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1 Impact of recreational fisheries management on fish biodiversity in gravel pit lakes
2 with contrasts to unmanaged lakes

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19

20 **Abstract**

21 Gravel pit lakes constitute novel ecosystems that can be colonized by fishes through
22 natural or anthropogenic pathways. Many of these man-made lakes are used by
23 recreational anglers and experience regular fish stocking. Recreationally unmanaged
24 gravel pits may also be affected by fish introductions, e.g., through illegal fish
25 releases, thereby contributing to the formation of site-specific communities. Our
26 objective was to compare the fish biodiversity in gravel pit lakes with and without the
27 recent influence of recreational fisheries management. We sampled 23 small (< 20

28 ha) gravel pit lakes (16 managed and 7 unmanaged) in north-western Germany and
29 compared fish community and diversity metrics obtained using littoral electrofishing
30 and multimesh gillnet catch per unit effort data. Given the size of the lakes we
31 sampled we expected species poor communities and elevated fish diversity in the
32 managed systems due to stocking. The two lake types were primarily mesotrophic
33 and did not differ in key abiotic and biotic environmental characteristics. Both lakes
34 types hosted similar fish abundance and biomass, but were substantially different in
35 terms of the fish community structure and species richness. Fish were present in all
36 lakes with at least three species. We discovered a higher α -diversity and a lower β -
37 diversity in managed gravel pit lakes compared to unmanaged lakes. Thus,
38 recreational fisheries management appeared to foster homogenization of fish
39 communities, likely because fisheries managers stock these lakes with desired fish
40 species (e.g., piscivorous fishes and large bodied cyprinids). However, we also
41 detected anthropogenic pathways in the colonization of unmanaged gravel pit lakes,
42 presumably from illegal releases by private people. Importantly, hardly any non-
43 native species were detected in the gravel pits we studied, suggesting that
44 recreational fisheries management not necessarily promotes the spread of exotic
45 species.

46 Key words:

47 Fish conservation; novel ecosystems; non-native species; fish stocking; recreational
48 fishing; fish community composition

49

50 **Significance Statement**

51 Little is known about fish communities in artificially created gravel pit lakes. We
52 compared those managed by recreational fishers with those lacking fisheries
53 management in north-western Germany. We found fishes in all gravel pit lakes and
54 demonstrated a higher α -diversity but more homogenized fish communities in
55 managed gravel pit lakes compared to unmanaged lakes. We did not detect the
56 establishment of relevant abundances of non-natives fishes despite intensive
57 fisheries management.

58

59 **1. Introduction**

60 Freshwater ecosystems have been strongly altered by humans (Dodds *et al.*, 2013).
61 While rivers in the temperate regions have experienced substantial biotic
62 homogenization and habitat loss (Vörösmarty *et al.*, 2010), lakes have mostly
63 suffered from eutrophication, pollution and climate change (Brönmark & Hansson,
64 2002). Moreover, invasions by non-native species have locally and regionally
65 become an important threat for freshwater ecosystems (Rahel, 2007). Today,
66 freshwater biodiversity is declining at an alarming rate with 37% of Europe's
67 freshwater fish species categorized as threatened (Freyhof & Brooks, 2011). Habitat
68 loss has been identified as one of the main stressor that impacts biodiversity
69 (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010). When properly managed
70 (Lemmens *et al.*, 2013), novel aquatic ecosystems, such as gravel pit lakes (i.e.,
71 lentic water bodies created by human use of sand, clay, gravel and other natural
72 resources), reservoirs and ponds, can counteract the freshwater biodiversity crisis by
73 creating secondary habitats for colonization and refuges in the case natural
74 ecosystems deteriorate (Dodson *et al.*, 2000; Santoul *et al.*, 2004, 2009; De Meester
75 *et al.*, 2005; Völkl, 2010; Emmrich *et al.*, 2014; Zhao *et al.*, 2016; Biggs *et al.*, 2017).

76 Gravel pits are often groundwater-fed and not necessarily connected to surrounding
77 river systems (Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Søndergaard
78 *et al.*, 2018); they thus display the interesting biogeographic feature of islands in a
79 landscape (Olden *et al.*, 2010). This characteristic causes a slow colonisation and a
80 potentially low species richness (Magnuson *et al.*, 1998).

81 In 2014, sand and gravel were extracted from over 28.000 quarries and pits in
82 Europe (UEPG, 2017) resulting in small and isolated gravel pit lakes as common
83 landscape elements in industrialized countries (Blanchette & Lund, 2016; Mollema &
84 Antonellini, 2016; Søndergaard *et al.*, 2018). In Lower Saxony, Germany, more than
85 37,000 gravel pit lakes smaller than 20 ha exist, and they cover about 70% of all
86 lentic habitats in this region (Manfrin, unpublished data). The fish species richness in
87 natural lakes in northern Germany has been found to be a function of areal size with
88 more species occurring in larger lakes due to higher habitat diversity (Eckmann,
89 1995). Thus, due to their normally small size below 50 ha, their recent origin after the
90 Second World War within the scope of further industrialization and often isolated
91 location, gravel pit lakes can also be naturally assumed to contain species-poor fish
92 communities, and when newly created may even lack fish populations at all (Scheffer
93 *et al.*, 2006; Søndergaard *et al.*, 2018).

94 There are several natural pathways for colonization of fishes in gravel pit lakes.
95 When connected with a river fishes can easily colonize these lakes (Molls &
96 Neumann, 1994; Staas & Neumann, 1994; Borcharding *et al.*, 2002). However, the
97 chances of fishes to colonize isolated, recently formed water bodies are low (Scheffer
98 *et al.*, 2006; Strona *et al.*, 2012). Natural colonization is then confined to rare events
99 like massive floods (Pont *et al.*, 1991; Olden *et al.*, 2010) or wind-based dispersal
100 through hurricanes (Bajkov, 1949). Another mean could be passive dispersal of eggs

101 through waterfowl. However, despite frequent claims, this introductory pathways has
102 not been documented with certainty (Hirsch *et al.*, 2018). Thus, it is likely that natural
103 colonization of isolated gravel pit lakes is a very slow process, potentially resulting in
104 species-poor fish communities (i.e., low α -diversity) and high among lake variation in
105 the species pool (i.e., high β -diversity) within a region (Whittaker, 1972; Baselga,
106 2010).

107 Human-induced processes like fish introductions, continuous fish stocking or
108 aquarium and bait bucket releases represent an anthropogenic pathways of
109 colonizing human-made freshwater systems (Copp *et al.*, 2010; Gozlan *et al.*, 2010;
110 Olden *et al.*, 2010; Hirsch *et al.*, 2018). In central Europe, by far the majority of gravel
111 pit lakes are managed by recreational anglers organized in clubs and associations
112 (Deadlow *et al.*, 2011). Managers of angling clubs and other fisheries stakeholders
113 regularly engage in fish stocking in lakes and rivers (Cowx, 1994), and this includes
114 gravel pit ecosystems (Arlinghaus, 2006; Arlinghaus *et al.*, 2015; Zhao *et al.*, 2016;
115 Søndergaard *et al.*, 2018). Moreover, illegal releases of garden ponds or aquaria
116 fishes represent the most common pathway of non-native fish dispersal in many
117 areas of the world (Copp *et al.*, 2010; Gozlan *et al.*, 2010; Olden *et al.*, 2010; Patoka
118 *et al.*, 2017) and may thus be widespread in gravel pits as well. Regular stocking may
119 increase α -diversity but reduce β -diversity through the process of biotic
120 homogenization (Radomski & Goeman, 1995; Rahel, 2000, 2002), particularly when
121 fisheries managers stock a common mix of highly desired species (e.g., top
122 predators, Eby *et al.*, 2006). A recent comparison of French gravel pit lakes indeed
123 revealed that the fish community composition was influenced by recreational angling
124 as managed gravel pit lakes hosted more non-native species of high fisheries value,

125 particularly top predators and common carp *Cyprinus carpio* L. compared to
126 unmanaged gravel pit lakes (Zhao *et al.*, 2016).

127 The objective of the present study was to compare the fish communities between
128 angler-managed and unmanaged gravel pit lakes in north-western Germany. We
129 hypothesized that recreational fisheries management would increase (1) species
130 richness, i.e. α -diversity, (2) the number of piscivorous and other highly desired
131 “game” species and (3) the number of non-native species, such as rainbow trout
132 *Oncorhynchus mykiss* (Walbaum 1792) and topmouth gudgeon *Pseudorasbora*
133 *parva* (Temminck & Schlegel 1846). We further hypothesized that the lakes managed
134 by anglers host more similar fish communities compared to the unmanaged lakes,
135 thereby hypothesizing that (4) recreational fisheries management decreases β -
136 diversity through biotic homogenization.

137

138 **2. Material and Methods**

139 2.1 Study lakes and fish sampling

140 We surveyed the fish communities and a range of limnological lake descriptors in 23
141 gravel pit lakes located in the lowlands of Lower Saxony, north-western Germany in
142 the Central Plain ecoregion (Fig. 1). For each lake, two ages were determined, the
143 start and the end of gravel mining, as gravel pits start filling up with water and
144 potentially become colonized by fishes already before the end of mining. The depth
145 was measured hydro-acoustically using a Hummingbird Sonar (Type 788ci) in
146 parallel transects spaced about 30 m apart. These data were used to calculate
147 contour maps using ordinary kriging in R (for further details see Supplementary of
148 Monk & Arlinghaus, 2017). The contour maps were used to extract key morphometric
149 variables of the lake (mean depth, maximum depth, shoreline length and area),

150 including estimation of areas covered by different depth strata according to the CEN
151 standard (2015) for the sampling of lake fish communities with multimesh gillnets (0 -
152 2.9 m, 3 - 5.9 m, 6 – 11.9 m, 12 – 19.9 m and 20 – 34.9 m). These data were also
153 used for the calculation of the shoreline development factor (Osgood, 2005) and the
154 extension of the littoral zone (defined as area between 0 and 2.9 m depth). We
155 mapped macrophytes in summer during full vegetation with a Simrad NSS7 evo2
156 echosounder with a Lowrance TotalScan Transducer in parallel transects spaced
157 about 30 m apart, similar to the contour maps. Macrophyte coverage and average
158 height were calculated by kriging using a commercial software (Winfield *et al.*, 2015;
159 Valley, 2016; www.gofreemarine.com/biobase/).

160 The fish communities were sampled using day-time electrofishing in the littoral
161 and multimesh gillnets in the benthic and profundal zones in autumn 2016 and 2017.
162 During each fish sampling campaign, the lake's Secchi depth, conductivity and pH-
163 value were measured. In addition, at the deepest point of the lake an oxygen-depth-
164 temperature profile was taken in steps of 50 cm using a WTW Multi 350i sensor,
165 WTW GmbH, Weilheim, Germany, and epilimnic water samples were taking for
166 analyzing total phosphorus concentrations (TP) and chlorophyll a (Chl a). In the
167 laboratory TP was determined using the molybdenum blue method (ISO, 2004;
168 Zwirnmann *et al.*, 1999) and Chl a was determined using high performance liquid
169 chromatograph (Mantoura & Llewellyn, 1983; Wright *et al.*, 1991).

170 Littoral electrofishing was conducted from a boat by a two person crew using a
171 FEG 8000 electrofishing device (8,0 kW; 150 - 300V / 300 - 600V; EFKO
172 Fischfanggeräte GmbH Leutkirch) with one anodic hand net (40 cm diameter and
173 mesh size 6 mm) and a copper cathode. Prior to sampling the shoreline was divided
174 in transects measuring between 50 and 120 m depending on the available shoreline
175 habitat. Shoreline habitats covered reeds, overhanging trees and branches,

176 submersed and emersed macrophytes, unvegetated littoral zones with no or low
177 terrestrial vegetation (in particular representing angling sites) and mixed habitats that
178 were not dominated by one of these structures. Each transect was sampled
179 separately. The number of transects varied between 4 and 27, depending on the lake
180 size. The length of all transects summed up to the whole lake shore except for the
181 two largest lakes where in total only about two thirds of the shoreline were fished
182 using random selection of transects. Littoral electrofishing was conducted in 16
183 managed and 4 unmanaged lakes in autumn 2016 (late August to early October
184 when the epilimnion temperature was $> 15^{\circ}\text{C}$) and multimesh gillnets were set
185 overnight for approximately 12 hours following CEN (2015). An additional
186 electrofishing sampling of the entire shoreline was carried out in autumn 2017 (late
187 August to mid-October). Additionally, in autumn 2017 three further unmanaged gravel
188 pit lakes (for a total sample of seven unmanaged lakes) were sampled by littoral
189 electrofishing of the whole shoreline and multimesh gillnets following the same
190 procedure as in 2016. Electrofishing data were standardized by meter shoreline
191 fished for estimation of lake-wide catch per unit effort data as relative abundance
192 index.

193 The multimesh gillnets differed slightly from the CEN standard (Appleberg,
194 2000; CEN, 2015) in a way that we used nets with four additional mesh sizes to
195 attempt to also representatively capture large fishes up to 530 mm total length
196 (Šmejkal *et al.*, 2015). The benthic gillnets had a length of 40 m, a height of 1.5 m
197 and were composed of 16 mesh-size panels each being 2.5 m long with mesh sizes
198 of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55, 70, 90, 110 and 135 mm. For
199 lakes < 20 ha the European gillnet sampling standard (CEN, 2015) considers a
200 minimum of 8 or 16 gillnets, depending on whether the maximum depth is below or
201 exceeds 12 m, respectively. Using such a fixed minimum number of nets would

202 strongly bias the fishing pressure in the substantially smaller systems that we
203 sampled, i.e., with 8 nets the encounter probabilities of a fish with a net would be
204 much higher in a small system of, say, 1 ha, compared to a larger ecosystem of 20
205 ha. This would bias the lake-wide CPUE estimates. Therefore, we adapted the
206 number of gillnets set in each lake by applying the minimum number of 16 standard
207 gillnets to the largest lake in our sample (Meitzer See), which is 19.6 ha and has a
208 maximum depth of 23.5 m. These dimensions are close to the smallest lake size of a
209 deep lake in the CEN standard of 20 ha. For this reference lake, we estimated the
210 quotient of area of the 16 gillnets to total lake area as a measure of “gillnet pressure”.
211 Using this target we calculated the appropriate gillnet numbers in smaller lakes to
212 achieve the same “gillnet pressure” in each lake.

213 The final number of gillnets set in each lake were distributed following a
214 stratified sampling design by depth strata, where number of gillnets by stratum were
215 set in proportion of the share of each depth stratum’s area to total lake surface area
216 (CEN, 2015). Gravel pit lakes with an area larger than 10 ha or a maximum depth of
217 ≥ 10 m were additionally sampled with pelagic multimesh gillnets to record open
218 water species not captured otherwise (CEN, 2015). One pelagic multimesh gillnet
219 was set in each of the following vertical depth strata: 0 - 1.5 m, 3 – 4.5 m, 6 – 7.5 m,
220 9 - 10.5 m and 12 – 13.5 m, but only if the depth strata contained >1 mg O₂ L⁻¹. Note
221 the pelagic gillnets were only used to complete the species inventory (presence-
222 absence data) as recommended in the CEN standard (CEN, 2015), but not used for
223 the lake wide fish abundance and biomass estimates. Lake-wide biomass and
224 abundance estimates were estimated as stratified means per area and night fished
225 as recommended by CEN (2015).

226 Total length of the fishes that were captured by electrofishing and gillnetting
227 were measured to the nearest mm and the weight was to the nearest g. In case of

228 higher sample sizes, at least 10 fish per species and 2 cm length class were
229 measured and weighted. Afterwards fishes were only measured and the weight was
230 calculated with length-weight regressions from that specific lake. Only in rare case of
231 catching several hundreds of 0+ fish by electrofishing, a subsample was measured
232 and weighted. Afterwards all the other fish were weighted together and the number
233 and length-frequency distribution of the whole sample was calculated using the
234 length-frequency distribution of the subsample.

235

236 2.2 Fish community descriptors

237 For all calculations and analyses, data from 2016 and 2017 were pooled. This results
238 in electrofishing data in 20 lakes from two years and in three lakes from only one
239 year. Furthermore, data from one autumn sampling per lake with multimesh gillnets
240 were analyzed.

241 Species richness, number of piscivorous species, number of small-bodied
242 non-game fish (after Emmrich *et al.*, 2014), number of threatened species (after the
243 Red List of Lower Saxony (LAVES, 2011), the Red List of Germany (Freyhof, 2009)
244 and the European Red List (Freyhof & Brooks, 2011)) and number of non-native
245 species (after Wiesner *et al.*, 2010 and Wolter & Röhr, 2010) were calculated to
246 describe the lake fish community based on electrofishing (littoral zone) and
247 multimesh gillnet data (benthic and for species richness also the pelagic zone). Perch
248 *Perca fluviatilis* (L.) > 150 mm and eel *Anguilla anguilla* (L.) > 500 mm total length
249 were accounted to the piscivorous fish guild, following Emmrich *et al.* (2014).
250 Cyprinid hybrids were listed as fish caught in the gravel pit lakes (Table 1), but
251 excluded from further analyses of species-specific patterns.

252 Species richness was used to compare the α -diversity between the lake types.
253 The number of piscivorous species was used as a fish community descriptor as

254 anglers prefer to catch predatory fishes and regularly stock those (Arlinghaus *et al.*
255 2015). We also assessed the number of small-bodied non-game fish species as
256 many of these species are relevant in a conservation context. Also, many small-
257 bodied species are pioneer colonizer of lakes, e.g. sunbleak *Leucaspius delineates*
258 (Heckel 1843) (Kottelat & Freyhof, 2007). The number of threatened species was
259 contrasted between the two lake types to assess the potential impact of fisheries
260 management on fish conservation objectives. Furthermore, the number of non-native
261 species was compared among lake types, as fish stocking is believed to promote the
262 spread of exotic fishes, particularly in gravel pit lakes (Zhao *et al.*, 2016;
263 Søndergaard *et al.*, 2018).

264 To compare the relative fish abundance and the abundance-based community
265 descriptors (piscivorous species, small-bodied non-game fish species, threatened
266 species, non-native species) as well as the Shannon diversity index (Shannon, 1948)
267 between the two lake types the mean lake-specific catch per unit effort (CPUE) with
268 individuals per shoreline length (N / 50 m) or gillnet area (N / 100 m²) was used
269 (number per unit effort, NPUE). CPUE data regarding the biomass per shoreline
270 length (g / 50 m) or gillnet area (N / 100 m²) were also calculated (biomass per unit
271 effort, BPUE). As NPUE data can be affected by the catch of a school of small fishes
272 and BPUE can be affected by the catch of single, large individuals, both calculations
273 were used in the analysis to provide a complete picture. In addition to species
274 numbers, NPUE and BPUE data from electrofishing and gillnetting as well as the
275 Shannon index were used to assess the fish biodiversity and community composition
276 between the two lake types.

277

278 2.3 Statistical analysis

279 To test for mean differences between the two lake types regarding the limnological
280 lake characteristics and the biodiversity descriptors of the fish community, a Welch
281 two sample t-test was conducted when raw variables or log₁₀-transformed variables
282 were normally distributed and showed homogeneity of variances. In all other cases, a
283 Wilcoxon rank sum test was performed.

284 Following Anderson *et al.* (2011), the β -diversity of the fish communities in managed
285 and unmanaged gravel pit lakes was visualized by non-metric multidimensional
286 scaling (nMDS; Kruskal, 1964) using Bray-Curtis distances on both species number
287 and abundance data. Afterwards a permutation test for homogeneity of multivariate
288 dispersions (permutations: N=9999) was performed to test for significant differences
289 in the fish community composition. With a similarity percentage analysis (SIMPER;
290 permutations: N=999; Clarke, 1993), the species strongly contributing to the average
291 dissimilarity between the two lake types were identified. All statistical analyses were
292 conducted using R version 3.2.2 (R Core Team, 2016) and the package *vegan*
293 (Oksanen *et al.*, 2018).

294

295 **3. Results**

296 Managed gravel pit lakes varied between 1.0 and 19.6 ha in size with a shoreline
297 length ranging from 415 to 2660 m; unmanaged gravel pit lakes ranged from 2.2 to
298 11.4 ha in size and varied between 727 and 2060 m in shoreline length. The two lake
299 types did not differ statistically in any morphological variable (Fig. 2): area (Welch two
300 sample t-test, $t = 0.728$; $p = 0.476$), shoreline length (Welch two sample t-test, $t =$
301 0.706 ; $p = 0.490$), shoreline development factor (Wilcoxon rank sum test, $W = 53.5$; p
302 $= 0.867$), mean depth (Welch two sample t-test, $t = 0.496$; $p = 0.635$), maximum
303 depth (Wilcoxon rank sum test, $W = 58$; $p = 0.922$) and share of the littoral (Welch
304 two sample t-test, $t = -0.748$; $p = 0.471$). While a difference in lake age in terms of

305 start of mining was detected (managed: 43.4 ± 8.7 a (mean \pm SD); unmanaged: 30.4
306 ± 9.7 a (mean \pm SD); Welch two sample t-test, $t = 3.03$, $p = 0.012$), no differences
307 were detected for the lake age at the end of mining (managed: mean = 29.4 ± 12.4 a
308 (mean \pm SD); unmanaged: mean = 21.6 ± 11.5 a (mean \pm SD); Welch two sample t-
309 test, $t = 1.475$, $p = 0.165$). Furthermore, no differences among lake types were
310 detected for the variables reflecting lake productivity: total phosphorus (TP; Welch
311 two sample t-test, $t = -0.285$, $p = 0.781$), chlorophyll a (Chl a; Welch two sample t-
312 test, $t = -1.433$, $p = 0.181$) and Secchi depth (Welch two sample t-test, $t = 0.530$, $p =$
313 0.608). The relatively low mean values of TP and Chl a indicated that the lakes were
314 predominantly mesotrophic. The two lake types also, on average, did not differ in
315 conductivity (Welch two sample t-test, $t = 0.903$, $p = 0.388$) and pH-value (Welch two
316 sample t-test, $t = -0.920$, $p = 0.383$). Macrophyte data revealed no differences
317 between the lakes types regarding macrophyte coverage (Welch two sample t-test, t
318 $= 0.916$, $p = 0.382$), however, the macrophyte height was larger in managed gravel pit
319 lakes (Welch two sample t-test, $t = 2.471$, $p = 0.036$).

320 In total 117,214 fishes were sampled, 108,148 individuals by electrofishing
321 and 9,066 by gillnetting. The fish community in the 23 gravel pit lakes consisted of 23
322 fish species and one hybrid (Table 1). All lakes contained at least three fish species.
323 *Perca fluviatilis* and roach *Rutilus rutilus* (L.) were found in all managed lakes, while
324 they were present in less than a third of the unmanaged lakes. Piscivorous species
325 such as pike *Esox Lucius* L., *Anguilla anguilla* and pikeperch *Sander lucioperca* (L.)
326 were also regularly found in managed, but only occasional or not at all in unmanaged
327 gravel pit lakes (Table 1). Littoral species, such as *Esox lucius*, *Anguilla anguilla* and
328 tench *Tinca tinca* (L.), were mainly or even exclusively caught by electrofishing, while

329 large individuals of less littoral-bound species such as *Perca fluviatilis* and *Rutilus*
330 *rutilus* as well as *Sander lucioperca* were better detected by gillnetting.

331 Of the 23 species, *Anguilla anguilla*, *Sander lucioperca*, ruffe *Gymnocephalus cernua*
332 (L.), white bream *Blicca bjoerkna* (L.), bitterling *Rhodeus amarus* (Bloch 1782),
333 European whitefish *Coregonus lavaretus* (L.), spined loach *Cobitis taenia* L. and
334 bleak *Alburnus alburnus* (L.) were only caught in managed gravel pits, while
335 sunbleak *Leucaspinus delineates* (Heckel 1843), nine-spined stickleback *Pungitius*
336 *pungitius* (L.), gudgeon *Gobio gobio* (L.), stone loach *Barbatula barbatula* (L.) and
337 brown bullhead *Ameiurus nebulosus* (Lesueur 1819) only occurred in unmanaged
338 gravel pits. However, non-native *Ameiurus nebulosus* was only detected as a single
339 individual.

340 On average, the species richness (Welch two sample t-test, $t = 7.61$, $p < 0.001$),
341 number of piscivorous species (Wilcoxon rank sum test, $W = 111$, $p < 0.001$) and
342 number of threatened species (Wilcoxon rank sum test, $W = 110$, $p < 0.001$) were
343 significantly higher in managed gravel pit lakes compared to unmanaged ones (Fig.
344 3). No differences between the two lake types were found in the number of small-
345 bodied non-game fish species (Wilcoxon rank sum test, $W = 37$, $p = 0.179$) and the
346 number of non-native species (Wilcoxon rank sum test, $W = 43.5$, $p = 0.153$).
347 However, in total, only four individual non-native fishes were caught, three specimens
348 of *Pseudorasbora parva* and one specimen of *Ameiurus nebulosus*. The Shannon
349 index revealed an overall greater diversity for the littoral fishes in terms of both
350 abundance and biomass (NPUE and BPUE) and for the whole lake fish community
351 biomass estimate (BPUE) in managed gravel pit lakes compared to unmanaged ones
352 (Table 2).

353 Significantly greater abundances (both NPUE and BPUE for both gear types) were
354 found for piscivorous fishes in managed gravel pit lakes compared to unmanaged
355 lakes (Table 2). By contrast, significantly larger abundances and biomasses of small-
356 bodied non-game fishes were detected in unmanaged gravel pit lakes compared to
357 managed ones, but only in the littoral community sampled by electrofishing. For
358 threatened species (*Anguilla anguilla*, *Esox lucius*, European catfish *Silurus glanis* L.,
359 *Rhodeus amarus* and *Cobitis taenia*) higher littoral abundances (NPUE and BPUE,
360 respectively) were detected in managed lakes compared to unmanaged lakes. Only
361 four non-native individuals were caught in the littoral by electrofishing and none by
362 multimesh gillnets, meaning that the abundance and biomass of non-natives
363 bordered detectability and accordingly did not differ among lake types.

364 To investigate differences of the gravel pit fish communities regarding β -diversity,
365 nMDS biplots were constructed by fishing gear using presence-absence data
366 (Appendix) and using abundance and biomass data (NPUE and BPUE; Fig. 4).
367 Permutation tests revealed significantly greater β -diversity for the littoral (NPUE: $F =$
368 6.615 , $p = 0.017$; BPUE: $F = 11.886$, $p = 0.002$) and benthic fish community (NPUE:
369 $F = 13.595$, $p = 0.001$; BPUE: $F = 10.106$, $p = 0.005$) in unmanaged gravel pit lakes
370 compared to managed lakes. These differences were revealed by all three means of
371 assessing the fish community (presence-absence, abundance and biomass).

372 *Leucaspinus delineatus*, *Perca fluviatilis*, rudd *Scardinius erythrophthalmus* (L.) and
373 *Pungitius pungitius* contributed 74.6% to the difference between the two lake types in
374 the littoral fish community assessed using electrofishing abundance data (NPUE;
375 Table 3). *Leucaspinus delineatus* and *Pungitius pungitius* were not detected in
376 managed gravel pit lakes, and their contribution to differences in the littoral fish
377 community among lake types was significant (*Leucaspinus delineatus*: $p = 0.014$,

378 *Pungitius pungitius*: $p = 0.013$). In terms of littoral fish biomass (electrofishing BPUE
379 data), *Anguilla anguilla*, Prussian carp *Carassius gibelio* (Bloch 1782) and *Esox*
380 *lucius* contributed most to the difference between the two lake types, but due to high
381 among lake variation in biomass for these species only littoral *Perca fluviatilis*
382 biomass significantly differentiated among managed and unmanaged gravel pit lakes
383 ($p = 0.037$) revealing significantly greater biomasses in managed lakes.

384 When taking the multimesh gillnet data (NPUE and BPUE) as metrics of whole lake
385 fish community descriptors, *Perca fluviatilis* and *Rutilus rutilus* revealed the highest
386 contribution to the difference in the fish community between the two lake types
387 (significant for *Perca fluviatilis*, $p = 0.020$ with higher whole-lake biomasses found in
388 managed gravel pit lakes). Furthermore, the whole-lake biomass of *Scardinius*
389 *erythrophthalmus* differed significantly among lake types, with greater average
390 abundance detected in unmanaged lakes ($p = 0.031$). In terms of abundance
391 (NPUE), *Leucaspinus delineatus* was a significantly discriminatory species who was
392 only found in multimesh gillnets in unmanaged lakes ($p = 0.013$).

393

394 **4. Discussion**

395 4.1 General findings

396 We compared the fish communities in angler-managed and unmanaged gravel pit
397 lakes. The results supported three out of four of our initial hypotheses. In particular,
398 species richness (H1) and the number of piscivorous species (H2; e.g., *Esox lucius*,
399 *Sander lucioperca*, *Silurus glanis*, *Perca fluviatilis* and *Anguilla anguilla*) as well as
400 the biomass of piscivorous fishes were significantly higher in managed gravel pit
401 lakes compared to unmanaged lakes. Furthermore, we found a larger number of

402 threatened species and higher littoral abundances and biomasses of threatened
403 fishes in managed gravel pit lakes, while there were no differences in the number of
404 small bodied non-game fish species among lake types. Hence, as hypothesized,
405 managed gravel pit lakes were found to contain a higher α -diversity compared to
406 unmanaged lakes. In contrast to our expectations (H3) the catches of non-native
407 fishes were negligible in both lake types and not significantly greater in managed
408 water bodies as initially assumed. In total four individuals of two species of a total of
409 117,214 sampled individuals were detected in three different gravel pit lakes. By
410 contrast, the final hypothesis (H4) received substantial support as the species-richer
411 fish communities in managed lakes were more similar to each other than the species-
412 poorer fish communities in unmanaged lakes, suggesting biotic homogenization
413 caused by recreational fisheries management.

414 4.2 Robustness of results to sampling methods

415 Both groups of gravel pits studied in our work, the ones managed by recreational
416 fishing clubs and the unmanaged lakes, were similar in key environmental
417 characteristics, such as morphology (e.g. lake area) and productivity – factors known
418 in shaping lentic fish communities in the temperate regions (e.g. Persson *et al.*, 1991;
419 Jeppesen *et al.*, 2000; Mehner *et al.*, 2005). This underscores that the fish
420 community differences we report were most likely a result of recreational fisheries
421 management. However, we collected data on the lake age with two different starting
422 points, the start of mining and the end of mining. While the end of mining – a variable
423 used in other studies to determine the gravel pit age (Zhao *et al.*, 2016; Søndergaard
424 *et al.*, 2018) - did not differ between the two lake types, the start of mining differed.
425 Therefore, managed gravel pit lakes had a higher chance to be colonized by chance
426 events due to their older age, which could also have contributed to the larger species

427 richness found in managed compared to unmanaged lakes. The second investigated
428 variable that differed between the lake types was macrophyte height, however, no
429 differences were detected for macrophyte coverage. As gillnets were set, if possible,
430 in areas without large macrophyte heights and only a low percentage of the
431 electrofished littoral was covered by significant amounts of macrophytes, we assume
432 the influence of the differences in macrophyte height between the lake types on our
433 data as quite low.

434 We used electrofishing and multimesh gillnetting to sample the fish community in the
435 gravel pit lakes as adequately as possible as it is known that multiple fishing gears
436 are needed to determine species richness and the habitat-specific abundance in
437 certain habitats of lakes (Barthelmes & Doering, 1996; Diekmann *et al.*, 2005; Jurajda
438 *et al.*, 2009; Achleitner *et al.*, 2012; Menezes *et al.*, 2013; Mueller *et al.*, 2017). Three
439 unmanaged gravel pit lakes were only sampled once in 2017 by electrofishing, while
440 all the other lakes, both managed and unmanaged, were electrofished twice in 2016
441 and 2017. The lower sampling effort in a subset of the unmanaged lakes likely
442 underestimated the presence of rare species and thus, the average species richness
443 metric in unmanaged lakes might suffer from a negative bias (Lyons, 1992;
444 Angermeier & Smogor, 1995; Paller, 1995). However, as a robustness check, when
445 confining the electrofishing data in all 23 lakes to just one sampling event in one year
446 and comparing the mean species richness of managed and unmanaged lakes,
447 identical results to the ones presented here with our increased sampling effort in 20
448 lakes were revealed (results not shown). Thus, even if we have underestimated
449 species richness in three of the seven unmanaged lakes that were sampled by
450 electrofishing only once, this bias would not be sufficient to alter our results. The

451 results on the lower species richness in unmanaged lakes in the littoral zone thus
452 appear robust to sampling bias.

453 Multimesh gillnets were used to sample the fish community of the benthic zone
454 following European standards (CEN, 2015) because the electrofishing is confined to
455 shallow littoral zones. We adapted the gillnet numbers to lake size to equalize fishing
456 pressure across lakes that varied twenty-fold in area. Following Šmejkal *et al.* (2015)
457 we also supplemented the standard mesh sizes in multimesh gillnets by a few larger
458 mesh size panels to sample fish up to 530 mm total length as representatively as
459 possibly, and importantly comparatively across lakes. However, certain species
460 known from previous studies to be present in Lower Saxonian gravel pit lakes
461 (Schälicke *et al.*, 2012) and other angler-managed stagnant water bodies in Germany
462 (Borkmann, 2001), such as the native *Cyprinus carpio* and the non-native Asian carp
463 grass carp *Ctenopharyngodon idella* (Valenciennes 1844), silver carp
464 *Hypophthalmichthys molitrix* (Valenciennes 1844) and bighead carp
465 *Hypophthalmichthys nobilis* (Richardson 1845), have probably been underestimated
466 in their biomass or even completely missed in our design. The reasons are twofold.
467 Some of these large-bodied cyprinids, such as carp, are not very vulnerable to gill-
468 nets and biomasses below 50 kg ha⁻¹ are below detectability (Bajer *et al.*, 2016).
469 More importantly, many of these large-bodied species are stocking-reliant and they
470 do not naturally recruit. Hence, these species do not produce individuals vulnerable
471 to the mesh sizes we used, and the fishes over 530 mm are largely invulnerable to
472 the sampling gear we used. It is thus very likely that we missed large-bodied
473 cyprinids and also underestimated the biomass present in large-bodied predators in
474 the managed lakes given the sampling gear we used. The effect on our results is
475 twofold. First, the underestimation of large-bodied cyprinid and predatory species in

476 managed lakes would support our findings as we revealed biotic homogenization
477 through the release of desired fish species and a higher biomass of predators in
478 managed lakes with our design. Second, we might have systematically
479 underestimated the presence and biomass of non-native cyprinids in both lakes
480 types. If in reality large-bodied, non-native cyprinids are only present in managed
481 lakes, our findings on the lack of relevant non-native fishes in managed gravel pit
482 lakes might need to be rethought. Further studies using much longer panels of large
483 mesh sizes are needed to detect large-bodied cyprinids in gravel pit lakes (Schälicke
484 *et al.*, 2012), and we recommend such studies in the future.

485 4.3 Species richness and presence of predators and other “game” species

486 Species richness and the number of piscivorous species were higher in gravel pit
487 lakes managed for recreational fisheries, supporting our first two hypotheses. In our
488 study, species richness functioned as a surrogate for α -diversity. Supporting our
489 results, a greater α -diversity in lakes managed by and for recreational fisheries has
490 previously been demonstrated for gravel pit lakes in southern France (Zhao *et al.*,
491 2016) and Minnesota lake fish assemblages (Radomski & Goeman, 1995).
492 Additionally, we also detected a higher Shannon diversity based on the littoral fish
493 abundance and the whole lake biomass estimate in managed gravel pit lakes, further
494 underscoring that managed lakes host larger fish biodiversity than unmanaged gravel
495 pit lakes. Fisheries managers tend to introduce and stock preferentially high trophic
496 level species (Eby *et al.*, 2006; Arlinghaus *et al.*, 2015) and additionally large-bodied
497 cyprinid fishes such as *Cyprinus carpio* and *Tinca tinca* in lakes (Arlinghaus *et al.*,
498 2015) to meet local angler demands (Arlinghaus & Mehner, 2004; Beardmore *et al.*,
499 2011; Donaldson *et al.*, 2011; Ensinger *et al.*, 2016). Therefore, as newly created
500 gravel pits are initially fish-free (Schurig, 1972), the documented higher number and

501 higher abundance and biomass of piscivorous species in managed gravel pit lakes is
502 explainable as a result of introductory and maintenance stocking of desired species
503 that eventually establish and self-recruit.

504 The high-demand species *Anguilla anguilla*, *Esox lucius* and *Perca fluviatilis* were
505 found in all or almost all managed gravel pits, and *Sander lucioperca* in half of the
506 lakes. Although natural colonization of gravel pits by naturally recruiting piscivorous
507 species such as *Esox lucius* and *Perca fluviatilis* is possible, the fact we found
508 *Anguilla anguilla* in almost all managed gravel pit lakes (which all lacked a connection
509 to a river) indicates that stocking must also have played a role. Moreover, it is well
510 known that the angling clubs in the region regularly stock piscivorous fishes such as
511 *Esox lucius* and *Sander lucioperca* (Arlinghaus *et al.*, 2015). These predators were
512 hardly found in unmanaged lakes and similarly no individuals of *Anguilla anguilla*
513 were detected in unmanaged gravel pits at all. The effect of stocking on the presence
514 of species is likely strongest in the early introductory phase when abundant
515 ecological niches are available for colonization. Recent research, however, has
516 shown that once a species is naturally recruiting, stocking with juveniles has no effect
517 on biomass and stock size, e.g., in *Esox lucius* (Johnston *et al.* in press; Hühn *et al.*,
518 2014). This means that once the initial establishment phase is over, continued angler
519 stocking should particularly affect non-naturally recruiting predatory fishes (Johnston
520 *et al.* in press), in our case *Anguilla anguilla*. Indeed, *Anguilla anguilla* represented
521 one of the major dissimilarities between the two lake types following our SIMPER
522 analyses. A higher relative frequency for *Anguilla anguilla* in gravel pit lakes as result
523 of stocking compared to natural lakes has also been reported previously (Emmrich *et*
524 *al.*, 2014; Arlinghaus *et al.*, 2016). Given the poor conservation status of eel in nature

525 (e.g. Bark *et al.*, 2007; Dekker, 2016), such stocking events into enclosed water
526 bodies seem questionable.

527 4.4 Small-bodied non-game and threatened species

528 Small-bodied fishes, such as *Rutilus rutilus*, *Alburnus alburnus* or small *Perca*
529 *fluviatilis*, are usually less desired by anglers compared to larger-bodied predators
530 (Arlinghaus & Mehner, 2004). However, for all species there are subgroups of
531 anglers that target the species preferentially (Beardmore *et al.*, 2011; Ensinger *et al.*,
532 2016). Moreover, smaller-bodied cyprinids are considered forage for predators and
533 are therefore also regularly stocked in lentic water bodies in Germany (Arlinghaus *et*
534 *al.*, 2015). We found some of these species, such as *Rutilus rutilus* and *Perca*
535 *fluviatilis*, to be present in all managed gravel pits, but they only selectively occurred
536 in a few unmanaged lakes. *Perca fluviatilis* and *Rutilus rutilus* are naturally common
537 in German lakes and have previously been documented to be widespread in lentic
538 water bodies in northern Germany and constitute key element of reference fish
539 communities in lakes (Mehner *et al.*, 2005; Emmrich *et al.*, 2014; Ritterbusch *et al.*,
540 2014). Although natural colonization is of course possible, it is also likely that
541 widespread small-bodied species were introduced through forage fish stockings or
542 through bait bucket releases in managed water bodies, leading to their common
543 distribution across Lower Saxonian gravel pit lakes in frequencies similar to their
544 distribution in managed natural lakes (Emmrich *et al.*, 2014; Ritterbusch *et al.*, 2014).
545 Therefore, it can be concluded that fisheries management also fosters the
546 establishment and spread of common and naturally widespread percid and cyprinid
547 species.

548 Small-bodied non-game fishes were also found in both lake types, but the non-game
549 species occurrence strongly differed between managed and unmanaged gravel pit

550 lakes. *Gymnocephalus cernua*, *Rhodeus amarus*, *Cobitis taenia* and *Alburnus*
551 *alburnus* exclusively occurred in managed lakes, while *Leucaspinus delineates*,
552 *Pungitius pungitius*, *Gobio gobio* and *Barbatula barbatula* were only caught in
553 unmanaged lakes. Furthermore, *Leucaspinus delineates* and *Pungitius pungitius*
554 common to unmanaged lakes strongly contributed to the average dissimilarity
555 between the two lake types. However, at the aggregate level both lakes types hosted
556 the same average number of non-game species. Lake-specific occurrences of
557 specific small-bodied non-game species either represents stochastic effects of
558 natural colonization (e.g., through flooding or influx from nearby creeks and canals)
559 or were additionally caused by stocking efforts of angling clubs. Angling clubs
560 regularly engage in the release of non-game fishes for species conservation
561 purposes, but the volume is small (Arlinghaus *et al.*, 2015) and the activity strongly
562 varies by angling club type (Theis, 2016; Theis *et al.*, 2017). Angling-club specific
563 release of non-game species and stochastic events related to establishment and
564 natural colonization (Copp *et al.*, 2010) can then explain the large variation in species
565 presence of small-bodied non-game species among lakes. The differences in non-
566 game species occurrence in the two lake types also explain the significant
567 differences in the abundances and biomasses of small-bodied non-game fishes
568 among lake types. The difference in abundance and biomass of small-bodied non-
569 game species were only detected in the littoral as multimesh gillnet do not
570 representative catch these small fishes, but also littoral habitats can favour different
571 species (Blaber *et al.*, 1989; Gratwicke & Speight, 2005). Furthermore, fish biomass
572 in lakes is primarily driven by bottom-up effects (e.g. Hanson & Leggett, 1982;
573 Lemmens *et al.*, 2018; Matsuzaki *et al.*, 2018) – a finding also revealed in our study
574 at the aggregate biomass level, which did not differ among lake types despite
575 radically different fish community composition. As species richness was substantially

576 lower in unmanaged lakes, the lake type-specific small-bodied non-game species
577 that colonized unmanaged lakes can reach higher biomasses and abundances in
578 these lakes types compared to managed lakes. It may also be possible that the
579 small-bodied non-game species in managed lakes may suffer from competitive
580 bottlenecks caused by competition for zooplankton with small-bodied “game”
581 cyprinids and be affected by predation through greater biomasses of piscivorous fish
582 in these lakes, thereby reducing their biomass in managed compared to unmanaged
583 lakes. However, it is similarly plausible that specific non-game species detected in
584 unmanaged lakes, but not occurring in managed lakes, may never have colonized
585 these lakes due to chance events.

586 The studied lakes hosted a total number of five regionally threatened species,
587 indicating their potential as biodiversity reservoir (Emmrich *et al.*, 2014). *Anguilla*
588 *anguilla*, *Rhodeus amarus* and *Cobitis taenia* occurred exclusively in managed lakes,
589 while *Esox lucius* and *Silurus glanis* were caught in both lake types. Note that none of
590 these regionally threatened species are listed in the German Red List of freshwater
591 fishes, yet the *Anguilla anguilla* is today globally threatened according to IUCN
592 criteria (Freyhof & Brooks, 2011). The number of regionally threatened species (as
593 judged by their presence on the regional Red List of Lower Saxony) and the littoral
594 abundance and biomasses were significantly higher in managed lakes compared to
595 unmanaged lakes, thereby suggesting managed lakes can function as secondary
596 habitat for hosting threatened species. In particular *Esox lucius* is worth highlighting,
597 as it was caught in 87.5% of the managed, but only in 14.3% of the unmanaged
598 gravel pit lakes. Fisheries management thus can foster the fish conservation value of
599 managed gravel pit lakes as *Esox lucius* typically establishes self-reproducing
600 population in gravel pit lakes after first introduction (Schälicke *et al.*, 2012). With

601 regards to eel, as mentioned above, the continued stocking in enclosed water bodies
602 seems problematic from a conservation standpoint as they do not enlarge the
603 spawning stock biomass.

604 4.5 Presence of non-native fishes

605 The hypothesized support of non-native species introductions and accumulation of
606 exotics by recreational fisheries management as revealed in a French gravel pit study
607 by Zhao *et al.* (2016) was not confirmed for artificial lakes in north-western Germany.
608 An examination of the French study revealed that the non-native species listed there
609 encompassed many species being native in Germany, but not in France, such as
610 *Cyprinus carpio*, *Sander lucioperca* and *Silurus glanis*. In our study, only two
611 individuals of non-native *Pseudorasbora parva* were found in one of 16 managed
612 lakes, which was most likely unwillingly introduced through poorly sorted stocking of
613 pond-reared *Cyprinus carpio* or poorly sorted wild stocking of cyprinids (e.g. Copp *et*
614 *al.*, 2005b; Wiesner *et al.*, 2010). In comparison, in two out of seven unmanaged
615 lakes, one individual of each of two non-native species, namely *Pseudorasbora parva*
616 and *Ameiurus nebulosus*, were detected, showing that also unmanaged lakes
617 receive propagule pressure by non-natives. Moreover, in a further unmanaged gravel
618 pit lake many individuals of a golden variant of *Scardinius erythrophthalmus*, common
619 as ornamental fish, were found. Illegal stocking (e.g. release of fish by owners of
620 garden ponds or local anglers interested in establishing desired species in a region)
621 has been shown to contribute as vector for fish dispersal around the globe (Johnson
622 *et al.*, 2009; Hirsch *et al.*, 2018), e.g. illegal goldfish *Carassius auratus* (L.) stocking in
623 Great Britain (Copp *et al.*, 2005a). This is further evidence that the unmanaged lakes
624 in our study were affected by illegal release of fishes by private people. Illegal
625 release, rather than organized fisheries management by fishing clubs, is today

626 believed to constitute the most important pathway for the transfer of non-natives
627 fishes across the world (Copp *et al.*, 2010). One reason for this is that release of non-
628 native fishes is banned in Germany based on Nature Conservation Law and most
629 fisheries are private property and run by trained fisheries managers, many of which
630 are alert of the need to constrain establishment of non-native fishes and rarely
631 engage in stocking non-natives (Arlinghaus *et al.*, 2015; Riepe *et al.*, 2017). While
632 such conditions still allow dispersal of fishes by private anglers illegally (Johnson *et*
633 *al.*, 2009), even if such activities occurred in our lakes, they have left a limited legacy
634 in the study region. This finding agrees with Wolter & Röhr (2010) who reported that
635 non-native fishes rarely have become invasive in Germany, with river populations of
636 gobies being an exception. We conclude that proper recreational fisheries
637 management is not per se a vector for non-native species establishment and that not
638 managing lakes is not a guarantee for the lack of establishment either.

639 4.6 Biotic homogenization caused by fisheries management

640 We found in agreement with our expectation that recreational fisheries management
641 contributed to the homogenization of fish faunas, reducing the β -diversity in fish
642 communities compared to unmanaged lakes. Homogenization of fish communities as
643 a result of a range anthropogenic influences (e.g., stocking, urbanization, habitat
644 simplification) has been repeatedly found across the world (Radomski & Goeman,
645 1995; Rahel, 2000; Villéger *et al.*, 2011). Our work shows that gravel pit lakes in
646 north-western Germany are no exception. But in contrast to other studies, we can
647 exclude non-fishing related impacts to have exerted substantial impacts on our
648 results as the environment of the lakes we studied was rather similar and only the
649 presence or absence of fisheries management discriminated among the lakes. Biotic
650 homogenization not only entails that fish communities become increasingly similar

651 across ecoregions and among ecosystems but that many ecosystems increasingly
652 host environmentally tolerant or species of high fisheries value, thereby increasing
653 the α -diversity locally, but decreasing β -diversity regionally. This result reflects that
654 management based on introductory stocking or maintenance stocking during the
655 management operations of a lake leads to the accumulation of a certain set of
656 desired species in gravel pit lakes that then establish and become self-reproducing
657 (Emmrich *et al.*, 2014) and collectively contribute to a homogenized community that
658 reduces β -diversity.

659 Homogenization in lentic fish communities over longer periods of time (e.g., 10.000
660 years after the last glaciation) may also be a natural phenomenon as evidenced by
661 fish community assessments of natural lakes across Europe and in northern
662 Germany who have shown that only a few key environmental gradients (e.g., lake
663 depth and productivity) discriminate among different lentic fish communities
664 (Diekmann *et al.*, 2005; Mehner *et al.*, 2005; Brucet *et al.*, 2013; Ritterbusch *et al.*,
665 2014). Put differently, lakes having similar limnological characteristics over time also
666 host very similar (i.e., homogenous) fish communities, supporting the results of our
667 managed lakes. One limitation to this statement is that also most of the natural lakes
668 assessed by Diekmann *et al.* (2005), Mehner *et al.* (2005) and Emmrich *et al.* (2014)
669 and used by Ritterbusch *et al.* (2014) to derive reference fish communities were
670 managed for fisheries presently or in the past. In that sense the newly created, yet
671 unmanaged gravel pit lakes with their lake-specific species poor communities do not
672 find any natural parallel in the existing studies. Therefore, we conclude that high β -
673 diversity maybe the natural conditions at least in the initial phases of the succession
674 in lakes. Similar to islands, the chances of fishes to naturally colonize isolated
675 freshwater habitats are low (Scheffer *et al.*, 2006; Strona *et al.*, 2012) and often

676 limited to rare events like massive floods (Pont *et al.*, 1991; Olden *et al.*, 2010), fish
677 rain (Bajkov, 1949) and less likely bird-based dispersal (Riehl, 1991; Hirsch *et al.*,
678 2018; Martin & Turner, 2018). A further colonization mechanism identified in our work
679 encompasses uncontrolled anthropogenic events, such as aquarium, garden pond and
680 bait bucket releases (Padilla & Williams, 2004; Copp *et al.*, 2005a; Hirsch *et al.*,
681 2018). Overall, also in light of the existing literature it seems that the high β -diversity
682 we found is special to young lake ecosystems in a pioneer status. Importantly,
683 however, as mentioned before, none of the unmanaged lakes were fish-free and they
684 contained at least three fish species, while often lacking piscivorous fish species.
685 Thus, one key message of our work is that also lakes not managed by and for
686 anglers will be colonized by fishes, through both natural and human-assisted means.
687 Our study differs from a recent Danish gravel pit study where the authors reported
688 fish-free systems, but the gravel pit lakes were on average much younger than the
689 ones in our study (Søndergaard *et al.*, 2018).

690 4.7 Conclusions and implications

691 Our findings offer two conclusions that vary depending on which perspective is taken.
692 First, ongoing homogenization of fish faunas globally (Rahel, 2002; Villéger *et al.*,
693 2011) can contribute to the freshwater biodiversity crisis (Dudgeon *et al.*, 2006) by
694 reducing the variation in lake fish communities among ecosystems. If such
695 perspective is taken, recreational fisheries management is one contributing factor to
696 homogenization, which may be judged as undesirable by some. Alternatively and
697 secondly, one has to realize that completely unmanaged lakes and angler-managed
698 lakes will be affected by similar drivers (e.g., introductory or illegal stocking). In a
699 highly urbanized environment it is an illusion to assume natural development of newly
700 created aquatic ecosystems without human impact is possible. If one then

701 acknowledges, based on our work, that proper management of recreational fisheries
702 does not necessarily lead to the development of artificial fish communities with many
703 non-native fishes, using newly created lakes for fisheries can be considered of
704 conservation value despite homogenization of fish communities being largely
705 inevitable. Importantly, recreational fisheries management promotes the rapid
706 establishment of fish communities in new ecosystems that largely resemble similarly
707 structured, managed natural lake ecosystems (Emmrich *et al.*, 2014; Ritterbusch *et*
708 *al.*, 2014). If new aquatic ecosystems would not be managed, the process of
709 establishment of fishes would likely take substantially longer and would strongly be
710 influenced by stochastic events.

711 Importantly, most standing waters in Germany are managed under fishing rights
712 laws. Under such conditions, recreational fisheries management contributes to
713 fulfilling state-specific fisheries objectives as specified in the laws, which demand
714 fisheries stakeholders to help establish and maintain near-natural fish communities
715 that match those to be expected under prevailing environmental conditions in natural
716 ecosystems (Arlinghaus, 2017). In all German states except Schleswig-Holstein,
717 gravel pit lakes are legally under the same demand as natural lakes as regards to the
718 goals of fisheries management. However, for artificial waters like gravel pit lakes no
719 reference fish community yet exists, and it is likely that this reference community is
720 species poorer than those documented in natural, managed lakes in Germany
721 (compare Emmrich *et al.* (2014) and Ritterbusch *et al.* (2014)). In the absence of this
722 information, fisheries operators could use fish communities present in
723 environmentally similar (in terms of depth, nutrient content, visibility, habitat structure)
724 natural ecosystems as benchmarks for the species pool expected to be developed in
725 in gravel pit lakes (Arlinghaus *et al.*, 2016). An alternative view maybe that the natural

726 condition of a gravel pit lake is initially fish-free, with slow accumulation of naturally
727 colonized species. While this perspective is valid, our work clearly showed that fish-
728 free lakes are not necessarily to be expected and that anthropogenic introductions
729 also happen in lakes that are not managed by recreational fisheries. Importantly, the
730 number of threatened species in managed and unmanaged lakes did not differ and
731 non-native fishes were rare, implicating that recreational fisheries management is not
732 necessarily a vector for the establishment of artificial fish communities that lack
733 species of conservation value.

734

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754

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756 SM: ideas, data generation, data analysis, manuscript preparation

757 ME: ideas, data generation, data analysis, manuscript editing

758 TK: data generation, manuscript editing, funding

759 CW: manuscript editing, funding

760 NW: ideas, data generation, data analysis

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1130 **Tables**

1131 Table 1: Common and scientific names, frequency of occurrence and relative frequency in the lake types of the fish species caught in 16 managed and 7
 1132 unmanaged gravel pit lakes using littoral electrofishing and benthic and pelagic gillnetting.

Common name	Scientific name	Frequency of occurrence in managed lakes	Frequency of occurrence in unmanaged lakes	Relative frequency in managed lakes (electrofishing)	Relative frequency in unmanaged lakes (electrofishing)	Relative frequency in managed lakes (gillnetting)	Relative frequency in unmanaged lakes (gillnetting)
Perch†	<i>Perca fluviatilis</i> L.	100.0	28.6	42.50	19.98	62.35	27.99
Roach	<i>Rutilus rutilus</i> (L.)	100.0	14.3	7.05	1.19	24.31	14.11
Tench	<i>Tinca tinca</i> (L.)	93.8	28.6	3.53	3.45	0.61	0.69
Eel†§	<i>Anguilla anguilla</i> (L.)	93.8	0.0	13.24	0.00	0.00	0.00
Pike†§	<i>Esox lucius</i> L.	87.5	14.3	3.88	5.42	0.28	0.00
Rudd	<i>Scardinius erythrophthalmus</i> (L.)	68.8	42.9	14.50	16.82	1.74	16.98
Bream	<i>Abramis brama</i> (L.)	68.8	14.3	6.77	0.00	5.21	0.17
Carp	<i>Cyprinus carpio</i> L.	56.3	42.9	0.35	0.15	0.17	1.24
Ruffe‡	<i>Gymnocephalus cernua</i> (L.)	56.3	0.0	0.31	0.00	2.69	0.00
Pikeperch†	<i>Sander lucioperca</i> (L.)	50.0	0.0	0.01	0.00	0.69	0.00
White bream	<i>Blicca bjoerkna</i> (L.)	43.8	0.0	1.91	0.00	1.71	0.00
Prussian carp	<i>Carassius gibelio</i> (Bloch 1782)	12.5	28.6	2.67	2.83	0.23	9.14
European catfish†§	<i>Silurus glanis</i> L.	12.5	14.3	0.06	0.00	0.02	0.00
Cyprinid hybrid	<i>Rutilus x Abramis</i>	12.5	0.0	0.00	0.00	0.00	0.00
Topmouth gudgeon‡¶	<i>Pseudorasbora parva</i> (Temminck & Schlegel 1846)	6.3	14.3	0.01	0.01	0.00	0.00
Bitterling‡§	<i>Rhodeus amarus</i> (Bloch 1782)	6.3	0.0	0.02	0.00	0.00	0.00
European whitefish	<i>Coregonus lavaretus</i> (L.)	6.3	0.0	0.00	0.00	0.00	0.00
Spined loach‡§	<i>Cobitis taenia</i> L.	6.3	0.0	0.39	0.00	0.00	0.00
Bleak‡	<i>Alburnus alburnus</i> (L.)	6.3	0.0	2.79	0.00	0.00	0.00
Sunbleak‡	<i>Leucaspis delineatus</i> (Heckel 1843)	0.0	42.9	0.00	27.51	0.00	15.18
Nine-spined stickleback‡	<i>Pungitius pungitius</i> (L.)	0.0	42.9	0.00	21.80	0.00	6.04
Gudgeon‡	<i>Gobio gobio</i> (L.)	0.0	28.6	0.00	0.72	0.00	4.69
Stone loach‡	<i>Barbatula barbatula</i> (L.)	0.0	14.3	0.00	0.08	0.00	3.76
Brown bullhead†¶	<i>Ameiurus nebulosus</i> (Lesueur 1819)	0.0	14.3	0.00	0.05	0.00	0.00

† Piscivorous species (perch > 15 cm total length (TL) and eel > 50 cm TL were classified piscivorous)

‡ Small-bodied non-game fish

§ Threatened species in Lower Saxony

¶ Non-native species

1133 Table 2: Comparison between the two management types for NPUE and BPUE of electrofishing and multimesh gillnet data on the total catch and the catch of the
 1134 selected fish community descriptors in gravel pit lakes in Germany.

		Mean (\pm S.D.)		Median (Range)		p-value
		Managed lakes	Unmanaged lakes	Managed lakes	Unmanaged lakes	
Littoral estimate (electrofishing) NPUE (N/50m)	Total abundance	30.4 (\pm 23.7)	538.4 (\pm 1306.7)	22.8 (7.3 - 94.7)	33.6 (3.8 - 3499.6)	0.368
	Piscivorous fishes	1.7 (\pm 1.2)	0.5 (\pm 0.7)	1.5 (0.2 - 4.2)	0.0 (0.0 - 1.6)	0.007
	Small-bodied non-game fishes	0.4 (\pm 1.6)	525.4 (\pm 1311.8)	0.01 (0.0 - 6.5)	12.7 (0.0 - 3498.5)	0.031
	Threatened fishes	2.8 (\pm 1.8)	0.4 (\pm 0.6)	2.8 (0.1 - 6.7)	0.0 (0.0 - 1.4)	0.001
	Non-native fishes	0.0 (\pm 0.01)	0.01 (\pm 0.02)	0.0 (0.0 - 0.06)	0.0 (0.0 - 0.1)	0.189
	Shannon index	1.1 (\pm 0.4)	0.5 (\pm 0.3)	1.1 (0.6 - 1.6)	0.6 (0.04 - 0.9)	0.002
Littoral estimate (electrofishing) BPUE (g/50m)	Total abundance	798.9 (\pm 525.6)	798.1 (\pm 829.9)	687.6 (55.9 - 2082.6)	472.9 (21.5 - 1920.8)	0.998
	Piscivorous fishes	451.4 (\pm 406.87)	94.4 (\pm 152.0)	318.8 (21.5 - 1556.4)	0.0 (0.0 - 360.5)	0.009
	Small-bodied non-game fishes	0.7 (\pm 1.8)	216.4 (\pm 523.1)	0.05 (0.0 - 7.3)	11.9 (0.0 - 1400.9)	0.026
	Threatened fishes	304.3 (\pm 248.8)	55.9 (\pm 134.8)	259.9 (25.9 - 973.8)	0.0 (0.0 - 360.5)	0.005
	Non-native fishes	0.01 (\pm 0.03)	22.3 (\pm 59.1)	0.0 (0.0 - 0.1)	0.0 (0.0 - 156.3)	0.154
	Shannon index	1.1 (\pm 0.3)	0.7 (\pm 0.3)	1.1 (0.4 - 1.6)	0.7 (0.2 - 1.0)	0.012
Whole lake estimate (multimesh gillnet) NPUE (N/100m ²)	Total abundance	104.5 (\pm 69.6)	76.9 (\pm 26.0)	91.8 (23.7 - 235.7)	77.1 (40.6 - 111.8)	0.624
	Piscivorous fishes	6.6 (\pm 4.9)	1.9 (\pm 3.4)	6.0 (0.3 - 19.3)	0.0 (0.0 - 8.2)	0.009
	Small-bodied non-game fishes	1.5 (\pm 2.3)	8.9 (\pm 12.9)	0.2 (0.0 - 6.6)	0.0 (0.0 - 33.5)	0.564
	Threatened fishes	0.2 (\pm 0.3)	0.0 (\pm 0.0)	0.0 (0.0 - 1.2)	0.0 (0.0 - 0.0)	0.105
	Non-native fishes	0.0 (\pm 0.0)	0.0 (\pm 0.0)	0.0 (0.0 - 0.0)	0.0 (0.0 - 0.0)	NA
	Shannon index	0.8 (\pm 0.3)	0.5 (\pm 0.4)	0.9 (0.04 - 1.4)	0.6 (0.07 - 1.0)	0.098
Whole lake estimate (multimesh gillnet) BPUE (g/100m ²)	Total abundance	3,481.1 (\pm 2,016.4)	3,048.8 (\pm 1,756.0)	2919.2 (496.2 - 6,999.9)	3707.7 (98.3 - 4,682.3)	0.613
	Piscivorous fishes	948.6 (\pm 771.6)	327.8 (\pm 694.1)	700.6 (12.1 - 2,602.3)	0.0 (0.0 - 1,857.9)	0.009
	Small-bodied non-game fishes	12.6 (\pm 22.7)	29.6 (\pm 39.4)	1.6 (0.0 - 76.8)	0.0 (0.0 - 89.8)	0.773
	Threatened fishes	53.9 (\pm 142.0)	0.0 (\pm 0.0)	142.0 (0.0 - 518.3)	0.0 (0.0 - 0.0)	0.105
	Non-native fishes	0.0 (\pm 0.0)	0.0 (\pm 0.0)	0.0 (0.0 - 0.0)	0.0 (0.0 - 0.0)	NA
	Shannon index	1.1 (\pm 0.3)	0.5 (\pm 0.4)	1.2 (0.6 - 1.7)	0.7 (0.02 - 1.1)	0.019

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1136 Table 3: Results of a similarity percentage analysis (SIMPER) for NPUE and BPUE data of
 1137 electrofishing and multimesh gillnetting, including average dissimilarity, cumulative % contribution to
 1138 the average dissimilarity, mean and standard deviation for managed and unmanaged gravel pit lakes.
 1139 Only species explaining more that 1% of the average dissimilarity are presented.

Data	Species	Average contribution to overall dissimilarity	Cumulative contribution %	Mean managed ± S.D.	Mean unmanaged ± S.D.	p-value
Littoral estimate (electrofishing) NPUE (N/50m)	<i>Leucaspis delineatus</i>	25.0	28.6	0.0 ± 0.0	515.2 ± 1307.1	0.014
	<i>Perca fluviatilis</i>	14.5	45.2	9.5 ± 7.3	2.2 ± 5.0	0.456
	<i>Scardinius erythrophthalmus</i>	14.0	61.2	7.2 ± 20.5	6.0 ± 12.3	0.516
	<i>Pungitius pungitius</i>	11.7	74.6	0.0 ± 0.0	6.4 ± 11.7	0.013
	<i>Anguilla anguilla</i>	4.8	80.1	2.6 ± 2.1	0.0 ± 0.0	0.356
	<i>Rutilus rutilus</i>	4.1	84.7	3.5 ± 8.8	0.4 ± 1.1	0.949
	<i>Abramis brama</i>	3.6	88.9	3.5 ± 10.4	0.0 ± 0.0	0.977
	<i>Carassius gibelio</i>	3.1	92.4	1.1 ± 3.2	3.0 ± 7.4	0.437
	<i>Tinca tinca</i>	2.5	95.2	1.3 ± 2.5	0.9 ± 2.3	0.688
	<i>Esox lucius</i>	1.4	96.9	0.7 ± 0.7	0.2 ± 0.5	0.619
Littoral estimate (electrofishing) BPUE (g/50m)	<i>Anguilla anguilla</i>	27.8	29.7	422.8 ± 467.1	0.0 ± 0.0	0.144
	<i>Carassius gibelio</i>	16.7	47.5	13.0 ± 46.8	383.7 ± 715.4	0.082
	<i>Esox lucius</i>	12.5	60.9	157.0 ± 200.7	4.4 ± 11.5	0.259
	<i>Leucaspis delineatus</i>	8.1	69.6	0.0 ± 0.0	198.1 ± 495.8	0.155
	<i>Scardinius erythrophthalmus</i>	6.9	76.9	22.9 ± 55.0	66.4 ± 99.8	0.104
	<i>Perca fluviatilis</i>	6.7	84.1	76.4 ± 48.5	22.9 ± 48.8	0.037
	<i>Cyprinus carpio</i>	3.8	88.1	32.9 ± 109.3	23.1 ± 61.2	0.503
	<i>Tinca tinca</i>	3.5	91.9	39.4 ± 36.5	6.0 ± 12.6	0.228
	<i>Rutilus rutilus</i>	2.3	94.4	26.9 ± 87.3	1.4 ± 3.6	0.553
	<i>Silurus glanis</i>	2.2	96.7	1.5 ± 5.2	51.5 ± 136.3	0.273
	<i>Ameiurus nebulosus</i>	1.2	97.9	0.0 ± 0.0	22.3 ± 59.1	0.252
Whole lake estimate (multimesh gillnet) NPUE (N/100m ²)	<i>Perca fluviatilis</i>	33.1	40.2	64.3 ± 59.3	24.4 ± 43.9	0.138
	<i>Rutilus rutilus</i>	16.4	60.1	24.5 ± 23.5	11.6 ± 30.6	0.136
	<i>Scardinius erythrophthalmus</i>	9.1	71.2	0.5 ± 1.3	15.8 ± 27.0	0.079
	<i>Leucaspis delineatus</i>	6.2	78.7	0.0 ± 0.0	9.0 ± 14.2	0.013
	<i>Carassius gibelio</i>	4.0	83.6	0.4 ± 1.6	5.3 ± 13.8	0.183
	<i>Abramis brama</i>	3.0	87.3	6.9 ± 17.6	0.1 ± 0.4	0.767
	<i>Pungitius pungitius</i>	2.9	90.8	0.0 ± 0.0	4.6 ± 11.9	0.173
	<i>Gobio gobio</i>	2.0	93.3	0.0 ± 0.0	2.8 ± 6.5	0.078
	<i>Barbatula barbatula</i>	1.3	94.9	0.0 ± 0.0	1.5 ± 4.0	0.139
		<i>Blicca bjoerkna</i>	1.2	96.4	3.7 ± 14.0	0.0 ± 0.0
Whole lake estimate (multimesh gillnet) BPUE (g/100m ²)	<i>Perca fluviatilis</i>	20.0	24.0	1240.3 ± 1032.8	435.0 ± 834.7	0.020
	<i>Rutilus rutilus</i>	16.5	43.9	988.7 ± 763.9	243.2 ± 643.4	0.153
	<i>Cyprinus carpio</i>	14.9	61.8	552.2 ± 791.0	848.7 ± 1191.5	0.152
	<i>Scardinius erythrophthalmus</i>	11.0	75.1	26.6 ± 70.6	690.3 ± 1332.1	0.031
	<i>Carassius gibelio</i>	9.0	86.0	18.7 ± 74.6	683.0 ± 1724.4	0.202
	<i>Abramis brama</i>	4.5	91.4	358.3 ± 724.0	0.9 ± 2.4	0.875
	<i>Sander lucioperca</i>	2.0	93.8	103.8 ± 147.0	0.0 ± 0.0	0.612
	<i>Tinca tinca</i>	1.4	95.6	16.2 ± 41.3	93.9 ± 238.6	0.227
	<i>Blicca bjoerkna</i>	1.0	96.8	75.9 ± 274.9	0.0 ± 0.0	0.667

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1141 **Figure captions**

1142 Figure 1: Location of the sampling lakes in Lower Saxony, north-western Germany, Europe

1143 Figure 2: Comparison of the environmental characteristics between managed (N=16) and unmanaged
1144 (N=7) gravel pit lakes. The boxes show the 25th to the 75th percentile and the whiskers extent to 1.5 *
1145 IQR (inter-quartile range). Median is marked as a solid line, mean as diamond and outliers as circles.
1146 Significance levels are * < 0.05; ** < 0.01; *** < 0.001 and n.s. = not significant.

1147 Figure 3: Descriptors of the fish community derived from electrofishing and multimesh gillnetting in
1148 managed (N=16) and unmanaged (N=7) gravel pit lakes. The boxplots show the 25th to the 75th
1149 percentile (box) and the whiskers extent up to 1.5 * IQR (where IQR is the inter-quartile range).
1150 Median is marked as a solid line, mean as diamond and outliers as circles. Significance levels are * <
1151 0.05; ** < 0.01; *** < 0.001 and n.s. = not significant.

1152 Fig. 4: Non-metric multidimensional scaling (nMDS) of the fish community structures with **A**
1153 electrofishing NPUE data, **B** electrofishing BPUE data, **C** gillnetting NPUE data and **D** gillnetting BPUE
1154 data. Solid triangles represent managed and open circle represent unmanaged gravel pit lakes. The
1155 ellipses show the 95% confidence intervals.

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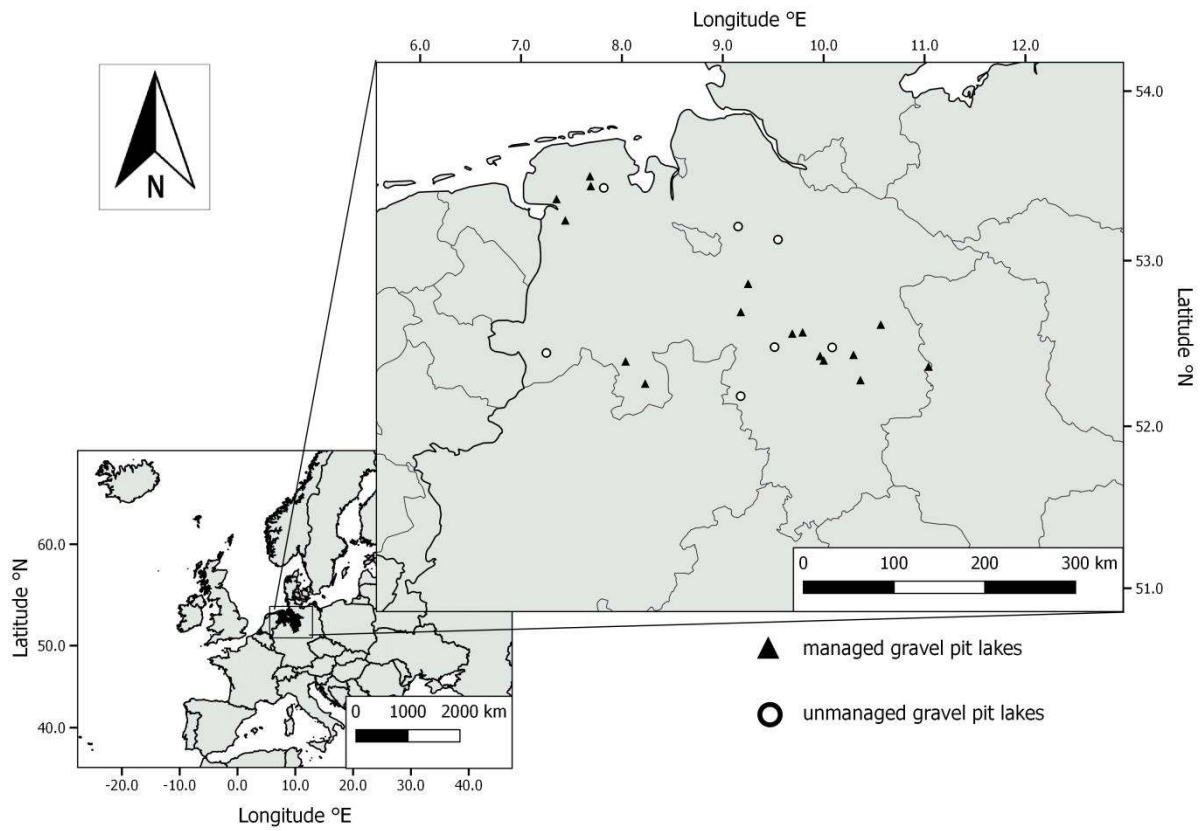
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1164 **Figures**



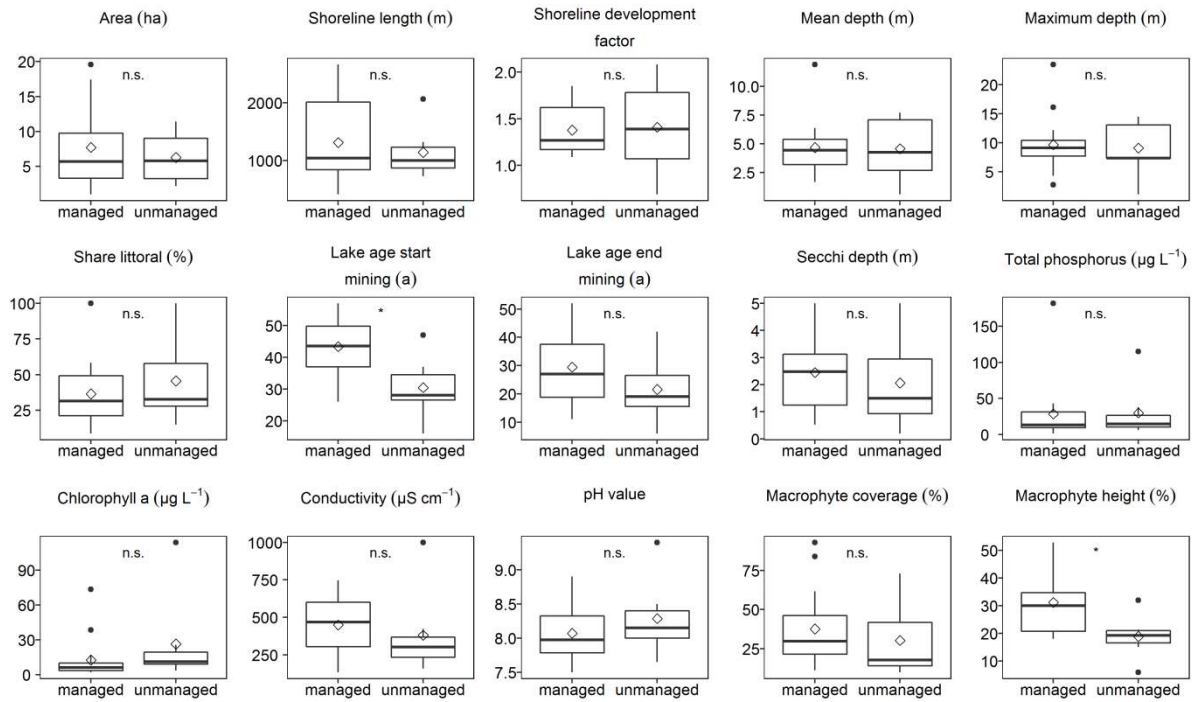
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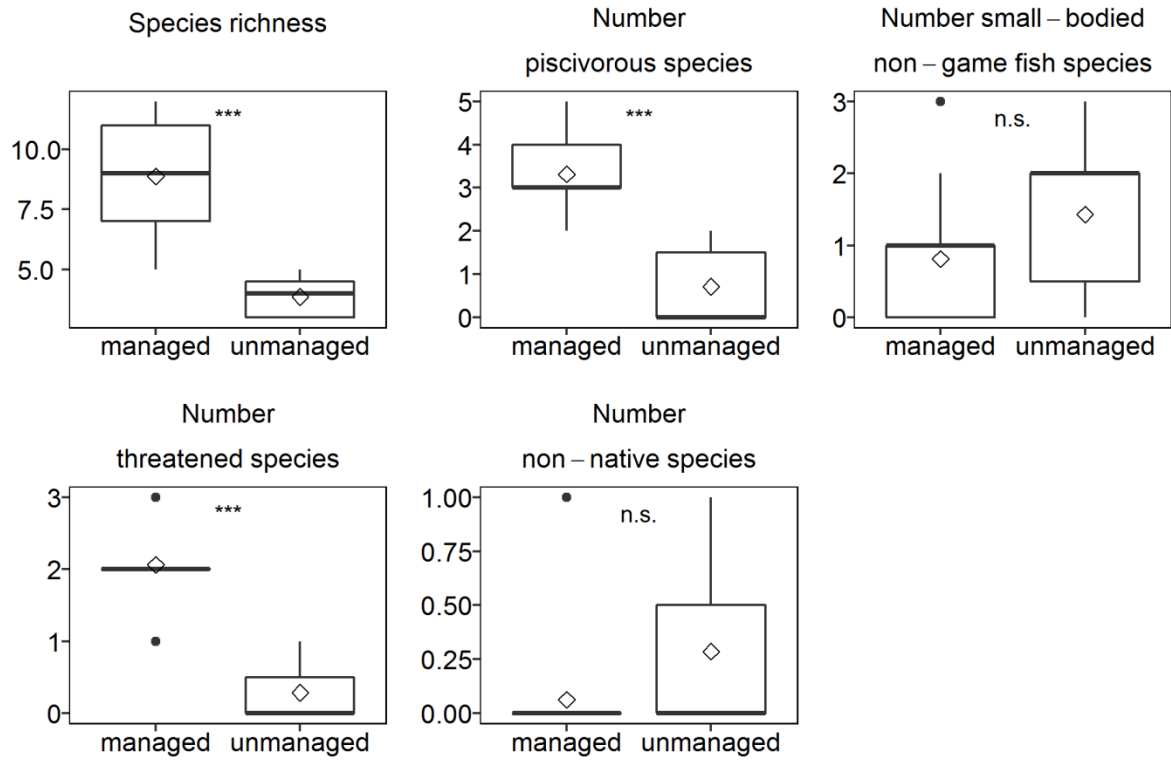
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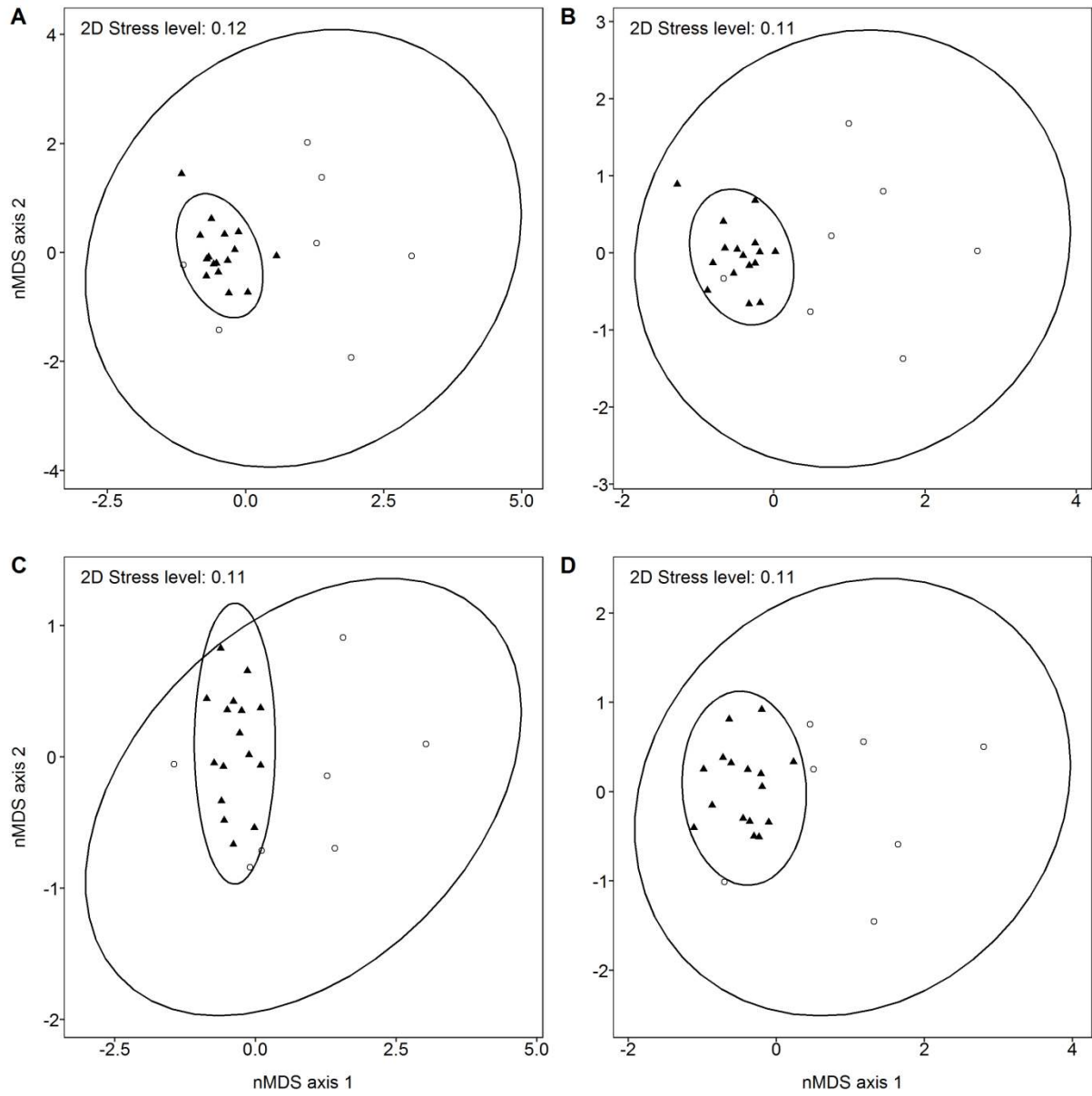
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