

# **Status of aquatic and riparian biodiversity in artificial lake ecosystems with and without management for recreational fisheries: implications for conservation**

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## Abstract

1 1. Humanity is facing a biodiversity crisis, with freshwater-associated biodiversity being in particularly  
2 dire state. Novel ecosystems created through human use of mineral resources, such as gravel pit  
3 lakes, can provide substitute habitats for conservation of freshwater and riparian biodiversity.  
4 However, many of these artificial ecosystems are managed for recreational fisheries and may exhibit  
5 high recreational use intensity, which may limit the biodiversity potential of gravel pit lakes.  
6 2. We assessed the species richness of several taxa present in gravel pit lakes and compared a range  
7 of taxonomic biodiversity metrics of lakes managed for recreational fisheries (N = 16) and  
8 unmanaged reference lakes (N = 10), while controlling for non-fishing related environmental  
9 variation.  
10 3. The average species richness of all examined taxa (plants, amphibians, dragonflies, damselflies,  
11 waterfowl, songbirds) was similar among both lake types and no faunal or floral breaks were  
12 revealed when examining the pooled species inventory of managed and unmanaged lakes. Similarly,  
13 there were no differences among management types in the presence of rare species and in the  
14 Simpson diversity index across all the taxa that we assessed.  
15 4. Variation in species richness among lakes was correlated with woody habitat, lake morphology  
16 (size and steepness) and land use, but not with the presence of recreational fisheries. Thus, non-  
17 fishing related environmental variables have stronger effects on local species presence than  
18 recreational-fisheries management or the presence of recreational anglers.  
19 5. Collectively, we found no evidence that anglers and recreational-fisheries management constrain  
20 the development of aquatic and riparian biodiversity in gravel pits of the study region.

## Keywords

amphibians, biodiversity, birds, disturbance, fishing, lake, littoral, recreation, riparian, vegetation

## 1. Introduction

21 Globally, biodiversity is in steep decline, creating a biodiversity crisis of unprecedented scale (Díaz et  
22 al., 2019; WWF, 2018). An estimated 1 million species are currently threatened by extinction (Díaz et  
23 al., 2019), and current species extinction rates are about 1000 times higher than the calculated  
24 background rate (Pimm et al., 2014). The biodiversity decline is particularly prevalent in freshwaters  
25 compared to marine and terrestrial environments (Sala et al., 2000; WWF, 2018). From 1970 to  
26 today, freshwater biodiversity has, on average, declined by 83% across thousands of populations  
27 (WWF, 2018). Although manifold reasons contribute to the freshwater biodiversity crisis (Reid et al.,  
28 2019), habitat alteration and fragmentation, pollution, overexploitation, invasive species and climate  
29 change constitute key drivers (Dudgeon et al., 2006; IPBES, 2019).

30 Artificially created aquatic habitats, such as gravel pit lakes or ponds, can play an important role in  
31 maintaining and increasing native biodiversity by providing refuge and secondary habitat for rare or  
32 endangered species (Damnjanović et al., 2018; Santoul, Gaujard, Angélibert, Mastrotillo, &  
33 Céréghino, 2009). Artificial lake ecosystems are often relatively recent in origin (less than 100 years  
34 of age; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2016) and created by mining of sand,  
35 clay, gravel and other mineral resources (Saulnier-Talbot & Lavoie, 2018). More than one billion tons  
36 of sand, gravel and other earthen materials were excavated in more than 24,500 quarries and pits  
37 within the EU-28 in 2017 alone (UEPG, 2017). The resulting numerous artificial lakes (for simplicity  
38 henceforth referred to as gravel pit lakes) have become common elements in many cultural  
39 landscapes across the industrialized world (Blanchette & Lund, 2016).

40 Lakes, including gravel pit lakes, provide a bundle of ecosystem services to humans (Reynaud &  
41 Lanzanova, 2017). These include provisioning services, such as fish yield, as well as a range of cultural  
42 services, in particular recreation (Meyerhoff, Klefoth, & Arlinghaus, 2019; Venohr et al., 2018).  
43 Although the benefits of water-based recreation can be substantial, the activity can also negatively  
44 impact on the biodiversity of freshwater ecosystems (Venohr et al., 2018). For example, human  
45 activities can reduce littoral and riparian habitat quality and thereby negatively affect associated taxa  
46 (Spyra & Strzelec, 2019). Water-based recreation has also been found to negatively impact birds and  
47 other mobile wildlife through fear reactions to humans (Dear, Guay, Robinson, & Weston, 2015; Frid  
48 & Dill, 2002), dogs (Randler, 2006) or pleasure boats (McFadden, Herrera, & Navedo, 2017; Wolter &  
49 Arlinghaus, 2003). Management and conservation of gravel pit lakes and other artificial waterbodies  
50 would benefit from jointly considering the well-being aquatic recreation produces to humans, while  
51 balancing these benefits with the possible negative biodiversity impacts that aquatic recreation can  
52 induce (Lemmens et al., 2013; Lemmens, Mergeay, Van Wichelen, De Meester, & Declerck, 2015).

53 Many gravel pit lakes located in central Europe are used by recreational fisheries (Emmrich,  
54 Schällicke, Hühn, Lewin, & Arlinghaus, 2014; Matern et al., 2019; Zhao et al., 2016). Anglers are not

55 only users, but in some regions of the world also managers of fish populations and habitats  
56 (Arlinghaus, Alós, et al., 2017). This particularly applies to Germany, where organizations of anglers,  
57 usually angling clubs and associations, are leaseholders or owners of freshwater fishing rights, and in  
58 this position are also legally entitled to manage fish stocks (Arlinghaus, Alós, et al., 2017). This entails  
59 the sovereignty to stock fish, to manage littoral habitat and introduce access and harvest regulations  
60 (Arlinghaus, Lorenzen, Johnson, Cooke, & Cowx, 2016). Because stocking of fish is particularly  
61 prevalent in freshwater recreational-fisheries management (Arlinghaus et al., 2015), key impacts of  
62 the presence of recreational fisheries and associated management activities can be expected at the  
63 fish stock and fish community levels (Matern et al., 2019; Zhao et al., 2016). Angler-induced changes  
64 of fish community composition and species richness typically include fostering elevated fish species  
65 richness through the release and introduction of large-bodied “game” fishes of high fisheries interest  
66 (Matern et al., 2019; Zhao et al., 2016). These changes might in turn affect submerged macrophytes,  
67 (e.g., due to introduction of benthivorous fish that uproot macrophytes; Bajer et al., 2016), and other  
68 taxa through predation (e.g., amphibians: Hecnar & M’Closkey, 1997; Miró, Sabás, & Ventura, 2018;  
69 invertebrates: Knorp & Dorn, 2016; Miller & Cowl, 2006; or birds: Cucherousset et al., 2012;  
70 Syväranta et al., 2009). In addition, anglers may modify littoral habitats through access to angling  
71 sites (Dustin & Vondracek, 2017), thereby affecting plant richness (O’Toole, Hanson, & Cooke, 2009),  
72 dragonflies (Z. Müller et al., 2003), or directly affect mobile taxa, such as birds, through angler-  
73 induced disturbances (Bell, Delany, Millett, & Pollitt, 1997; Cryer, Linley, Ward, Stratford, &  
74 Randerson, 1987). Indirectly, angler presence can also inadvertently kill non-targeted wildlife, e.g.,  
75 through lost fishing gear that is ingested by birds or where birds become entangled (Franson et al.,  
76 2003; Sears, 1988). Therefore, anglers can both be seen as stewards of aquatic ecosystems (Granek  
77 et al., 2008) as well as a potential threat to certain aquatic taxa depending on the local angling  
78 intensity and other conditions (Reichholf, 1988; Venohr et al., 2018).

79 In Germany, fisheries (including recreational angling) are regulated by Federal state-specific fisheries  
80 law, while protection of species and habitat types is regulated by Federal and state-specific nature  
81 conservation legislation. Conflicts with angler interests regularly occurs when nature conservation  
82 authorities implement rules to achieve conservation goals that partially or fully constrain access to  
83 water bodies (Arlinghaus, 2005). Conservation-motivated constraints of angling or recreational-  
84 fisheries-management actions (e.g., stocking) are not only motivated by the implementation of  
85 national or international conservation law (e.g., Natura 2000 legislation of the European Community;  
86 92/43/EWG, 1992) in natural ecosystems, but are increasingly commonplace in relation to artificial  
87 lake ecosystems. For example, in some regions of Germany recreational fisheries have been excluded  
88 from potential use of newly created gravel pit lakes already during the process of licensing the sand  
89 or gravel extraction (H. Müller, 2012). Such bans of the future angling use is typically justified by the

90 assumption that angling is particularly impactful for disturbance-sensitive taxa (e.g., waterfowl) or  
91 habitats of special conservation concern (H. Müller, 2012; Reichholf, 1988; Wichmann, 2010).

92 To contribute to this ongoing conservation debate, here the taxonomic biodiversity present in and  
93 around gravel pit lakes was studied using a space-for-time substitution design comparing lakes  
94 managed and used by recreational fisheries with lakes that do not experience recreational fisheries  
95 actions and lack angler presence. Our study goal was to examine the aggregate impact of  
96 recreational fisheries on the taxonomic aquatic and riparian biodiversity detectable at typical gravel  
97 pit lakes in north-western Germany. The specific objective was to estimate the effect of recreational  
98 fisheries on species richness, faunal and floral composition, community diversity and conservation  
99 value across a range of aquatic and riparian taxa that are protected by national and European  
100 conservation legislation (e.g., birds, amphibians, dragonflies). Because the absence of recreational  
101 fisheries in a given gravel pit lake does not mean the ecosystems remain undisturbed from other  
102 recreational uses (e.g., swimming, walking), it was hypothesized that the presence of recreational  
103 fisheries and associated management activities will, on average, not affect species richness and  
104 conservation value of taxa that are not specifically targeted by anglers (Odonata, amphibians,  
105 submerged and riparian vegetation, waterfowl and songbirds). This hypothesis was formulated as a  
106 statistical null hypothesis to be falsified by empirical data.

## 2. Methods

### 107 *Study area and lake selection*

108 Our study was conducted in the Central Plain ecoregion of Lower Saxony in north-western Germany  
109 (Figure 1). Lower Saxony has 8 million inhabitants at a population density of 167 inhabitants per km<sup>2</sup>.  
110 The total area of the Federal state encompasses 47,710 km<sup>2</sup>, of which 27,753 km<sup>2</sup> constitute  
111 agricultural farmland and 10,245 km<sup>2</sup> managed forests (Landesamt für Statistik Niedersachsen (LSN),  
112 2018). Natural lentic waters are scarce. In fact, of 35,048 ha total standing waters in Lower Saxony 73  
113 % by area and more than 99 % by number are artificial lakes, mainly ponds and small gravel pit lakes  
114 with less than 10 ha surface area (Manfrin et al., unpublished data).

115 Most gravel pit lakes in Lower Saxony, and Germany as a whole, are managed for recreational  
116 fisheries by angler associations and clubs. These lakes are thus exposed to regular stocking with  
117 species of fisheries interests and experience access and harvest rules, regular controls by fisheries  
118 inspectors, and fishing club activities like collecting litter and cleaning and development of the littoral  
119 zone (Theis, 2016). Similar activities are absent in gravel pit lakes not used for recreational fisheries,  
120 which are much rarer in number but still occur in Lower Saxony and elsewhere across Germany. For  
121 our study, we selected a set of gravel pit lakes managed by recreational fisheries (defined as  
122 managed lakes) and another set of lakes not experiencing any form of legal angling and recreational  
123 fishing-related management (defined as unmanaged lakes, Table 1).

124 We identified managed lakes through a survey of all angling clubs organized in the Angler Association  
125 of Lower Saxony. Lakes were selected according to the following criteria. The lake shall be in  
126 ownership of a fishing club, of small size (1-20 ha) and with no dredging in the last ten years (“old  
127 age”). This approach yielded N = 16 managed lakes as study sites spread across Lower Saxony in 10  
128 angling clubs (Table 1, Figure 1). The angler density (number of anglers per unit water area) for these  
129 clubs ranged from 8 to 43 anglers per hectare (mean ± SE: 21 ± 3.6 anglers per ha). These average  
130 angler densities correspond to averages known for German and Lower Saxonian angling clubs with 24  
131 ± 2.5 and 22 ± 10.8 anglers per ha, respectively. All selected angler-managed lakes experienced  
132 regular angling activities and fisheries-management actions, including annual stocking of a range of  
133 fish species and regular shoreline development activities.

134 Gravel pits not managed by and for anglers were identified in close vicinity to the managed lakes  
135 (Figure 1). The number of unmanaged lakes available was much smaller than the number of managed  
136 lakes. Overall, we identified N = 10 unmanaged lakes that were of similar age, size and other  
137 environmental conditions to the managed lakes, but differed from the managed ones by the absence  
138 of an angling club and any form of legal angling and fisheries-management for at least 5 years prior

139 to the onset of our study (Table 1, Figure 1). Both lakes types were accessible to non-angling  
140 recreation as they were not fenced.

141 In a subset of the selected lakes, Matern et al. (2019) previously conducted fish faunistic surveys  
142 revealing identical fish abundances and biomasses in both lakes types, but larger local fish species  
143 richness and significantly more abundant game fishes (particularly predators and large-bodied  
144 cyprinids such as carp, *Cyprinus carpio*) in managed lakes compared to unmanaged ones. These data  
145 showed that the angler-managed lakes included in our study were indeed more intensively managed  
146 in terms of fish stocking and hosted a substantially different fish community. This finding was a  
147 relevant precondition of the study design to show that managed and unmanaged lakes particularly  
148 differed in traces left by fisheries-management and fisheries use both in terms of fish community  
149 composition and angler presence in the littoral zone.

150 Despite our attempt to select lakes as similar as possible in terms of the environment (e.g., age, size,  
151 trophic state), just differentiated by the presence or not of recreational fisheries, we statistically  
152 controlled for possible confounding factors affecting the taxonomic biodiversity at both lake types.  
153 To that end, a set of environmental variables were assessed and integrated into the statistical  
154 analyses to more carefully isolate the possible impact of recreational-fisheries management on  
155 biodiversity, while controlling for other key environmental differences among lakes that could also  
156 affect the community composition of specific taxa (e.g., morphometry, land use). We in turn describe  
157 the assessment of the various environmental indicators.

#### 158 *Land use*

159 Several indicators of land use and spatial arrangement in Lower Saxony across catchments were  
160 assessed to account for potential land use effects on the studied aquatic and riparian taxa. Shortest-  
161 path distances of lakes to nearby cities, villages, lakes, canals and rivers were calculated in Google  
162 Maps (© 2017). Subsequently, a share of different land use categories within 100 m around each lake  
163 (buffer zone) was calculated in QGIS 3.4.1 with GRASS 7.4.2 using ATKIS® land use data with a 10 x 10  
164 meter grid scale (© GeoBasis-DE/BKG 2013; Adv, 2006). The ATKIS®-object categories were merged  
165 to seven land use classes: (1) urban (all anthropogenic infrastructures like buildings, streets, railroad  
166 tracks etc.), (2) agriculture (all arable land like fields and orchards but not meadows or pastures), (3)  
167 forest, (4) wetland (e.g., swamp lands, fen, peat lands), (5) excavation (e.g., open pit mine), (6) water  
168 (e.g., lakes, rivers, canals) and (7) other (not fitting in previous classes like succession areas, grass  
169 land, boulder sites etc.).

#### 170 *Recreational use intensity*

171 The lake-specific recreational use intensity was assessed by counting the type and number of  
172 recreationists during each site visit (between six and nine visits per lake, see biodiversity sampling

173 below). Indirect use intensity metrics encompassed measures of accessibility and litter, which were  
174 assessed as follows: the pathways around every lake were enumerated with a measuring wheel  
175 (NESTLE-Cross-country Model 12015001, 2 m circumference, 0.1% accuracy), measuring the length of  
176 all trails and paths at each lake. These variables were summed and normalized to shoreline length.  
177 Angling sites and other open spaces accessible to other recreationists (e.g., swimmers) along the  
178 shoreline were counted, and all litter encountered along paths and sites was counted and assigned to  
179 (1) angling-related (e.g., lead weight, nylon line, artificial bait remains) and (2) other litter not directly  
180 angling-related (e.g., plastic packaging, beer bottles, cigarette butts). More intensively used lakes  
181 were expected receiving larger amount of litter and being more easily accessible through paths and  
182 trampled sites, which could affect biodiversity negatively.

### 183 *Age and morphology*

184 The age of each lake was assessed through records in the angling clubs and by interviewing owners of  
185 lakes and regional administration or municipalities. Bathymetry and the size of each lake was  
186 mapped with a SIMRAD NSS7 evo2 echo sounder paired with a Lawrence TotalScan transducer  
187 mounted on a boat driving at 3 – 4 km/h along transects spaced at 25-45 m depending on lake size  
188 and depth. The data were processed using BioBase (Navico), and the post-processed data (depth and  
189 gps-position per ping) were used to calculate depth contour maps using ordinary kriging with the  
190 gstat-package in R (Gräler, Pebesma, & Heuvelink, 2016; R Core Team, 2013). Maximum depth and  
191 relative depth ratio (Damjanović et al., 2018) were extracted from the contour maps. Shoreline  
192 length and lake area were estimated in QGIS 3.4.1 and used to calculate the shoreline development  
193 factor (Osgood, 2005).

### 194 *Water chemistry and nutrient levels*

195 During spring overturn, epilimnic water samples were taken for analyzing total phosphorus  
196 concentrations (TP), total organic carbon (TOC), ammonium and nitrate concentrations ( $\text{NH}_4$ ,  $\text{NO}_3$ )  
197 and chlorophyll a (Chl-a) as a measure of algal biomass. TP was determined using the ammonium  
198 molybdate spectrophotometric method (EN ISO 6878, 2004; Murphy & Riley, 1962), TOC was  
199 determined with a nondispersive infrared detector (NDIR) after combustion (DIN EN 1484, 1997),  
200 ammonium and nitrate were assessed using the spectrometric continuous flow analysis (DIN EN ISO  
201 13395, 1996; EN ISO 11732, 2005), and Chl-a was quantified using high performance liquid  
202 chromatography (HPLC), where the phaeopigments (degradation products) were separated from the  
203 intact chlorophyll a and only the concentration of the latter was measured (Mantoura & Llewellyn,  
204 1983; Wright, 1991). Also during spring overturn, the lake's conductivity and pH were measured in  
205 epilimnic water with a WTW Multi 350i sensor probe (WTW GmbH, Weilheim, Germany), and  
206 turbidity was assessed using a standard Secchi-disk.



207 *Littoral and riparian habitat assessment*

208 Riparian structures and littoral dead wood was assessed using a plot design inspired by Kaufmann &  
209 Whittier (1997). Each plot consisted of a 15 x 4 meter riparian sub-plot, a 1 x 4 meter shoreline band,  
210 and a 4-meter-wide littoral transect extending into the lake to a maximum of ten meters or a water  
211 depth of three meters. At each lake the position of the first plot was randomly selected and  
212 subsequent plots placed every 100 (or 150 meters for larger lakes) apart along the shoreline until the  
213 lake was surrounded, resulting in 4-20 plots per lake (depending on lake size). In each riparian sub-  
214 plot and shoreline band, all plant structures (e.g., trees, tall herbs, reed) were assessed following the  
215 protocol of Kaufmann & Whittier (1997) as 0 - absent, 1 - sparse (< 10 % coverage), 2 - moderate (10-  
216 39 % coverage), 3 - dominant (40-75 % coverage), and 4 - very dominant (> 75 % coverage). In each  
217 littoral transect all dead wood was counted, and length and bulk diameters measured. Additionally,  
218 the width and height of each coarse woody structure was assessed, and each piece assigned to either  
219 (1) simple dead wood (bulk diameter < 5 cm and length < 50 cm, no or very low complexity), or (2)  
220 coarse woody structure (bulk diameter > 5 cm and/or length > 50, any degree of complexity)  
221 following the criteria of DeBoom & Wahl (2013). Further, for each dead wood structure the volume  
222 was calculated using the formula for a cylinder for simple dead wood and for an ellipsoid for coarse  
223 woody structure.

224 *Riparian plant species*

225 All lakes were sampled for riparian plant species at four transects (one per cardinal direction) in May.  
226 Each transect was 100 m long and contained five evenly spaced (20 m distance) 1 m<sup>2</sup>-plots. Along the  
227 transects trees (>2 m high) were identified using Spohn, Golte-Bechtle, & Spohn (2015) and counted.  
228 Within each sampling plot, riparian vascular plants (<2 m high) were identified following the same  
229 key (Spohn et al., 2015) and their abundance assessed following Braun-Blanquet (1964): “r” = 1  
230 individual, “+” = 2 – 5 individuals but < 5 % coverage, “1” = 6 – 50 individuals but < 5 % coverage,  
231 “2m” = > 50 individuals but < 5 % coverage, “2a” = 5 – 15 % coverage, “2b” = 16 – 25 % coverage, “3”  
232 = 26 – 50 % coverage, “4” = 51 – 75 % coverage, “5” = 76 – 100 %. The regional species pool was  
233 estimated from the Red Lists of Lower Saxony (Garve, 2004) in combination with their expected  
234 occurrence according to habitat type and species habitat preferences.

235 *Submerged macrophytes*

236 All lakes were sampled for submerged macrophytes between late June and late August, following the  
237 sampling protocol of Schaumburg et al. (2014). Every lake was scuba dived and snorkeled along  
238 transects set perpendicular to the shoreline from the bank (depth = 0 m) to the middle of the lake  
239 until the deepest point of macrophyte growth was reached. The position of the first transect was  
240 randomly chosen and all other transects spaced evenly along the shoreline at 80-150 m distances

241 depending on lake size, resulting in 4-20 transects sampled per lake. Along each transect, in every  
242 depth stratum (0-1 m, 1-2 m, 2-4 m, 4-6 m) the dominance of submerged macrophyte species was  
243 visually estimated following the Kohler scale: “0 – absent”, “1 – very rare”, “2 – rare”, “3 –  
244 widespread”, “4 – common”, “5 – very common” (Kohler, 1978). No macrophytes were found below  
245 6 m depth. Macrophytes were identified under water according to Van de Weyer & Schmitt (2011). If  
246 this was not possible, samples were taken and identified under a stereomicroscope following Van de  
247 Weyer & Schmitt (2011). Stonewort species were only identified to the genus level (*Chara* spec. or  
248 *Nitella* spec.), thus exact species numbers might be underestimated. Macrophytes dominance was  
249 transformed to percent coverage for each transect (Van der Maarel, 1979). The average coverage per  
250 stratum was extrapolated to the total lake using the contour maps. The total macrophyte coverage in  
251 the littoral zone was calculated using the extrapolated coverage from strata between 0 m and 3 m  
252 depth. The regional species pool was estimated from the Red Lists of Lower Saxony in combination  
253 with the expected species for gravel pit lakes following the list of plant species associations in Lower  
254 Saxony (Garve, 2004; Korsch, Doege, Raabe, & van de Weyer, 2013; Preising et al., 1990).

#### 255 *Amphibians*

256 Amphibians were sampled during the mating-seasons (from March to May). Every lake was sampled  
257 twice: (1) during the day with an inflatable boat driving slowly along the shore searching for adults,  
258 egg-balls (frogs) and egg-lines (toads), (2) after sunset by feet around the lake searching for calling  
259 adults. Each observation (adult or eggs) was marked with a GPS (Garmin Oregon 600), identified in  
260 the field or photographed for later identification following Schlüpmann (2005). Numbers were  
261 recorded (adults) or estimated (eggs), assuming 700 to 1500 eggs per egg-ball (frogs) or 10,000 eggs  
262 per (100 % covered) m<sup>2</sup> of egg-line-assemblages (toads). The egg numbers were calculated from  
263 pictures taken in the field and verified with literature (Trochet et al., 2014). The regional species pool  
264 was estimated from the Red List of Lower Saxony in combination with their expected distribution  
265 (Podloucky & Fischer, 2013).

#### 266 *Odonata*

267 Dragonflies and damselflies were sampled once per lake between early- and mid-summer. At each  
268 lake, the whole shoreline was intensively searched during mid-day. Sitting or flushing imagines were  
269 caught with a hand net (butterfly net, 0.2 mm mesh size, bioform), identified using Lehmann & Nüss  
270 (2015), and released without being harmed. The regional species pool was estimated from the Red  
271 List of Lower Saxony in combination with their expected habitat preferences (Altmüller & Clausnitzer,  
272 2010; Hein, 2018).

273 *Waterfowl and songbirds*

274 Waterfowl were identified following Dierschke (2016), counted and protocolled at every visit  
275 (between six and nine visits per lake). Songbirds were sampled once per lake between early- and  
276 mid-summer using a point-count sampling combined with a bioacoustics approach which was also  
277 used in other studies (Rempel, Hobson, Holborn, Van Wilgenburg, & Elliott, 2005; Wilson, Barr, &  
278 Zagorski, 2017). We took 2-minutes audio-recordings (ZOOM Handy Recorder H2, Surround 4-  
279 Channel setting, 44.1kHz sampling frequency, 16 bit quantification) at sampling points placed 200 m  
280 apart around the whole lake, assuming each sampling point covers a radius of 100 m. Sampling  
281 points were marked with GPS. At each point all birds seen or heard were protocolled when identified  
282 following Dierschke (2016). The audio-records were analyzed in the lab, and singing species were  
283 identified using reference audio samples ([www.deutsche-vogelstimmen.de](http://www.deutsche-vogelstimmen.de); [www.vogelstimmen-wehr.de](http://www.vogelstimmen-wehr.de)) and a birdsong-identifying software (BirdUp - Automatic Birdsong Recognition, developed  
284 by Jonathan Burn, Version 2018). The regional species pools for waterfowl and songbirds were  
285 estimated from the Red List of Lower Saxony (e.g. waders; Krüger & Nipkow, 2015) in combination  
286 with their expected occurrence according to habitat type and preferences.  
287

288 *Diversity metrics*

289 We focused on the analysis of species presence-absence data to arrive at measures of taxonomic  
290 species richness to serve as an aggregate index of species diversity. Additionally, using relative  
291 abundance data by species we computed the Simpson diversity index (Pielou, 1969) to consider the  
292 dominance of certain species within the taxa-specific community. We were not interested in whether  
293 a particular species detected actually recruits in a given gravel pit lake, rather we were interested in  
294 the species inventory present, assuming our estimates represented a minimal estimate of local  
295 richness as rare species likely remained undetected. To weigh rare and threatened species more, we  
296 additionally computed the richness of threatened species and estimated an index of taxon-specific  
297 conservation value for the study region following Oertli et al. (2002). To that end, each species was  
298 ranked according to its threat status on the Red Lists of Lower Saxony (Altmüller & Clausnitzer, 2010;  
299 Garve, 2004; Korsch et al., 2013; Krüger & Nipkow, 2015; Podlucky & Fischer, 2013). Species of least  
300 concern were ranked lowest ( $c(0) = 2^0 = 1$ ). All species classified with an increasing threat status  
301 category  $r$  according to the regional Red List were weighted exponentially more strongly as  $c(r) = 2^r$   
302 (Table 2) following Oertli et al. (2002)**Error! Reference source not found.** For each lake, the final  
303 taxon-specific conservation value ( $CV$ ) was calculated as the sum of all values for the observed  
304 species  $S_i$  ( $S_1, S_2, S_3, \dots, S_n$ ) divided by the total number of species ( $n$ ) for a given taxon:

305

$$CV = \frac{1}{n} * \sum_{S_i=1}^{S_n} c(r_{S_i}).$$

306 The conservation index value increases with more species of a given taxon being threatened or rare.  
307 We tested a range of different allocations of threat status to estimate the conservation value, using  
308 also national and European red lists; however, the results remained robust. For space reasons, we  
309 just report the regional index here.

310 Finally, to test for differences in species composition across all lakes, the pooled species inventory by  
311 lake type (managed and unmanaged) was used and the Sørensen index (Sørensen, 1948) as a  
312 measure of community similarity was calculated. The Sørensen index ranges from 0 (no species in  
313 common among the two lake types) to 1 (all species the same) and is calculated as  $\frac{2a}{2a+b+c}$ , with  $a$   
314 being the number of shared species and  $b$  and  $c$  being the numbers of unique species to each lake  
315 type, respectively. Following Matthews (1986), faunal or floral breaks, i.e. substantial (i.e.,  
316 biologically meaningful) differences in species composition, among lake types were assumed to occur  
317 when the Sørensen index was  $< 0.5$ .

### 318 *Statistical analysis*

319 The impact of the presence of recreational-fisheries management on aquatic and riparian  
320 biodiversity was tested in two steps.

321 First, differences in taxon-specific species richness, Simpson diversity index, richness of threatened  
322 species, conservation value and as well as key environmental variables between lake types (managed  
323 and unmanaged gravel pits) were assessed with univariate statistics. To that end, mean differences  
324 among lake types were tested using Student's  $t$  (in case of variance homogeneity) or Welch-F (in case  
325 of variance heterogeneity) whenever the error term was normally distributed (Shapiro-Wilk-test).  
326 Otherwise, a Mann-Whitney-U-test of median differences was used. P-values were Sidak-corrected  
327 (Šidák, 1967) for multiple comparisons. Significance was assessed at  $p < 0.05$ .

328 Second, we modelled the among-lake variation in species richness as a function of management type  
329 and a set of lake-specific environmental descriptors. These analyses aimed at further isolating an  
330 impact of fisheries management and type of recreational uses on species inventory across all taxa  
331 and lakes in a joint model that included other predictor variables of the lake environment. To reduce  
332 the dimensionality of the environmental variables, a Principal Component Analyses (PCA) was  
333 conducted without rotations (PCA; Mardia, Kent, & Bibby, 1979) in "classes of environmental  
334 variables" (e.g., morphology, productivity, habitat structure, land use, recreational use).  
335 Environmental variables forming Principal Components (PC) were considered correlated, their  
336 loadings identified, the axis meanings interpreted, and the PC scores used as indicator variables. We  
337 then conducted multivariate Redundancy Analyses (RDA; Legendre & Legendre, 2012) to examine if  
338 recreational fisheries management explains variation in either environmental variables or species  
339 richness across multiple taxa in the multivariate space. In addition to management type, all relevant

340 environmental variables (e.g., trophic state, lake size/steepness, land use, riparian/littoral habitat  
341 structure, water chemistry), recreational use intensity, gravel pit age, and catchment were included  
342 in the multivariate analysis of species richness. With the RDA, we used a forward selection process  
343 (Blanchet, Legendre, & Borcard, 2008) to identify the most explaining environmental predictors of  
344 species richness across different taxa and lakes, including management as a key variable of interest in  
345 this study. Using the variance inflation factor (VIF; Neter, Kutner, Nachtsheim, & Wasserman, 1996)  
346 correlated environmental variables were removed before model building. All data were scaled and  
347 centered (z-transformation) prior to analyses. The degree of explanation was expressed using the  
348 adjusted coefficient of multiple determination ( $R^2_{adj.}$ ). Variables significantly explaining variation in  
349 richness across lakes were also assessed using ANOVA (Analysis of variance, Chambers & Hastie,  
350 1992) at a significance level of  $p < 0.05$ . All calculations and analyses were carried out in R using the  
351 vegan-package (Oksanen et al., 2018; R Core Team, 2013).

### 3. Results

#### 352 *Description of lake types in relation to the environment*

353 The studied lakes were, on average, small (mean  $\pm$  SD, area  $6.5 \pm 5.2$  ha, range 0.9 – 19.5 ha), shallow  
354 (maximum depth  $9.6 \pm 5.2$  m, range 1.1 – 23.5 m) and mesotrophic (TP  $26.3 \pm 30.9$   $\mu\text{g/l}$ , range 8 - 160  
355  $\mu\text{g/l}$ ) with moderate visibility (Secchi depth  $2.4 \pm 1.4$  m, range 0.5 – 5.5 m) (Table 3). The land use in a  
356 100 m buffer around the lake was, on average, characterized by low degree of forestation (mean  $16 \pm$   
357  $21$  %, range 0 – 72.6 %) and high degree of agricultural land use (mean  $27 \pm 22$  %, range 2.4 – 79 %).  
358 Lakes were, on average, situated close to both human settlements (mean distance to the next village  
359  $618.3 \pm 533.4$  m, range 20 – 1810 m) and other water bodies (mean distance to next lake, river, or  
360 canal  $55.8 \pm 84.7$  m, range 1 – 305 m). Gravel pit lakes were all in an advanced stage of succession  
361 and on average  $27.3 \pm 13.3$  years old (range 6 – 54 years, see Tables S1-S4 for detailed lake-specific  
362 environmental variables). The study lakes belong to four different watersheds (small North Sea  
363 tributaries and the catchments of the rivers Ems, Weser and Elbe; Table 1, Figure 1).

#### 364 *Environmental characteristics of managed and unmanaged gravel pit lakes*

365 Both lake types did not statistically differ in age, size, trophic state, and land use (Table 3). A similar  
366 result was revealed in a multivariate RDA, which confirmed the absence of significant differences  
367 between managed and unmanaged lakes in “classes of environmental variables” (i.e., PC scores, for  
368 details see Tables S5, S6) representing morphology (an index of steepness and water body size;  $R^2_{\text{adj.}}$   
369 = -0.005,  $F = 0.86$ ,  $p = 0.470$ ), trophic state ( $R^2_{\text{adj.}}$  = -0.006,  $F = 0.86$ ,  $p = 0.544$ ), proximity to  
370 alternative water bodies ( $R^2_{\text{adj.}}$  = -0.023,  $F = 0.45$ ,  $p = 0.867$ ), proximity to human presence ( $R^2_{\text{adj.}}$  =  
371 0.035,  $F = 1.90$ ,  $p = 0.143$ ) and land use variables ( $R^2_{\text{adj.}}$  = 0.033,  $F = 1.85$ ,  $p = 0.135$ ). However, in  
372 multivariate space the habitat structure differed significantly among managed and unmanaged lakes  
373 along the first PC axis (Dim 1), which represented a vegetation gradient below and above water  
374 (Figure 2). Along this axis, managed lakes were found to be more vegetated than unmanaged ones in  
375 both the riparian and the littoral zones ( $R^2_{\text{adj.}}$  = 0.056,  $F = 2.48$ ,  $p = 0.022$ ).

#### 376 *Recreational uses of managed and unmanaged lakes*

377 The two lake types differed strongly in terms of recreational use intensity, particularly in relation to  
378 the observed angling intensity. As intended by our study design, managed lakes revealed, on  
379 average, significantly higher angling use intensity indexed by a diverse set of variables like angling  
380 litter density, extension of open sites, paths and trails and number of anglers observed (Table 4). By  
381 contrast, the average recreational use intensity of managed and unmanaged lakes by non-angling  
382 recreationists (e.g., swimmers) did not statistically differ when analyzed by univariate statistics on a  
383 variable-by-variable level (Table 4). However, when all indicator variables of the recreational use,

384 both angling and non-angling, were combined in a multivariate RDA analysis as a function of  
385 management type, managed lakes separated from unmanaged lakes along PC axis 1. This axis  
386 represented differences in recreational use intensity by both anglers and other recreationists  
387 (particularly swimmers) and extension of trails and paths (Figure 3,  $R^2_{adj.} = 0.16$ ,  $F = 5.76$ ,  $p < 0.001$ ).  
388 Note that there was no differentiation among lake types along the second PC axis of the recreational  
389 variables (Figure 3), which represented shoreline inaccessibility.

#### 390 *Species diversity and taxon-specific conservation value in managed and unmanaged gravel pit lakes*

391 In total 41 submerged macrophytes species were detected, 191 riparian vascular plants, 44 trees, 3  
392 amphibians, 33 Odonata, 36 songbirds and 34 waterfowl species. This species inventory represented  
393 a substantial fraction of the regional species pool of trees (59 %), Odonata (56 %) and waterfowl (45  
394 %). By contrast, only one third or less of the regional species pool of vascular plant species (12 %),  
395 submerged macrophytes (33 %), songbirds (33 %) and amphibians (38 %) was detected. Only few  
396 species non-native to Lower Saxony or Germany were found: 4 submerged macrophyte species (e.g.,  
397 *Elodea nuttallii*, [Planch.] H. St. John, which is invasive), 4 riparian tree species, 2 waterfowl species  
398 (e.g., *Alopochen aegyptiaca*, L., which is invasive), 1 riparian vascular plant species, and 1 dragonfly  
399 species.

400 Based on the pooled species inventories (gamma diversity), unique species (i.e. species present in  
401 only one lake or only one lake type) were found in all taxa except amphibians (Table 5). Managed  
402 lakes hosted more unique species within most taxa than unmanaged lakes, while unmanaged lakes  
403 had more unique Odonata. No faunal or floral breaks were detected between managed and  
404 unmanaged lakes using the Sørensen index (all indices  $\geq 0.5$ ; Table 5). The average taxon-specific  
405 species richness (alpha-diversity), the Simpson diversity index, the average number of threatened  
406 species and the average taxon-specific conservation value were statistically similar in managed and  
407 unmanaged lakes across all taxa when analyzed using univariate statistics (Table 6).

#### 408 *Environmental correlates of among-lake variation in species richness*

409 Across lakes, species richness of amphibians, Odonata, songbirds and riparian vascular plant species  
410 covaried along the first axis (Figure 4), collectively representing riparian diversity (for full PCA results,  
411 see Table S8). The second PCA axis represented mainly submerged macrophytes (Figure 4). The third  
412 axis was related to the diversity of riparian tree species and the fourth mainly to waterfowl diversity  
413 (Figure 5). Therefore, lakes offering high riparian species richness were not necessarily rich in in-lake  
414 biodiversity (represented by submerged macrophytes and waterfowl) or tree biodiversity. The RDA  
415 analysis to explain the among-lake variation in species richness as a function of management type  
416 alone revealed no influence of this factor on among-lake richness across several taxa (RDA,  $R^2_{adj.} =$   
417  $0.028$ ,  $F = 1.73$ ,  $p = 0.114$ ).

418 All environmental variables subsumed by PC-scores into environmental predictors and lake age had  
419 acceptable inflation factors ( $VIF < 5$ , maximum: 4.98, supplement Table S7) and were used along with  
420 watershed association and management type in the full RDA analysis to explain among-lake species  
421 richness jointly across all taxa. The RDA-based forward model selection retained a few environmental  
422 variables as key correlates of species richness of multiple taxa across lakes, but management type  
423 dropped from the best model (Table 7). Therefore, among lake variation in richness across several  
424 aquatic and riparian taxa was solely explained by environmental factors unrelated to either  
425 management type or recreation-related variables. Specifically, the coverage of woody habitat along  
426 the littoral was negatively correlated with riparian species richness and positively correlated with  
427 tree diversity along the first axis in Figure 4. The extent of agricultural land use (representing also  
428 more rural conditions, supplementary Table S6) was positively associated with riparian species  
429 richness (Figure 4). Lake steepness (representing also small lake size and low shoreline development  
430 factor, supplementary Table S5) was negatively correlated with waterfowl species richness (Figure 5).  
431 All other environmental variables, including lake age and watershed were not significant (Table 7).  
432 The best model explained 36 % of the total variance in the multivariate species richness. In this  
433 model, neither management type nor any of the recreational use variables explained variation in  
434 species richness of a range of aquatic and riparian taxa among lakes.



#### 4. Discussion

435 We found support for our study hypotheses. Specifically, in line with initial expectations we found no  
436 differences in species richness, Simpson diversity and conservation value across all examined taxa  
437 among managed and unmanaged gravel pit lakes, and we found a similar species pool to be present  
438 in both lake types. Collectively, our study did not reveal that recreational-fisheries management  
439 (through impacts on fish communities) or the presence of anglers (through disturbance effects on  
440 shoreline habitat and wildlife or lethal impacts through lost fishing gear) significantly constrains the  
441 development of diverse communities of amphibians, birds, submerged macrophytes, terrestrial  
442 plants and Odonata relative to those expected at lakes that are not managed for recreational  
443 fisheries. Instead, we found the best predictors of the variation in species richness among lakes  
444 related to land use variables, the extent of woody habitat at the lake shores and the lake morphology  
445 (size and steepness). Therefore, our study suggests that for the taxa and lake types that we examined  
446 broader environmental factors and land use, and not the presence of recreational fisheries and its  
447 management of fish stocks and littoral zones, shape taxonomic diversity of plants, birds, amphibians,  
448 and dragonflies.

##### 449 *Biodiversity potential of gravel pit lakes*

450 We found gravel pit lakes in Lower Saxony, Germany, to host a substantial species diversity and  
451 fraction of the regional species' pools of aquatic and riparian taxa, in particular trees, Odonata and  
452 waterfowl. This finding supports related work in other areas of Europe (Damnjanović et al., 2018;  
453 Santoul et al., 2009; Spyra & Strzelec, 2019). Yet, only small fractions of the regional species' pools  
454 were detected for vascular plant species, submerged macrophytes, songbirds and amphibians. In  
455 particular amphibians are considered very sensitive to predation from fish (Hecnar & M'Closkey,  
456 1997; Miró et al., 2018). Many amphibian species depend on shallow water and best develop in  
457 small, temporary waters (Porej & Hetherington, 2005; Shulse, Semlitsch, Trauth, & Williams, 2010;  
458 Temple & Cox, 2009). None of our study lakes, however, were free of fish (Matern et al., 2019). Our  
459 gravel pits were also relatively steeply-sloped with small fractions of littoral areas, disconnected from  
460 rivers, placed in agricultural landscapes and close to anthropogenic infrastructure. All of these factors  
461 are negative for amphibian diversity and can explain the low species richness we detected for this  
462 taxon (Porej & Hetherington, 2005; Shulse et al., 2010; Temple & Cox, 2009). Importantly, with our  
463 study results however, management by recreational fisheries and the substantially different fish  
464 communities in managed and unmanaged lakes can be excluded as an additional stressor.

465 *Environmental differences among managed and unmanaged lakes*

466 The gravel pit lakes we studied were similar in the majority of the environmental factors that we  
467 examined (including age) except the coverage of submerged macrophytes, which was more prevalent  
468 in managed gravel pit lakes compared to unmanaged ones. Submerged macrophytes have been  
469 reported to be strongly affected by fish stocking of benthivorous species, such as common carp  
470 (Bajer et al., 2016; Miller & Crowl, 2006). However, in a subset of the same gravel pit lakes presented  
471 in this paper, Matern et al. (2019) found similar biomasses of fishes in managed and unmanaged  
472 lakes. Due to the sampling gear used in the study by Matern et al. (2019), the authors likely  
473 underestimated the abundance and biomass of common carp and other large benthivorous fish  
474 (Ravn et al., 2019). Although no absolute biomass data of carp or other species in our study lakes are  
475 available, the fact that submerged macrophytes were more diverse and more developed in the  
476 angler-managed lakes suggests that co-existence of carp and other game fish with a species rich  
477 submerged macrophyte community, also in terms of threatened stonewort species (*Chara sp.*, *Nitella*  
478 *sp.*), is possible. This disagrees with expectations expressed elsewhere that managing lakes with  
479 benthivorous fish necessarily harms submerged macrophytes (Van de Weyer, Meis, & Krautkrämer,  
480 2015). The more developed submerged macrophytes in managed lakes revealed in this study instead  
481 suggests that critical biomass thresholds for benthivorous fish after which macrophytes typically  
482 vanish or strongly decline (about 100 kg/ha; Vilizzi, Tarkan, & Copp, 2015) might not have been  
483 reached in our study lakes. Alternatively, the transferability of typically mesocosm studies that have  
484 reported substantial impacts of carp on macrophytes to occur after reaching about 100 kg/ha may  
485 not hold under conditions in the wild (Arlinghaus, Hühn, et al., 2017). We speculate the regular  
486 shoreline development activities by anglers and angling clubs to maintain access to angling sites may  
487 create “disturbances” (Dustin & Vondracek, 2017; O’Toole et al., 2009) that regularly interrupt the  
488 succession of tree stands, thereby reducing the shading effects in the littoral zone (Balandier et al.,  
489 2008; Monk & Gabrielson, 1985). Reduced shading of the shallow littoral can promote growth of  
490 submerged macrophytes. Another factor promoting macrophyte growth could be angler-induced  
491 nutrient inputs (Niesar, Arlinghaus, Rennert, & Mehner, 2004), although this factor is unlikely, given  
492 that the trophic variables did not differ among managed and unmanaged lakes in our study.

493 Lake shorelines managed by anglers were previously reported to be heavily modified to  
494 accommodate angling sites and access to anglers (Dustin & Vondracek, 2017; O’Toole et al., 2009).  
495 Although improved accessibility in angler-managed lakes was supported in our study, the amount of  
496 aquatic and riparian vegetation was nevertheless significantly larger in angler-managed systems  
497 compared to unmanaged lakes. This indicates that maintaining accessibility of lakeshores to anglers  
498 does not necessarily mean degraded riparian or littoral habitat quality. In fact, anglers have an  
499 interest to maintain access to lakes to be able to fish, but there is also an interest in developing  
500 suitable habitats for fish (Meyerhoff et al., 2019) and maintaining sites that promise solitude during

501 the experience (Beardmore, Hunt, Haider, Dorow, & Arlinghaus, 2015), which indirectly may also  
502 support biodiversity. The littoral zone is the most productive habitat of lakes (Winfield, 2004), and  
503 fish species depend on submerged macrophytes and other structures for spawning and refuge  
504 (Lewin, Mehner, Ritterbusch, & Brämick, 2014; Lewin, Okun, & Mehner, 2004). At the same time,  
505 crowding is a severe constraint that reduces angler satisfaction (Beardmore et al., 2015). Therefore,  
506 although anglers regularly engage in shoreline development activities and angling site maintenance,  
507 the data of this study suggest they do so to a degree that may maintain or even foster aquatic and  
508 riparian vegetation.

#### 509 *Differences in recreational use of managed and unmanaged lakes*

510 Managed lakes were found to have more developed tracks, paths, parking places and other facilities  
511 that attract anglers and other recreationists. Thus, angler-managed lakes were generally more  
512 accessible to water-based recreationists, although these differences were not always statistically  
513 significant among the two lake types for recreational uses other than angling. Importantly, despite  
514 managed lakes receiving regular fisheries-management activities such as stocking and angler use,  
515 neither “management type” nor the index of general recreational use intensity were related with  
516 species richness across multiple taxa and lakes. Thus, for the diversity metrics and the taxa we  
517 examined (vegetation, odonata, amphibians, birds), our study does not suggest that the use of gravel  
518 pits by recreational fisheries significantly constraints the development of aquatic and riparian  
519 biodiversity across a range of taxa. Clearly, species-specific effects on disturbance-sensitive species  
520 (e.g., selected bird species; Knight, Anderson, & Marr, 1991) may still occur, which our aggregate  
521 metrics of taxonomic richness or the Simpson community diversity index might have been too  
522 insensitive to detect. Further work on community differences among managed and unmanaged lakes  
523 is warranted and will form the basis of a future paper.

#### 524 *Differences in biodiversity among managed and unmanaged lakes*

525 Across all the taxa we examined, no statistical differences were found in species richness, number of  
526 threatened species, conservation value and Simpson diversity between managed and unmanaged  
527 lakes. This result was unexpected. Recreational-fisheries management can affect aquatic and riparian  
528 biodiversity through various pathways, first through supporting and enhancing fish stocks that exert  
529 predation pressure (e.g., on tadpoles and Odonata larvae; Hecnar & M’Closkey, 1997; Knorp & Dorn,  
530 2016), second through indirect fish-based effects (e.g., uprooting macrophytes through benthivorous  
531 feeding; Bajer et al., 2016), third through direct removal or damage of submerged and terrestrial  
532 plants during angling activities (O’Toole et al., 2009), which may have knock-on effects on dragonflies  
533 (Z. Müller et al., 2003), and forth through activity-based disturbance effects or lethal impacts through  
534 lost fishing sinkers in particular on birds (Cryer et al., 1987; Sears, 1988). Our study design was not  
535 tailored towards directly measuring disturbance effects on particular species; instead we choose to

536 aggregately look at a range of taxonomic richness indices for communities present at gravel pit lakes  
537 that are associated with recreational fisheries compared to ecologically similar lakes that do not.  
538 When judged against these aggregate biodiversity metrics, our work does not support the idea that  
539 recreational-fisheries management and angler presence has important impacts that modify species  
540 inventories to a degree that strongly depart from situations expected at unmanaged lakes without  
541 anglers. Previous work has reported relevant reductions in bird biodiversity from lakes exposed to  
542 human disturbances due to recreation including angling (Bell et al., 1997; Newbrey, Bozek, &  
543 Niemuth, 2005). However, we found similar species richness and conservation value of both  
544 waterfowl and riparian songbirds in managed and unmanaged lakes. This does not exclude the  
545 possibility that for example the breeding success of specific disturbance-sensitive taxa might have  
546 been impaired in angler-managed lakes (Park, Park, Sung, & Park, 2006; Reichholf, 1988). But if such  
547 effects were present, they were not strong enough to substantially alter species richness, not to be  
548 confused with species identity. Overall, against the metrics we choose, our findings supported the  
549 initial hypothesis of no impacts from recreational fishing on non-targeted taxa in gravel pits situated  
550 in agricultural landscapes.

551 *Environmental determinants of aquatic and riparian biodiversity in gravel pit lakes*

552 The species richness of different taxa did not uniformly vary among lakes, in contrast to a study of  
553 managed shallow ponds by Lemmens et al. (2013). While examining strictly aquatic taxa  
554 (zooplankton, submerged and emerged aquatic macrophytes, benthic invertebrates), Lemmens et al.  
555 (2013) revealed uniform responses in species richness across taxa and ponds. The much broader  
556 trophic and habitat requirements of aquatic and riparian taxa studied in our work resulted in  
557 significantly more variable biotic responses. For example, lakes rich in riparian biodiversity were not  
558 necessarily rich in submerged macrophytes and waterfowl. The reason is that the biodiversity of  
559 aquatic and riparian biodiversity respond to many more variables than in-lake variables. Our  
560 multivariate analyses revealed the variation in species richness across multiple taxa was driven by  
561 structural variables of the habitat quality, lake morphometry (size and steepness) and land use in a  
562 buffer zone around the lake, but not by recreational use intensity or the presence of recreational-  
563 fisheries management activities. Thus, environmental factors unrelated to recreational fishing seem  
564 to overwhelm any specific impacts of angling, at least for the taxonomic diversity metrics and the  
565 taxa examined in our work.

566 Mosaics of different habitats (reeds, overhanging trees etc.) along the shoreline support species  
567 richness and diversity for most taxa (Kaufmann, Hughes, Whittier, Bryce, & Paulsen, 2014), and the  
568 presence of endangered biodiversity increase the recreational value of gravel pit as perceived by  
569 anglers (Meyerhoff et al., 2019). Extended woody habitat both in water and particularly in the  
570 riparian zone was correlated with increased tree diversity, but reduced riparian species richness of  
571 vascular plants, amphibians, Odonata and songbirds. This might be explained by the shading effect of

572 trees on herbal vegetation (Balandier et al., 2008; Monk & Gabrielson, 1985). Odonata, songbirds  
573 and amphibian species benefited from more vegetated littoral habitats, in agreement with previous  
574 work (Paracuellos, 2006; Remsburg & Turner, 2009; Shulse et al., 2010). The species richness of  
575 waterfowl was strongly governed by lake area and steepness of the littoral, with larger and shallower  
576 lakes having a higher waterfowl species richness, confirming earlier findings by Elmberg, Nummi,  
577 Poysa, & Sjoberg (2006) and Paszkowski & Tonn (2000). The three dominant waterfowl species  
578 (occurring on 85 % or more of sampled lakes) were either omnivorous (mallard, *Anas platyrhynchos*,  
579 L.) or herbivorous-invertivorous (common coot, *Fulica atra*, L., and tufted duck, *Aythya fuligula*, L.). In  
580 addition, 77 % of the lakes were used by grey goose (*Anser anser*, L.), which feeds on terrestrial  
581 plants. Thus, it can be concluded that the dominant waterfowl detected at our studied lakes benefit  
582 from submerged macrophytes or riparian plants, both found to be more abundant at managed lakes.

583 Collectively, our data do not support substantial negative impacts of recreational fisheries  
584 management on the species richness and community diversity of waterfowl and songbirds present at  
585 gravel pit lakes. In a related study from Welsh reservoirs Cryer, Linley, Ward, Stratford, & Randerson  
586 (1987) observed only distributional changes of waterfowl to the presence of anglers and no changes  
587 in abundance. Similarly negligible effects of anglers on piscivorous birds at Canadian natural lakes  
588 were reported by Somers, Heisler, Doucette, Kjoss, & Brigham (2015). Specifically for gravel pit lakes,  
589 Bell et al. (1997) failed to find evidence for impacts of recreational fishing on the community  
590 structure of waterfowl, although in particular diving waterfowl reduced their abundance during  
591 presence of anglers and other recreationists. In that study, similar to ours, habitat quality and lake  
592 size were more important for waterfowl diversity than the bank use by anglers, and their shoreline  
593 management rather supported grazing waterfowl by opening up sites (Bell et al., 1997). This does not  
594 mean that recreational fishing will not impact bird populations at all as for example the breeding  
595 success of disturbance sensitive species might still be impaired (Park et al., 2006; Reichholf, 1988).  
596 Our study design was not designed to examine the breeding success of particular species and rather  
597 focused on aggregate diversity metrics.

### 598 *Limitations*

599 The strength of our study design is the focus on multiple taxa, which is rare in the recreational  
600 ecology literature related to freshwaters. The limitation is that we did not focus on specific species,  
601 and our sampling design does not answer whether the detected mobile species (e.g., birds or  
602 Odonata) recruited in the study lakes or only used them temporarily as feeding or resting habitat.  
603 Moreover, because of adjustments in taxa-specific sampling schemes, in our sampling we might have  
604 underestimated seasonal taxa (amphibians, Odonata) and we likely missed rare species (Yoccoz,  
605 Nichols, & Boulinier, 2001; Zhang et al., 2014). However, even if this is the case the conclusions of  
606 our work are robust because this systematic error affected both management types that we  
607 compared in our study.

608 Our study used a comparative approach where lakes were not randomly allocated to either angler-  
609 managed lakes or controls. However, because the sample of our lakes were all from the same  
610 geographical area and the age of our lakes and the wider environmental factors were mainly similar,  
611 the key differences among lake types related to the presence of recreational fishing. Therefore, we  
612 content that our design would have been able to differentiate strong angling-induced biodiversity  
613 effects would they exist in reality.

614 A further limitation is that our design did not include entirely unused lakes where recreation  
615 whatsoever is prohibited. Our data have to be interpreted against the possibility that gravel pits  
616 situated in reserves with strictly no human access might show higher species diversity than revealed  
617 in our sample lakes. All the lakes were situated in agricultural environments and all were exposed to  
618 a certain recreational use. Background disturbance (Liley, Underhill-Day, Panter, Marsh, & Roberts,  
619 2015) might have affected the observed species pool, affecting the detectability of species in our  
620 study region.

621 The conclusions of our work are also confined to the environmental gradients that we could observe.  
622 For example, higher angler use intensities than found in the present work might reveal different  
623 results.

624 Finally, the recreational use intensity was mainly recorded during weekdays when the field visits  
625 were done. Thus, potential high intensity phases at weekends might be unrepresented. However,  
626 this would even strengthen our conclusions, if the real recreational use of managed lakes was well  
627 beyond what was considered in our analyses.

## 628 *Conclusions*

629 Our study shows that recreational-fisheries management does not constrain the establishment of a  
630 rich biodiversity of aquatic and riparian taxa in and around gravel pit lakes relative to conditions  
631 expected at ecologically similar unmanaged lakes. Environmental variables related to habitat quality,  
632 land use and lake morphometry rather than recreation-related drivers were key in driving the species  
633 richness for multiple taxa across lakes. Our study thus shows that co-existence of recreational  
634 fisheries and aquatic and riparian biodiversity of high conservation value and richness is possible, at  
635 least under the specific ecological conditions of gravel pit lakes in agricultural landscapes.

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## Tables

Table 1: Descriptors of gravel pits sampled in Lower Saxony. Trophic state was determined using Riedmüller, Hoehn, & Mischke (2013).

No.	Lake name	Lake type	water-shed	End of mining	Trophic state	Maximum depth [m]	Lake area [ha]	pH value	Conductivity [S/cm]	Main recreationists and activities identified during on-site visits
01	Chodhemster Kolk	Managed	Ems	1971	Mesotrophic	10.1	3.2	6.7	208	dog walkers
02	Collrunge	Managed	SNST <sup>1</sup>	1982	Mesotrophic	8.6	4.3	7.9	200	Anglers, dog walkers
03	Donner Kiesgrube 3	Managed	Weser	2000	Eutrophic	5.2	1.0	7.8	632	cyclists
04	Kiesteich Brelingen	Managed	Weser	1999	Mesotrophic	8.7	8.5	7.5	299	Anglers, dog walkers
05	Kolshorner Teich	Managed	Weser	1980	Mesotrophic	16.1	4.3	7.6	547	Anglers, horses
06	Linner See	Managed	Ems	2000	Mesotrophic	11.2	17.7	8.5	301	Anglers
07	Meitzer See	Managed	Weser	2006	Oligotrophic	23.5	19.5	7.9	618	Anglers, dog walkers, swimmers
08	Neumanns Kuhle	Managed	Ems	1970	Polytrophic	6.2	6.9	8.6	585	Anglers, dog walkers
09	Plockhorst	Managed	Weser	1998	Eutrophic	8.2	14.3	8.0	338	Anglers, dog walkers, horses
10	Saalsdorf	Managed	Weser	1995	Mesotrophic	9.2	9.0	9.0	566	Anglers, dog walkers
11	Schleptruper See	Managed	Ems	1965	Mesotrophic	10.1	4.0	8.2	502	Anglers, dog walkers
12	Stedorfer Baggersee	Managed	Weser	1983	Eutrophic	2.8	1.9	7.5	352	Anglers, dog walkers
13	Steinwedeler Teich	Managed	Weser	1978	Mesotrophic	9.1	10.4	7.5	742	Anglers, dog walkers, cyclists
14	Wahle	Managed	Weser	1990	Mesotrophic	12.1	8.1	7.6	728	Anglers, dog walkers, cyclists, horses
15	Weidekampsee	Managed	Weser	1994	Oligotrophic	4.3	2.9	8.0	461	Anglers, dog walkers
16	Wiesedermeer	Managed	SNST <sup>1</sup>	1990	Mesotrophic	9.2	2.9	8.0	136	Anglers, dog walkers
17	Bülstedt	Unmanaged	Weser	1991	Polytrophic	1.1	2.4	7.6	285	Birdwatchers
18	Goldbeck	Unmanaged	Elbe	1992	Eutrophic	5.0	2.3	7.9	293	Owner/friends, horses, swimmers
19	Handorf	Unmanaged	Weser	2004	Eutrophic	23.0	13.6	9.2	666	Horses, dogs (commercial)
20	Hänigsen	Unmanaged	Weser	2011	Mesotrophic	12.3	6.2	8.6	437	Swimmers, dog walkers, anglers, campfires, dumping ground
21	Heeßel	Unmanaged	Weser	1963	Eutrophic	7.4	0.9	8.2	537	No
22	Hopels	Unmanaged	SNST <sup>1</sup>	1998	Mesotrophic	14.5	5.5	7.7	215	Swimmers, dog walkers
23	Lohmoor	Unmanaged	Weser	1991	Eutrophic	7.4	4.1	8.2	159	Birdwatchers
24	Pfütze	Unmanaged	Weser	2000	Mesotrophic	7.3	10.6	7.7	342	Dog walkers, canoes, swimmers, cyclists
25	Schwicheldt	Unmanaged	Weser	2007	Mesotrophic	10.0	1.7	8.4	895	Owner/hunter, dog walkers
26	Xella	Unmanaged	Weser	1975	Mesotrophic	7.3	2.1	7.5	957	No (restricted access)

<sup>1</sup>Small North Sea Tributaries

Table 2: Ranking of Red List categories used for calculation of conservation values.

<b>Red List categories of Lower Saxony</b>	<b>Rank <i>r</i></b>	<b>Weight <i>c</i></b>
1 – critically endangered	4	16
2 – endangered R – rare	3	8
3 – vulnerable G – indeterminate	2	4
V – near threatened	1	2
* – least concern – – data deficient	0	1

Table 3: Univariate comparison of environmental variables between managed and unmanaged gravel pit lakes. P-values are Sidak-corrected to account for multiple comparisons within classes of environmental variables, **significant ones ( $p < 0.05$ ) are bolded**, *statistical trends ( $p < 0.1$ ) are in italics*.

Class	Environmental variable (abbreviation)	mean $\pm$ standard deviation (minimum - maximum)		Comparison		
		Managed (N = 16)	Unmanaged (N = 10)	Test *	Statistic	p-value
Morphology	maximum depth in m (MaxDep)	9.7 $\pm$ 4.9 (2.8-23.5)	9.5 $\pm$ 6.0 (1.1-23.0)	U-test	W = 89	0.986
	lake area in ha (LArea)	7.4 $\pm$ 5.6 (1.0-19.5)	4.9 $\pm$ 4.2 (0.9-13.6)	U-test	W = 105	0.592
	shoreline development factor (SDF)	1.5 $\pm$ 0.3 (1.1-2.2)	1.6 $\pm$ 0.3 (1.3-2.2)	t-test	t = -1.0	0.824
	relative depth ratio (RelDepR)	0.04 $\pm$ 0.01 (0.02-0.07)	0.04 $\pm$ 0.02 (0.01-0.07)	t-test	t = -1.1	0.754
Trophic state	total phosphorus in $\mu\text{g/l}$ (TP)	25.7 $\pm$ 36.5 (8-160)	27.2 $\pm$ 20.9 (12-72)	U-test	W = 63.5	0.983
	total organic carbon in mg/l (TOC)	6.6 $\pm$ 2.8 (2.5-13)	6.0 $\pm$ 2.5 (2.9-12.4)	U-test	W = 93	0.997
	mean chlorophyll a in $\mu\text{g/l}$ (CHLa)	11.6 $\pm$ 15.9 (2.05-65.3)	21.2 $\pm$ 26.1 (2.6-90.6)	U-test	W = 53	0.765
	Secchi depth in m (Secchi)	2.6 $\pm$ 1.5 (0.5-5.5)	2.0 $\pm$ 1.1 (0.5-4.5)	t-test	t = 0.9	0.972
	ammonium in $\mu\text{g/l}$ (NH4)	56.9 $\pm$ 71.2 (15.0-240.0)	84.0 $\pm$ 164.8 (15.0-550.0)	U-test	W = 75	1.000
	nitrate in $\mu\text{g/l}$ (NO3)	283.8 $\pm$ 380.4 (5.0-1040.0)	733.0 $\pm$ 984.1 (5.0-2940.0)	U-test	W = 50	0.604
	conductivity in mS/cm (Con)	0.5 $\pm$ 0.2 (0.1-0.7)	0.5 $\pm$ 0.3 (0.2-1.0)	t-test	t = -0.3	1.000
	pH value (pH)	7.9 $\pm$ 0.5 (6.7-9)	8.1 $\pm$ 0.5 (7.5-9.2)	t-test	t = -1	0.967
Habitat structure	volume-% of simple dead wood (SDW_Vol)	0.005 $\pm$ 0.009 (0-0.035)	0.008 $\pm$ 0.010 (0.001-0.028)	U-test	W = 65.5	0.973
	volume-% of coarse woody structure (CWS_Vol)	1.5 $\pm$ 1.4 (0.02-5.6)	1.7 $\pm$ 2.0 (0.02-6.2)	U-test	W = 86.5	1.000
	mean riparian tree coverage on an ordinal scale from 0 to 4 (Rip_Trees)	1.0 $\pm$ 0.2 (0.4-1.5)	0.9 $\pm$ 0.3 (0.4-1.2)	t-test	t = 0.9	0.942
	mean litoral reed coverage on an ordinal scale from 0 to 4 (Reed)	1.3 $\pm$ 0.9 (0-2.5)	0.8 $\pm$ 0.7 (0-1.7)	t-test	t = 1.25	0.779
	mean riparian vascular plants coverage on an ordinal scale from 0 to 4 (Rip_Herbs)	1.7 $\pm$ 0.4 (1.1-3.0)	1.0 $\pm$ 0.7 (0.1-1.9)	U-test	W = 118	0.225
	<i>submerged macrophyte coverage in the littoral zone in % (MP_Cov)</i>	39.3 $\pm$ 19.9 (12.5-82.3)	21.1 $\pm$ 27.5 (0-85.2)	U-test	W = 126	0.083
Age	Lake age in years by 2017 (Age)	29.4 $\pm$ 12.4 (11-52)	23.8 $\pm$ 14.7 (6-54)	t-test	t = 1.05	0.303

\* t-test = Student's t-test / U-test = Mann-Whitney-U-test

Table 4: Univariate comparison of environmental variables between managed and unmanaged gravel pit lakes. P-values are Sidak-corrected to account for multiple comparisons within classes of environmental variables, **significant ones ( $p < 0.05$ ) are bolded**, *statistical trends ( $p < 0.1$ ) are in italics*.

Class	Environmental variable (abbreviation)	mean $\pm$ standard deviation (minimum - maximum)		Comparison		
		Managed (N = 16)	Unmanaged (N = 10)	Test *	Statistic	p-value
Land use	excavation within 100m- buffer in % (Excav)	4.8 $\pm$ 7.2 (0-21.3)	9.4 $\pm$ 14.6 (0-39.0)	U-test	W = 63	0.718
	agriculture within 100m- buffer in % (Agric)	22.8 $\pm$ 19.9 (2.4-55.9)	33.8 $\pm$ 25.4 (3.5-79.0)	U-test	W = 58	0.598
	forest within 100m-buffer in % (Forest)	22.0 $\pm$ 25.1 (0-72.6)	5.6 $\pm$ 6.0 (0-15.5)	U-test	W = 118	0.132
	urban area within 100m- buffer in % (Urban)	27.8 $\pm$ 29.2 (0-87.5)	17.4 $\pm$ 24.5 (0-59.5)	U-test	W = 99	0.767
Water	wetland within 100m-buffer in % (Wetland)	0.9 $\pm$ 3.6 (0-14.4)	5.1 $\pm$ 14.1 (0-45.1)	U-test	W = 61.5	0.504
	water surface within 100m- buffer in % (Water)	9.7 $\pm$ 12.5 (0.9-50.4)	8.7 $\pm$ 8.8 (0.5-30.1)	U-test	W = 80	1.000
	distance to next lake in m (DistLake)	164.1 $\pm$ 236.4 (5-850)	264.1 $\pm$ 440.6 (1-1280)	U-test	W = 87	0.999
	distance to next river in m (DistRiver)	5226.1 $\pm$ 9805.2 (25-29,900)	3999.5 $\pm$ 9841.6 (220-31,920)	U-test	W = 92	0.980
	distance to next canal in m (DistCanal)	312.4 $\pm$ 462.3 (1-1630)	224.5 $\pm$ 367.9 (5-1180)	U-test	W = 84	1.000
Human presence	distance to next road in m (DistRoad)	265.3 $\pm$ 314.4 (15-1010)	558.0 $\pm$ 510.1 (30-1530)	U-test	W = 50.5	0.416
	distance to next settlement in m (DistVille)	504.1 $\pm$ 407.8 (20-1400)	801.0 $\pm$ 673.0 (60-1810)	t-test	t = -1.4	0.530
	distance to next city in m (DistCity)	7135.0 $\pm$ 4087.6 (170-13,130)	5859.0 $\pm$ 4488.3 (1070-15,110)	t-test	t = 0.8	0.917
Recreational use	<b>litter related to angling in numbers per m shore (A_Lit)</b>	<b>0.05 <math>\pm</math> 0.05 (0-0.20)</b>	<b>0.002 <math>\pm</math> 0.007 (0-0.021)</b>	U-test	<b>W = 140.5</b>	<b>0.007</b>
	litter unrelated to angling in numbers/m shore (NonA_Lit)	0.70 $\pm$ 0.50 (0.02-1.48)	0.34 $\pm$ 0.71 (0-2.29)	U-test	W = 126	0.124
	<b>angling-sites and open spaces in % of shoreline(open_sites)</b>	<b>18.5 <math>\pm</math> 19.8 (3.6-87.7)</b>	<b>8.4 <math>\pm</math> 14.4 (0-48.6)</b>	U-test	<b>W = 133</b>	<b>0.044</b>
	<b>trails and paths per shoreline in m/m (Trails)</b>	<b>0.9 <math>\pm</math> 0.1 (0.6-1.1)</b>	<b>0.4 <math>\pm</math> 0.5 (0-1.4)</b>	U-test	<b>W = 138</b>	<b>0.019</b>
	<b>anglers per lake per visit (Anglers)</b>	<b>1.6 <math>\pm</math> 1.6 (0-5.1)</b>	<b>0.1 <math>\pm</math> 0.2 (0-0.8)</b>	U-test	<b>W = 143</b>	<b>0.006</b>
	dog walkers per lake per visit (Dogs)	1.7 $\pm$ 1.9 (0-6)	0.5 $\pm$ 1.0 (0-3.3)	U-test	W = 123.5	0.154
	<i>swimmers per lake per visit (Swimmers)</i>	<i>2.9 <math>\pm</math> 2.6 (0-10)</i>	<i>0.7 <math>\pm</math> 1.0 (0-3.1)</i>	U-test	W = 129.5	0.075
	<i>other recreationists per lake per visit (other_people)</i>	<i>2.9 <math>\pm</math> 3.2 (0.3-11.9)</i>	<i>0.9 <math>\pm</math> 1.4 (0-3.8)</i>	U-test	W = 128.5	0.087

\* t-test = Student's t-test / U-test = Mann-Whitney-U-test

Table 5: Overview about unique species of different taxa found at managed and unmanaged gravel pits in Lower Saxony, Germany. The numbers in brackets refer to single-lake observations, i.e. the number of species found at only one lake each.

Taxon	Species number found only in ...		Sørensen index (similarity)
	...managed lakes	...unmanaged lakes	
submerged macrophytes	15 (13)	10 (9)	0.58
riparian vascular plants	55 (35)	31 (23)	0.73
riparian trees	6 (4)	5 (4)	0.86
amphibians	0 (0)	0 (0)	1.00
Odonata	5 (3)	8 (4)	0.76
songbirds	9 (7)	6 (5)	0.74
waterfowl	10 (3)	6 (3)	0.69

Table 6: Univariate comparison of species richness, Simpson index, threatened species and taxon-specific conservation values in managed and unmanaged gravel pit lakes. **Statistical differences of Sidak-corrected p-values < 0.05 are bolded.**

Diversity measure	Taxa	mean ± standard deviation (minimum - maximum)		Test *	Comparison	
		managed (N = 16)	unmanaged (N = 10)		statistic	p-value
species richness	submerged macrophytes	6.4 ± 3.2 (2-14)	5.2 ± 3.6 (0-11)	t-test	t = 0.91	0.962
	riparian vascular plants	42.3 ± 12.6 (15-57)	49.2 ± 11.2 (30-64)	t-test	t = -1.43	0.718
	riparian trees	12.8 ± 2.1 (9-17)	12.6 ± 5.3 (3-24)	F-test	t = 0.08	1.000
	amphibians	1.6 ± 0.5 (1-2)	2.2 ± 0.8 (1-3)	U-test	W = 43	0.220
	- reproducing	1 ± 0.6 (0-2)	1.4 ± 0.8 (0-3)	U-test	W = 59	0.832
	Odonata	7.9 ± 2.8 (2-12)	9 ± 4.3 (4-18)	t-test	t = -0.77	0.985
	- damselflies	4.3 ± 1.3 (2-6)	4.4 ± 1.3 (3-7)	t-test	t = -0.29	1.000
	- dragonflies	3.7 ± 2.1 (0-7)	4.6 ± 3.4 (1-12)	t-test	t = -0.84	0.975
	songbirds	9.2 ± 2.8 (5-14)	11.3 ± 3 (7-17)	t-test	t = -1.81	0.452
waterfowl	9.5 ± 2.8 (3-13)	9.1 ± 3.5 (2-13)	t-test	t = 0.32	1.000	
Simpson index	submerged macrophytes	0.6 ± 0.2 (0.1-0.9)	0.5 ± 0.3 (0-1)	t-test	t = 0.32	1.000
	riparian vascular plants	0.9 ± 0.1 (0.8-0.9)	0.9 ± 0.0 (0.8-0.9)	U-test	W = 79	1.000
	riparian trees	0.7 ± 0.2 (0.2-0.8)	0.7 ± 0.1 (0.4-0.9)	U-test	W = 94	0.990
	amphibians	0.1 ± 0.1 (0-0.4)	0.3 ± 0.2 (0-0.6)	U-test	W = 46	0.382
	- reproduction	0.2 ± 0.4 (0-1)	0.2 ± 0.3 (0-1)	U-test	W = 69.5	0.997
	damselflies	0.5 ± 0.1 (0.3-0.6)	0.6 ± 0.1 (0.4-0.8)	t-test	t = -2	0.339
	dragonflies	0.6 ± 0.3 (0-1)	0.5 ± 0.4 (0-0.9)	U-test	W = 87	1.000
	songbirds	0.8 ± 0.0 (0.7-0.9)	0.9 ± 0.0 (0.8-0.9)	t-test	t = -2.41	0.156
waterfowl	0.7 ± 0.1 (0.3-0.8)	0.7 ± 0.1 (0.4-0.9)	U-test	W = 81	1.000	
threatened species	submerged macrophytes	1.3 ± 1.1 (0-4)	0.6 ± 1.0 (0-3)	U-test	W = 109	0.565
	riparian vascular plants	0.6 ± 0.7 (0-2)	0.5 ± 0.7 (0-2)	U-test	W = 88	0.999
	riparian trees	0 ± 0 (0-0)	0.1 ± 0.3 (0-1)	U-test	W = 72	0.848
	amphibians	0.4 ± 0.5 (0-1)	0.8 ± 0.4 (0-1)	U-test	W = 51	0.440
	Odonata	0.8 ± 0.8 (0-2)	1.3 ± 1.2 (0-4)	U-test	W = 61.5	0.929
	- damselflies	0.3 ± 0.4 (0-1)	0.1 ± 0.3 (0-1)	U-test	W = 92	0.963
	- dragonflies	0.6 ± 0.7 (0-2)	1.2 ± 1.2 (0-4)	U-test	W = 54.5	0.692
	songbirds	0.3 ± 0.5 (0-1)	0.5 ± 0.5 (0-1)	U-test	W = 65	0.958
waterfowl	1.1 ± 1.0 (0-3)	0.9 ± 1.0 (0-3)	U-test	W = 88	1.000	
conservation value	submerged macrophytes	2.0 ± 0.8 (1-3.5)	1.6 ± 1.2 (1-4.6)	U-test	W = 99.5	0.571
	riparian vascular plants	1.1 ± 0.2 (1-1.9)	1.0 ± 0.0 (1-1.1)	U-test	W = 94.5	0.978
	riparian trees	1.0 ± 0.0 (1-1)	1.0 ± 0.1 (1-1.3)	U-test	W = 72	0.848
	amphibians	1.7 ± 0.8 (1-2.5)	2.2 ± 0.9 (1-4)	U-test	W = 61.5	0.924
	Odonata	1.5 ± 0.5 (1-2.3)	1.7 ± 0.5 (1-2.6)	U-test	W = 59.5	0.901
	- damselflies	1.2 ± 0.4 (1-2.2)	1.1 ± 0.2 (1-1.8)	U-test	W = 91.5	0.972
	- dragonflies	1.7 ± 0.9 (1-3.3)	2.2 ± 1.0 (1-3.8)	U-test	W = 55.5	0.889
	songbirds	1.2 ± 0.2 (1-1.6)	1.2 ± 0.1 (1-1.3)	U-test	W = 72.5	1.000
waterfowl	2.2 ± 1.0 (1.1-3.9)	2.2 ± 0.8 (1.2-3.2)	U-test	W = 79	1.000	

\* t-test = Student's t-test / F-Test = Welch-F-test / U-test = Mann-Whitney-U-test



Table 7: ANOVA results of forward selection of RDA models explaining species richness across taxa.

Variables are ordered by their  $R^2_{adj}$ -value. **Significant variables ( $p < 0.05$ ) are bolded.**

Modelling step	Variable	Variance explained	$R^2_{adj}$ *	F-statistic	p-value
full model	<b>woody_habitat</b>	<b>14.7%</b>	<b>0.112</b>	<b>6.63</b>	<b>&lt; 0.001</b>
	<b>watershed</b>	<b>14.8%</b>	<b>0.080</b>	<b>2.22</b>	<b>0.028</b>
	<b>acidity</b>	<b>6.9%</b>	<b>0.063</b>	<b>3.12</b>	<b>0.019</b>
	<b>agricultural_extent</b>	<b>9.1%</b>	<b>0.060</b>	<b>4.10</b>	<b>0.003</b>
	age	3.6%	0.050	1.63	0.165
	<b>lake_steepness</b>	<b>6.9%</b>	<b>0.043</b>	<b>3.12</b>	<b>0.015</b>
	management	2.3%	0.028	1.04	0.424
	vegetated_habitat	3.8%	0.024	1.73	0.145
	conductivity	4.2%	0.015	1.91	0.116
	nitrogen	3.7%	0.012	1.65	0.160
	wetland	2.3%	0.009	1.04	0.406
	lake_shallowness	3.5%	0.009	1.57	0.186
	inaccessibility	2.2%	0.000	1.00	0.431
	trophic_state	1.1%	-0.004	0.48	0.825
	rural	3.7%	-0.007	1.66	0.163
	general_recreational_use_intensity	2.1%	-0.011	0.96	0.466
	forest_extent	2.4%	-0.015	1.10	0.379
	distance_to_next_river	1.4%	-0.016	0.65	0.694
	best model	<b>woody_habitat</b>	<b>14.7%</b>		<b>5.05</b>
<b>agricultural_extent</b>		<b>11.8%</b>	<b>0.271</b>	<b>4.06</b>	<b>0.001</b>
<b>lake_steepness</b>		<b>9.3%</b>		<b>3.20</b>	<b>0.004</b>

\*  $R^2_{adj}$ -values are shown for single-variable-models and the best model. The full model has an  $R^2_{adj}$ -value of 0.445.

## Figure legends

Figure 1: Map of study sites in Lower Saxony (Germany) together with the watersheds (green = Ems, orange = Weser, magenta = Elbe, blue = SNST/small North Sea tributaries) and main rivers (dark blue; Ems, Weser, Elbe).

Figure 2: Principal component analysis (PCA) by category of environmental variables visualized for habitat structure (SDW\_Vol = volume-% of simple dead wood, CWS\_Vol = volume-% of coarse woody structure, Rip\_Trees = mean riparian tree coverage, Herb = mean riparian vascular plants coverage, Reed = mean littoral reed coverage, MP\_Cov = submerged macrophyte coverage in the littoral zone; Table 3). Percentages in brackets show the proportional variance explained by each axis respectively. Numbers reflect the different lakes (Table 1). The centroids of management types are plotted as supplementary variables that did not influence the ordination. The 95% confidence-level around centroids are plotted to visualize differences between lake types.

Figure 3: Principal component analysis (PCA) by category of environmental variables visualized for recreational use intensity (A\_Lit = litter related to angling, NonA\_Lit = litter unrelated to angling, open\_sites = angling-sites and open spaces, Trails = trails and paths per shoreline, Anglers = angling people per visit, Dogs = dog walkers per visit, Swimmers = swimming people per visit, other\_people = other recreationists per visit; Table 4). Percentages in brackets show the proportional variance explained by each axis respectively. Numbers reflect the different lakes (Table 1). The centroids of management types are plotted as supplementary variables that did not influence the ordination. The 95% confidence-level around centroids are plotted to visualize differences between lake types.

Figure 4: Principal component analysis (PCA) of species richness plotted for the first two axes (only relevant, i.e. highly contributing, variables are shown). Percentages in brackets show the proportional variance explained by each axis respectively. Numbers reflect the different lakes (Table 1). The centroids of management types and the explanatory variables from redundancy analysis (RDA, slashed purple lines, only the important ones for Dim1 and Dim2 are shown) are plotted as supplementary variables to not influence the ordination. The 95% confidence-level around centroids are plotted to visualize differences between lake types.

Figure 5: Principal component analysis (PCA) of species richness plotted for the third and fourth axis (only relevant, i.e. highly contributing, variables are shown). Percentages in brackets show the proportional variance explained by each axis respectively. Numbers reflect the different lakes (Table 1). The centroids of management types and the explanatory variables from redundancy analysis (RDA, slashed purple lines, only the important ones for Dim3 and Dim4 are shown) are plotted as supplementary variables to not influence the ordination. The 95% confidence-level around centroids are plotted to visualize differences between lake types.









