporal beta diversity in watersheds with reduced forest cover, implying that higher basin
480 forest covers may buffer changes through time when comparing pre-industrial and contemporary
481 times (Winegardner et al. 2017).

482

483 Changes in individual lakes may also have influenced the TBIs in our study, especially during the
484 period between the 1940s and 1970s. The slight lowering of the water level in some lakes and the end
485 of grazing in shore areas (Toivonen 1985) have probably had effect on temporal losses and temporal
486 gains of aquatic plant species. It is also highly likely that in a few lakes, some species, such as *Iris*
487 *pseudacorus*, have been deliberately moved to these lakes for ornamental plants. One, somewhat
488 challengingly measurable, factor has also been the introduction and dispersal of the non-native
489 muskrat (*Ondatra zibethicus*) to this area. The dynamics of muskrat populations have probably caused
490 changes in plant species abundances due to the grazing and housing behaviour of these aquatic

491 mammals. Especially, muskrats have impacted dominant plant species, for example, by preferential
492 grazing on *Schoenoplectus lacustris*, *Equisetum fluviatile* and *Nymphaea alba* ssp. *candida*, which
493 again have contributed to the increase of *Phragmites australis*, *Nuphar lutea* and, particularly, *Typha*
494 *latifolia* in these lakes (Toivonen and Meriläinen 1980). In addition, the nesting and feeding habits of
495 muskrats create patches to vegetation, thereby creating different successional stages and increasing
496 the number of small helophytes and other weak competitors. This might be one reason for the gain of
497 species from the 1940s to the 1970s. After the 1980s, muskrat population sizes have decreased in this
498 area (Toivonen and Meriläinen 1980). However, these changes are not visible in the absence-presence
499 plant data, but these might be the reason behind the variation in temporal losses and gains of species
500 across the landscape (hypothesis 3).

501

502 Furthermore, in 2017, the spring and early summer were relatively cold, and the thermal growing
503 season was slightly late compared to the situation in the 2000s sampling period (Finnish
504 Meteorological Institute 2020a, b). This can be one reason why the loss of species was prominent in
505 the lakes from the 2000s to the latest sampling period. Late-maturing plant species that are
506 challenging to identify in their early phases were not necessarily properly developed during the field
507 work, including *Sparganium* species or some small helophytes (e.g. *Eleocharis acicularis*,
508 *Alopecurus aequalis*). It is thus possible that one exceptional year can hinder detecting overall long-
509 term trends in changes of community composition. Because of this issue, we are reluctant to make
510 further conclusions on the patterns detected between the 2000s and the 2010s.

511

512 Despite the ecological stressors in the study lakes, one reason for the small changes in the TBIs can
513 be the high ecological resilience of the lakes (Holling 1973), which is in accordance with the idea that
514 species can keep pace with the changes in the environment (for lakes, see a review by Heino et al.
515 2020). Connectivity is essential for the resilience of freshwater biota and environments (Heino et al.

2017). Our study lakes have high connectivity to other small lakes and, more importantly, to the two largest water bodies in the area, lakes Roine and Pyhäjärvi (Fig. S1), which can act as colonization sources for aquatic plant species. Because of the high dispersal ability of aquatic plants by seed and vegetative propagules and owing to flexible reproductive systems (Eckert et al. 2016), spatial connectivity might enhance the landscape-level ecological resilience (Allen et al. 2016). Also, due to high phenotypic plasticity, both morphological and ecological (Lacoul and Freedman 2006), aquatic plant species can probably adapt to modest changes in the environment (Lindholm et al. 2020c). This issue combined with multiple interacting lake-scale stressors, the complex community-environment relationships and stochastic processes might also explain why the environmental variables in our models cannot explain variation in the TBI between the 1940s and the 1970s. In addition, when the possible effects of climate change (temporary warming in the 1930s and current warming trend) are added to the list of these factors, a multidimensional puzzle is created (Heino et al. 2009).

528

Limitations of temporal studies and future study needs

The main limitation of temporal biodiversity studies is the lack of appropriate long-term datasets (Magurran et al. 2019) and problems with the quality of existing temporal datasets (Dornelas et al. 2013). The most common limitations of temporal studies are related to temporal extent, as long time series are often unavailable. Our dataset covers a wide temporal extent, including five different decades, but we still are unaware whether major changes have taken place between the specific survey periods (e.g., during the 1960s or the 1980s). In addition, as the baseline in our study was the 1940s, the full range of impacts of major anthropogenic pressures are probably underestimated (Mihoub et al. 2017) due to already existing human impacts in some of the study lakes. Too few sampling points in time can also limit interpretations, as our results showed that one exceptional year regarding weather conditions can hinder detecting overall long-term trends in changes of community composition. As climate change has been predicted to cause more extreme weather conditions

541 (Seneviratne et al. 2012), this issue may become even more relevant in the future and affect studies
542 based on only a single field season. Moreover, if we had looked only at the first (1940s) and the last
543 (2010s) survey decades, we might have thought that both temporal losses and gains of species had
544 been equally present. However, inspecting the different decades between this 70-year long time
545 period, we gained a more detailed picture of temporal beta diversity patterns. These issues further
546 highlight the fact that relying only on one or two survey points in time can result in limited knowledge
547 of the ecological phenomenon under study.

548

549 A general issue in temporal studies is sampling variation, as long time series of replicated surveys are
550 quite rare (Magurran 2011). It is possible that there is some sampling variation between the surveys
551 done in the 1940s and those in the other decades. Thus, it is possible that changes in temporal beta
552 diversity may be due to this sampling variation to some extent. Closely related to sampling variation
553 is the precision of data. We focused on presence-absence data, as with historical datasets focusing on
554 the whole lake area, presence-absence data are a more reliable source of information compared to
555 coverage information representing abundance. However, using only binary coefficients, i.e., those
556 based on presence-absence data, instead of quantitative forms of the indices can also produce less
557 sensitive results (Legendre 2014). Also, Hillebrand et al. (2018) stated that we cannot rely only on
558 presence-absence data. Also, it is likely that there have been changes in a species' abundance long
559 before this species is completely lost from the site. Ot'ahel'ová et al. (2011) found that during a 34-
560 year time period, aquatic plant species richness did not change much in floodplain lake ecosystems,
561 although the abundance of aquatic plants fluctuated over the years. Therefore, using abundance data
562 would reveal a more detailed picture of temporal ecological change.

563

564

565

566 **Conclusion**

567

568 There is an urgent need for information on how biodiversity is changing in time. In addition, to
569 comprehensively understand the impact of anthropogenic activities on biodiversity, we must
570 understand how biodiversity has changed over time and what are the underlying processes. In
571 conclusion, we found that the temporal change in aquatic plant communities has been modest through
572 decades, as the main changes occurred from the 1940s to the 1970s due to the temporal gain of
573 species. Nevertheless, it seems that even relatively modest changes in the environment seem to be
574 affecting temporal gains of species and losses of species at the lake level. For example, aquatic plant
575 species seem to benefit from the decrease in agricultural area with declining nutrient inputs in small
576 boreal lakes. In addition, our results showed that relying only two survey points in time can result in
577 limited knowledge of the ecological phenomenon under study, and an exceptional year in terms of
578 weather conditions can mask overall long-term trends in compositional changes, especially under the
579 ongoing climate change. Thus, future studies should try to utilize data from several decades to
580 overcome the limitations of temporal information (Dornelas et al. 2019).

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Tables and Figures

Table 1. Summary of results of beta regression analyses. This table shows the estimates, the standard errors, z-values of these coefficients and their significance. Response variable = Temporal beta diversity index (TBI) between survey decade pairs. Explanatory variables = Elevation from earlier decade, other variables are representing the change from earlier decade to a later one (calculated by subtracting the earlier decade's values from the later decade's values (i.e. 1970-1940)). *P<0.05, **P<0.01, ***P<0.001. Pseudo R² = maximum likelihood coefficients of determination were obtained through an iterative process.

		Estimate	Std. error	z	p	AIC	Pseudo R ²	Log- likelihood	p
1940– 1970	Intercept	-2.352	1.198	-1.964	0.050*	-49.135	0.090	32.568	0.823
	Elevation (m)	0.006	0.010	0.597	0.550				
	pH	-0.052	0.231	-0.223	0.823				
	Water transparency (m)	0.132	0.225	0.586	0.558				
	Agriculture (%)	0.004	0.032	0.112	0.911				
	Built area (%)	0.145	0.292	0.498	0.619				
	Ditches	0.288	0.199	1.450	0.147				
1970– 1990	Intercept	-0.741	1.632	-0.454	0.650	-123.450	0.367	69.725	<0.001***
	Elevation (m)	-0.009	0.013	-0.682	0.495				
	pH	-2.513	0.842	-2.984	0.003**				
	Water transparency (m)	-0.917	0.286	-3.205	0.001**				
	Agriculture (%)	-0.068	0.033	-2.055	0.040*				
	Built area (%)	0.900	0.273	3.298	<0.001***				
	Ditches	-0.919	0.363	-2.528	0.0115*				
1990– 2000	Intercept	-0.403	1.114	-0.362	0.718	-65.578	0.121	40.789	0.029*
	Elevation (m)	-0.022	0.010	-2.113	0.035*				
	pH	-1.136	0.591	-1.923	0.055				
	Water transparency (m)	-0.097	0.223	-0.437	0.662				
	Agriculture (%)	-0.027	0.035	-0.764	0.445				
	Built area (%)	-0.610	0.400	-1.525	0.127				
	Ditches	0.339	0.178	1.907	0.057				
2000– 2010	Intercept	-0.936	1.952	-0.480	0.632	-81.101	0.359	48.550	<0.001***
	Elevation (m)	-0.005	0.020	-0.257	0.797				
	pH	2.800	1.215	2.304	0.021*				
	Water transparency (m)	1.302	0.590	2.209	0.027*				
	Agriculture (%)	-0.250	0.103	-2.436	0.015*				
	Built area (%)	-0.604	0.669	-0.904	0.366				
	Ditches	0.751	0.578	1.299	0.194				
1940– 2010	Intercept	-0.323	0.689	-0.468	0.640	-58.215	0.389	37.108	0.055
	Elevation (m)	-0.007	0.006	-1.081	0.280				
	pH	-0.326	0.161	-2.028	0.043*				
	Water transparency (m)	-0.265	0.132	-2.012	0.044*				
	Agriculture (%)	0.013	0.007	1.817	0.069				
	Built area (%)	0.005	0.075	0.071	0.943				
	Ditches	-0.047	0.072	-0.662	0.508

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783 **Figure 1.** Changes in vascular aquatic plant community compositional dissimilarity (D) and its gain
 784 and loss components between the survey pairs of decades: the 1940s and the 1970s, the 1970s and
 785 the 1990s, the 1990s and the 2000s, and the 2000s and the 2010s. B/den represent losses and C/den
 786 gains of species

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Figure 2. Maps showing the location of the study area and the lakes (N=27) studied and the losses (B/den statistics) and gains (C/den statistics) computed from the species occurrence data between the aquatic plant surveys. The sizes of the points are proportional to the TBI indices (Sørensen D). The plus (+) sign indicates that the gains of species is dominated and minus (-) signs the loss of species. Names of the lakes can be found from Table S3

Fig. 3. B-C plots representing the species losses (B) and gains (C) between survey pairs of decades.

a) 1940s–1970s, b) 1970s–1990s, c) 1990s–2000s, d) 2000s–2010s, e) 1940s–2010s. Names of the lakes can be found in Table S3. Lakes are coloured by elevation of 100 m. a. s. l. The sites are

800 represented by symbols corresponding to where the loss of species (triangle) and gain of species
801 (square) has been dominant. The green line represents the theoretical positions of sites where gains
802 would equal losses. The red line has been drawn parallel to the green line and passing through the
803 centroid of all points. Its position above the green line indicates that, on average, species gains
804 dominated over losses from the 1940s to the 1970s (a). The red line below the green line indicates
805 species losses from the 2000s to the 2010s (d)

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807 **Fig 4.** Canonical ordination plot obtained by using dbRDA on the aquatic plant data from the five
 808 decades and 27 sites, constrained by a factor representing the five survey decades. The lakes (open
 809 circles) for each decade are surrounded by 60 % coverage ellipses