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. Humanity is facing a biodiversity crisis, with freshwater-associated biodiversity in a particularly dire state. Novel ecosystems created through human use of mineral resources, such as gravel pit lakes, can provide substitute habitats for conservation of freshwater and riparian biodiversity. However, many of these artificial ecosystems may exhibit high recreational use intensity, which may limit their biodiversity potential.

2. The species richness of several taxa (plants, amphibians, dragonflies, damselflies, waterfowl, songbirds) was assessed and a range of taxonomic biodiversity metrics were compared between gravel pit lakes managed for recreational fisheries (N = 16) and unmanaged reference lakes (N = 10), while controlling for non-fishing related environmental variation.

3. The average species richness of all examined taxa was similar among both lake types and no substantial differences in species composition were revealed when examining the pooled species inventory. Similarly, there were no differences among lake types in the presence of rare species and in the Simpson diversity index across all the taxa that were assessed.

4. Variation in species richness among lakes was correlated with woody habitat, lake morphology (surface area and steepness) and land use, but not correlated with the presence of recreational fisheries. Thus, non-fishing related environmental variables had stronger effects on local species presence than recreational-fisheries management or the presence of recreational anglers.

5. Collectively, no evidence was found that anglers and recreational-fisheries management constrain the development of aquatic and riparian biodiversity in gravel pit lakes in the study region. Conservation of species diversity at gravel pit lakes could benefit from an increasing reliance on habitat enhancement activities.

Keywords

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

1. Introduction

Globally, biodiversity is in steep decline, with an estimated 1 million species currently threatened by
extinction (Díaz et al., 2019). The biodiversity decline is particularly prevalent in freshwaters (Reid et
al., 2019), where habitat alteration and fragmentation, pollution, biological invasions and climate
change are key drivers (Dudgeon et al., 2006).

Artificially created aquatic habitats, such as gravel pit lakes or ponds, could maintain and increase
native freshwater biodiversity by providing refuge and secondary habitats for rare or endangered
species (Damnjanović et al., 2018; Oertli, 2018). The origins of artificial lake ecosystems are often
relatively recent (less than 100 years of age; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset,
2016), where artificial lakes are often created by mining for mineral resources (Saulnier-Talbot &
Lavoie, 2018). More than one billion tonnes of sand and gravel were excavated in more than 24,500
quarries and pits within the European Union in 2017 alone (European Aggregates Association (UEPG),
2017). The resulting numerous artificial lakes (for simplicity henceforth referred to as gravel pit lakes)
have become common elements in many cultural landscapes across the industrialized world (Oertli,
2018).

Lakes, including gravel pit lakes, provide many ecosystem services to humans. These include
provisioning services, such as fish yield, as well as a range of cultural services, such as recreation
(Meyerhoff, Klefoth, & Arlinghaus, 2019; Venohr et al., 2018). Although the benefits of water-based
recreation can be substantial, water-based activities can also negatively impact the biodiversity of
freshwater ecosystems (Venohr et al., 2018). For example, human activities can reduce littoral and
riparian habitat quality and thereby negatively affect associated taxa (Spyra & Strzelec, 2019). Water-
based recreation has also been found to negatively impact birds through fright responses to humans
(Dear, Guay, Robinson, & Weston, 2015), dogs (Randler, 2006) or pleasure boats (McFadden,
Herrera, & Navedo, 2017). Therefore, the management of gravel pit lakes and other artificial
waterbodies would benefit from the joint consideration of the well-being aquatic recreation
generates for humans and the possible negative biodiversity impacts from aquatic recreation.

Many gravel pit lakes located in central Europe are used for recreational fisheries (Matern et al.,
2019; Zhao et al., 2016). In some regions of the world anglers are not only resource users, but also
managers of fish populations and habitats (Arlinghaus, Müller, Rapp, & Wolter, 2017). This
particularly applies to Germany, where organizations of anglers, usually angling clubs and
associations, are leaseholders or owners of freshwater fishing rights, and in this position are also
legally entitled to manage fish stocks (Arlinghaus, Müller, et al., 2017). This entails the sovereignty to
stock fish, to manage littoral habitat and introduce access and harvest regulations (Arlinghaus,
Müller, et al., 2017). Because stocking of fish is particularly prevalent in freshwater recreational-

fisheries management, key impacts of the presence of recreational fisheries and associated
management activities can be expected at the fish stock and fish community levels (Matern et al.,
2019; Zhao et al., 2016). Angler-induced changes typically elevate fish species richness through the
release and introduction of large-bodied "game" fishes of high fisheries interest (Matern et al., 2019;
Zhao et al., 2016). In turn, the altered fish community may affect submerged macrophytes, (e.g., due
to introduction of benthivorous fish that uproot macrophytes; Bajer et al., 2016), and other taxa
through predation (e.g., birds: Cucherousset et al., 2012; amphibians: Hecnar & M'Closkey, 1997; or
invertebrates: Knorp & Dorn, 2016). In addition, anglers may modify littoral habitats to create access
to angling sites, thereby affecting species richness of plants (O'Toole, Hanson, & Cooke, 2009) and
dragonflies (Z. Müller et al., 2003), or affecting mobile taxa, such as birds, through direct contact and
disturbances (Bell, Delany, Millett, & Pollitt, 1997; Cryer, Linley, Ward, Stratford, & Randerson, 1987).
Indirectly, angler presence can also inadvertently kill non-targeted wildlife, e.g., through lost fishing
gear that is ingested by birds or where birds become entangled (Franson et al., 2003; Sears, 1988).
Therefore, anglers can both be seen as stewards of aquatic ecosystems (Granek et al., 2008) as well
as a potential threat to certain aquatic taxa depending on the local angling intensity and other
conditions (Reichholf, 1988).

In Germany, fisheries (including recreational angling) are regulated by fisheries laws specific to the
Federal state, while the protection of species and habitat types is regulated by Federal and state-
specific nature conservation legislation. Conflicts with angler interests regularly occur when nature
conservation authorities implement rules that partially or fully constrain access to water bodies to
achieve conservation goals (Arlinghaus, 2005). Conservation-motivated constraints of angling or
recreational-fisheries-management actions (e.g., stocking) are increasingly applied within artificial
lake ecosystems through the implementation of national or international conservation law (e.g., the
European Habitats Directive; Council of the European Communities, 1992). For example, in some
regions of Germany recreational fisheries have been excluded from follow-up use of newly created
gravel pit lakes during the process of licensing the sand or gravel extraction (H. Müller, 2012). Such
bans of future angling use are often justified by the assumption that angling is particularly impactful
for disturbance-sensitive taxa (e.g., waterfowl) or for habitats of special conservation concern (H.
Müller, 2012; Reichholf, 1988).

To contribute to this ongoing debate, the work presented here has studied the taxonomic
biodiversity associated with gravel pit lakes using a space-for-time substitution design comparing
lakes managed and used by recreational fisheries with lakes that do not experience recreational
fisheries actions and therefore lack angler impacts. The study goal was to examine the impact of
recreational fisheries on the taxonomic aquatic and riparian biodiversity detectable at typical gravel
pit lakes in north-western Germany. The specific objective was to estimate the effect of recreational
fisheries on species richness, faunal and floral composition, community diversity and conservation

value across a range of aquatic and riparian taxa that are protected by national and European conservation legislation (e.g., birds, amphibians, dragonflies). Because the absence of recreational fisheries in a given gravel pit lake does not mean the ecosystems remain undisturbed from other recreational uses (e.g., swimming, walking), it was hypothesized that the presence of recreational fisheries and associated management activities would, on average, not affect species richness and conservation value of taxa that are not specifically targeted by anglers (Odonata, amphibians, submerged and riparian vegetation, waterfowl and songbirds). This hypothesis was formulated as a statistical null hypothesis to be falsified by empirical data.

2. Methods

Study area and lake selection

This study was conducted in the Central Plain ecoregion of Lower Saxony in north-western Germany (Figure 1), where natural lentic waters are scarce. Of 35,048 ha of total standing waters in Lower Saxony 73 % by area and more than 99 % by number are artificial lakes. These artificial waterbodies consist of mainly ponds and small gravel pit lakes with less than 10 ha surface area (Nikolaus et al., in review).

Most gravel pit lakes in Lower Saxony, and Germany as a whole, are managed for recreational fisheries by angler associations and clubs. These lakes are thus exposed to regular stocking with species of fisheries interest and are subject to access and harvest rules, regular controls by fisheries inspectors, and fishing club activities like collecting litter and cleaning and development of the littoral zone (Arlinghaus, Müller, et al., 2017). Similar activities are largely absent in gravel pit lakes not used for recreational fisheries, which are much rarer in number but still occur in Lower Saxony and elsewhere across Germany. For this study, a set of gravel pit lakes managed by recreational fisheries (defined as managed lakes) was selected, and compared to another set of gravel pit lakes not experiencing any form of legal angling and recreational fishing-related management (defined as unmanaged lakes, Table 1).

Managed lakes were identified through a survey of all angling clubs organized in the Angler Association of Lower Saxony. Lakes were selected according to the following criteria: the lake was owned by a fishing club, of small size (1-20 ha) and had no dredging in the last ten years ("old age"). This approach yielded N = 16 managed lakes as study sites spread across Lower Saxony in 10 angling clubs (Table 1, Figure 1).The angler density (number of anglers per unit water area) for these clubs ranged from 8 to 43 anglers per hectare (mean ± SE: 21 ± 3.6 anglers per ha). These angler densities correspond to averages known for German and Lower Saxonian angling clubs, which are 24 ± 2.5 and 22 ± 10.8 anglers per ha, respectively. All selected angler-managed lakes experienced regular angling

activities and fisheries-management actions, including annual stocking of a range of fish species and

regular shoreline development activities, such as mowing of angling sites and litter removal.

Gravel pits not managed by and for anglers were identified in close vicinity to the managed lakes

where available (Figure 1). The number of unmanaged lakes in the state was much smaller than the

number of managed lakes. Overall, N = 10 unmanaged lakes were identified, which were of similar

age, size and other environmental conditions to the managed lakes, but differed from the managed

ones by the absence of an angling club and any form of legal angling and fisheries-management for at

least five years prior to the onset of our study (Table 1, Figure 1). Both lake types were accessible to

non-angling recreation as they were not fenced.

In a subset of the selected lakes, Matern et al. (2019) previously conducted fish faunistic surveys

revealing identical fish abundances and biomasses in both lakes types, but larger local fish species

richness and significantly more abundant game fishes (particularly predators and large-bodied

cyprinids such as carp, *Cyprinus carpio*) in managed lakes compared to unmanaged ones. These data

showed that the angler-managed lakes included in this study were indeed more intensively managed

in terms of fish stocking and hosted a substantially different fish community. This finding was a

relevant precondition of the study design in that managed and unmanaged lakes differed in traces

left by fisheries-management and fisheries use, both in terms of fish community composition and

angler presence in the littoral zone.

Despite the attempt to select lakes as similar as possible in terms of the environment (e.g., age,

surface area, trophic state), a set of environmental variables was assessed and integrated into the

statistical analyses to more carefully isolate the possible impact of recreational-fisheries

management on biodiversity, while controlling for other key environmental differences among lakes

that could also affect the community composition of specific taxa (e.g., morphometry, land use,

habitat structure).

Land use

Several indicators of land use and spatial arrangement in Lower Saxony across catchments were

assessed. Shortest-path distances of lakes to nearby cities, villages, lakes, canals and rivers were

calculated in Google Maps (© 2017). Subsequently, a share of different land use categories within

100 m around each lake (buffer zone) was calculated in QGIS 3.4.1 with GRASS 7.4.2 using ATKIS®

land use data with a 10 x 10 meter grid scale (© GeoBasis-DE/BKG 2013; AdV - Working Committee

of the Surveying Authorities of the States of the Federal Republic of Germany, 2006). The ATKIS®-

object categories were merged to seven land use classes: (1) urban (all anthropogenic infrastructures

like buildings, streets, railroad tracks etc.), (2) agriculture (all arable land like fields and orchards but

not meadows or pastures), (3) forest, (4) wetland (e.g., swamp lands, fen, peat lands), (5) excavation

(e.g., open pit mine), (6) water (e.g., lakes, rivers, canals) and (7) other (not fitting in previous classes

like succession areas, grass land, boulder sites etc.).

Recreational use intensity

The lake-specific recreational use intensity was assessed by counting the type and number of

recreationists during each site visit (between six and nine visits per lake, see biodiversity sampling

below). Indirect use intensity metrics encompassed measures of accessibility and litter, which were

assessed as follows: the pathways around every lake were enumerated with a measuring wheel

(NESTLE-Cross-country Model 12015001, 2 m circumference, 0.1% accuracy), measuring the length of

all trails and paths at each lake. These variables were summed and normalized to shoreline length.

Angling sites and other open spaces accessible to other recreationists (e.g., swimmers) along the

shoreline were counted, and all litter encountered along paths and sites was counted and assigned to

(1) angling-related (e.g., lead weight, nylon line, artificial bait remains) and (2) other litter not directly

angling-related (e.g., plastic packaging, beer bottles, cigarette butts). More intensively used lakes

were expected to receive large amounts of litter and be more easily accessible through paths and

trampled sites, which could affect biodiversity negatively.

Age and morphology

The age of each lake was assessed through records in the angling clubs and by interviewing owners of

lakes and regional administration or municipalities. Bathymetry and the size of each lake was

mapped with a SIMRAD NSS7 evo2 echo sounder paired with a Lawrence TotalScan transducer

mounted on a boat driving at $3 - 4$ km/h along transects spaced at 25-45 m depending on lake size

and depth. The data were processed using BioBase (Navico), and the post-processed data (depth and

gps-position per ping) were used to calculate depth contour maps using ordinary kriging with the

gstat-package in R version 3.5.1 (Gräler, Pebesma, & Heuvelink, 2016; R Core Team, 2013). Maximum

depth and relative depth ratio (Damnjanović et al., 2018) were extracted from the contour maps.

Shoreline length and lake area were estimated in QGIS 3.4.1 and used to calculate the shoreline

development factor (*SDF*), which is the ratio of the lakes shoreline length (*L*) to the circumference of

a circle with the same area (*A*): $SDF = \frac{L}{2\sqrt{\pi A}}$

Water chemistry and nutrient levels

During spring overturn, epilimnic water samples were taken to analyze total phosphorus

concentrations (TP), total organic carbon (TOC), ammonium and nitrate concentrations (NH_4, NO_3)

and chlorophyll a (CHLa; three samples per lake) as a measure of algal biomass. TP was determined

using the ammonium molybdate spectrophotometric method (EN ISO 6878, 2004; Murphy & Riley,

1962), TOC was determined with a nondispersive infrared detector (NDIR) after combustion (DIN EN

1484, 1997), ammonium and nitrate were assessed using the spectrometric continuous flow analysis

(DIN EN ISO 13395, 1996; EN ISO 11732, 2005), and CHLa was quantified using high performance
liquid chromatography (HPLC), where the phaeopigments (degradation products) were separated
from the intact chlorophyll a and only the concentration of the latter was measured (Mantoura &
Llewellyn, 1983; Wright, 1991). For CHLa the mean of three samples per lake was determined for
each sampling. Also during spring overturn, each lake's conductivity and pH were measured in
epilimnic water with a WTW Multi 350i sensor probe (WTW GmbH, Weilheim, Germany), and
turbidity was assessed using a standard Secchi-disk. For all variables, the mean values of two years
(i.e. two samplings) were used in the analyses.

Littoral and riparian habitat assessment

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

Riparian plant species

All lakes were sampled for riparian plant species at four transects (one per cardinal direction) in May.
Each transect was 100 m long and contained five evenly spaced (20 m distance) 1 m^2-plots. Along the
transects trees (>2 m high) were identified following Spohn, Golte-Bechtle, & Spohn (2015) and
counted. Within each sampling plot, riparian vascular plants (<2 m high) were identified following the
same key (Spohn et al., 2015) and their abundance assessed following Braun-Blanquet (1964). The
regional species pool was estimated from the Red Lists of Lower Saxony (Garve, 2004), which
includes a full species inventory, in combination with their expected occurrence according to habitat
type and species' habitat preferences.

Submerged macrophytes

All lakes were sampled for submerged macrophytes between late June and late August, following the

sampling protocol of Schaumburg, Schranz, Stelzer, & Vogel (2014). Every lake was scuba dived and

snorkeled along transects set perpendicular to the shoreline from the bank (depth = 0 m) to the

middle of the lake until the deepest point of macrophyte growth was reached. The position of the

first transect was randomly chosen and all other transects spaced evenly along the shoreline at 80-

150 m distances depending on lake size, resulting in 4-20 transects sampled per lake. Along each

transect, in every depth stratum (0-1 m, 1-2 m, 2-4 m, 4-6 m) the dominance of submerged

macrophyte species was visually estimated following the Kohler scale (Kohler, 1978). No

macrophytes were found below 6 m depth. Macrophytes were identified directly under water or if

this was not possible, samples were taken and identified under a stereomicroscope following Van de

Weyer & Schmitt (2011). Stonewort species were only identified to the genus level (*Chara* and

Nitella), thus exact species numbers might be underestimated.   Macrophyte dominance was

transformed to percent coverage for each transect (Van der Maarel, 1979). The average coverage per

stratum was extrapolated to the total lake using the contour maps. The total macrophyte coverage in

the littoral zone was calculated using the extrapolated coverage from strata between 0 m and 3 m

depth. The regional species pool was estimated from the Red Lists of Lower Saxony, which include

full species inventories, in combination with the expected species for gravel pit lakes following the

list of plant species associations in Lower Saxony (Garve, 2004; Korsch, Doege, Raabe, & van de

Weyer, 2013; Preising et al., 1990).

Amphibians

Amphibians were sampled during the mating-seasons (from March to May). Every lake was sampled

twice: (1) during the day with an inflatable boat driving slowly along the shore searching for adults,

egg-balls (frogs) and egg-lines (toads), (2) after sunset by foot around the lake searching for calling

adults. Each observation (adult or eggs) was marked with a GPS (Garmin Oregon 600) and identified

in the field or photographed for later identification following Schlüpmann (2005). Numbers were

recorded (adults) or estimated (eggs), assuming 700 to 1500 eggs per egg-ball (frogs) or 10,000 eggs

per (100 % covered) m^2 of egg-line-assemblages (toads). The egg numbers were calculated from

pictures taken in the field and verified with literature (Trochet et al., 2014). The regional species pool

was estimated from the Red List of Lower Saxony, which includes a full species inventory, in

combination with their expected distribution (Podloucky & Fischer, 2013).

Odonata

Dragonflies and damselflies were sampled once per lake between early- and mid-summer. At each

lake, the whole shoreline was intensively searched during mid-day. Sitting or flushing adult

individuals were caught with a hand net (butterfly net, 0.2 mm mesh size, bioform), identified using
Lehmann & Nüss (2015), and released without being harmed. The regional species pool was
estimated from the Red List of Lower Saxony, which includes a full species inventory, in combination
with their expected habitat preferences (Altmüller & Clausnitzer, 2010; Lehmann & Nüss, 2015).

Waterfowl and songbirds

Waterfowl were identified following Dierschke (2016) and counted at every visit (between six and
nine visits per lake). Songbirds were sampled once per lake between early- and mid-summer using a
point-count sampling combined with a bioacoustics approach which was also used in other studies
(Rempel, Hobson, Holborn, Van Wilgenburg, & Elliott, 2005; Wilson, Barr, & Zagorski, 2017). Two-
minutes audio-recordings were taken (ZOOM Handy Recorder H2, Surround 4-Channel setting,
44.1kHz sampling frequency, 16 bit quantification) at sampling points placed 200 m apart around the
whole lake, assuming each sampling point covers a radius of 100 m. Sampling points were marked
with GPS. At each point all birds seen (or heard while not recording) were also noted when identified
following Dierschke (2016). The audio-records were analyzed in the lab, and singing species were
identified using reference audio samples (www.deutsche-vogelstimmen.de; www.vogelstimmen-
wehr.de) and a birdsong-identifying software (BirdUp - Automatic Birdsong Recognition, developed
by Jonathan Burn, Version 2018). The regional species pools for waterfowl and songbirds were
estimated from the Red List of Lower Saxony (Krüger & Nipkow, 2015) , which includes a full species
inventory, in combination with their expected occurrence according to habitat type and preferences
(Dierschke, 2016).

Diversity metrics

The analysis focused on species presence-absence data to arrive at measures of taxonomic species
richness, an aggregate index of species diversity. Additionally, the Simpson diversity index (Pielou,
1969) was computed using relative abundance data by species to consider the dominance of certain
species within each taxa-specific community. There was no consideration in whether a particular
species detected actually recruits in a given gravel pit lake, rather only consideration in the species
inventory present, assuming the estimates represented a minimal estimate of local richness as rare
species likely remained undetected. To weigh rare and threatened species more heavily, additionally
the richness of threatened species was computed, and an index of taxon-specific conservation value
for the study region was estimated following Oertli et al. (2002). To that end, each species was
ranked according to its threat status on the Red Lists of Lower Saxony (Altmüller & Clausnitzer, 2010;
Garve, 2004; Korsch et al., 2013; Krüger & Nipkow, 2015; Podloucky & Fischer, 2013). Species of least
concern were ranked lowest ($c(0) = 2^0 = 1$). All species classified with an increasing threat status
category r according to the regional Red List were weighted exponentially more strongly as $c(r) = 2^r$
(Table **2**) following Oertli et al. (2002). For each lake, the final taxon-specific conservation value (CV)

was calculated as the sum of all values for the observed species s_i ($s_1, s_2, s_3, ... , s_n$) divided by the total

number of species (n) for a given taxon:

$$CV = \frac{1}{n} * \sum_{s_{i=1}}^{s_n} c(r_{s_i}).$$

The conservation index value increases with more species of a given taxon being threatened or rare.

A range of different allocations of threat status were tested to estimate the conservation value, using

also national and European red lists; however, the results remained robust. For space reasons, just

the regional index is reported here.

Finally, to test for differences in species composition across all lakes, the pooled species inventory by

lake type (managed and unmanaged) was used, and the Sørensen index (Sørensen, 1948) as a

measure of community similarity was calculated. The Sørensen index ranges from 0 (no species in

common among the two lakes types) to 1 (all species the same) and is calculated as $\frac{2a}{2a+b+c}$, with a

being the number of shared species and b and c being the numbers of unique species to each lake

type, respectively. As an indicator for whether species compositions are substantial (i.e., biologically

meaningful) different or not, so called "faunal brakes" as well as "floral breaks" were searched for.

Following Matthews (1986) faunal or floral brakes among lake types were assumed to occur when

the Sørensen index was < 0.5.

Statistical analysis

The impact of the presence of recreational-fisheries management on aquatic and riparian

biodiversity was tested in two steps.

First, differences in taxon-specific species richness, Simpson diversity index, richness of threatened

species, conservation value and as well as key environmental variables between lake types (managed

and unmanaged gravel pits) were assessed with univariate statistics. To that end, mean differences

among lake types were tested using Student's t (in case of variance homogeneity) or Welch-F (in case

of variance heterogeneity) whenever the error term was normally distributed (Shapiro-Wilk-test).

Otherwise, a Mann-Whitney-U-test of median differences was used. *P*-values were Sidak-corrected

(Šidák, 1967) for multiple comparisons. Significance was assessed at $P < 0.05$.

Second, the among-lake variation in species richness was modelled as a function of lake type and a

set of lake-specific environmental descriptors. These analyses aimed at further isolating an impact of

fisheries management and type of recreational uses on species inventory across all taxa and lakes in

a joint model that included other predictor variables of the lake environment. To reduce the

dimensionality of the environmental variables, multiple Principal Component Analyses (PCA) without

rotations were conducted on related classes of environmental variables respectively (groups were

structured into variables related to morphology, productivity, habitat structure, land use, and

recreational use). Environmental variables forming Principal Components (PC) were considered

correlated, their loadings identified, the axis meanings interpreted, and the PC scores used as

indicator variables. A multivariate Redundancy Analyses (RDA) was then conducted to examine if

recreational fisheries management explains variation in either environmental variables or species

richness across multiple taxa in the multivariate space. In addition to lake type, all relevant

environmental variables (e.g., trophic state, surface area/steepness, land use, riparian/littoral habitat

structure, water chemistry), recreational use intensity, gravel pit age, and catchment were included

in the multivariate analysis of species richness. With the RDA, a forward selection process (Blanchet,

Legendre, & Borcard, 2008) was used to identify the environmental predictors that explained the

most variance in species richness across different taxa and lakes, including management as a key

variable of interest in this study. Using the variance inflation factor (VIF; Neter, Kutner, Nachtsheim,

& Wasserman, 1996) correlated environmental variables were removed before model building. All

data were scaled and centered (z-transformation) prior to analyses. The degree of explanation was

expressed using the adjusted coefficient of multiple determinations ($R^2_{adj.}$). Variables significantly

explaining variation in richness across lakes were also assessed using ANOVA (Analysis of variance) at

a significance level of $P < 0.05$. All calculations and analyses were carried out in R version 3.5.1 using

the vegan-package (Oksanen et al., 2018; R Core Team, 2013).

3. Results

Description of lake types in relation to the environment

The studied lakes were, on average, small (mean ± SD, area 6.5 ± 5.2 ha, range 0.9 – 19.5 ha), shallow

(maximum depth 9.6 ± 5.2 m, range 1.1 – 23.5 m) and mesotrohic (TP 26.3 ± 30.9 µg/l, range 8 - 160

µg/l) with moderate visibility (Secchi depth 2.4 ± 1.4 m, range 0.5 – 5.5 m) (Table 3). The land use in a

100 m buffer around the lake was, on average, characterized by low degree of forestation (mean 16 ±

21 %, range 0 – 72.6 %) and high degree of agricultural land use (mean 27 ± 22 %, range 2.4 – 79 %).

Lakes were, on average, situated close to both human settlements (mean distance to the next village

618.3 ± 533.4 m, range 20 – 1810 m) and other water bodies (mean distance to next lake, river, or

canal 55.8 ± 84.7 m, range 1 – 305 m). Gravel pit lakes were all in an advanced stage of succession

and on average 27.3 ± 13.3 years old (range 6 – 54 years, see Tables S1-S4 for detailed lake-specific

environmental variables). The study lakes belong to four different catchments (small North Sea

tributaries and the catchments of the rivers Ems, Weser and Elbe; Table 1, Figure 1).

Environmental characteristics of managed and unmanaged gravel pit lakes

Both lake types did not statistically differ in age, size, trophic state, and land use (Table 3). A similar

result was revealed in a multivariate RDA, which confirmed the absence of significant differences

between managed and unmanaged lakes in "classes of environmental variables" (i.e., PC scores, for

details see Tables S5, S6) representing morphology (an index of steepness and water body size; $R^2_{adj.}$
= -0.005, F = 0.86, P = 0.470), trophic state ($R^2_{adj.}$ = -0.006, F = 0.86, P = 0.544), proximity to
alternative water bodies ($R^2_{adj.}$ = -0.023, F = 0.45, P = 0.867), proximity to human presence ($R^2_{adj.}$ =
0.035, F = 1.90, P = 0.143) and land use variables ($R^2_{adj.}$ = 0.033, F = 1.85, P = 0.135). However, in
multivariate space the habitat structure differed significantly among managed and unmanaged lakes
along the first PC axis (Dim 1), which represented a vegetation gradient below and above water
(Figure 2). Along this axis, managed lakes were found to be more vegetated than unmanaged ones in
both the riparian and the littoral zones ($R^2_{adj.}$ = 0.056, F = 2.48, P = 0.022).

Recreational uses of managed and unmanaged lakes

The two lake types differed strongly in terms of recreational use intensity, particularly in relation to
the observed angling intensity. As intended by the study design, managed lakes revealed, on average,
significantly higher angling use intensity indexed by a diverse set of variables like angling litter
density, extension of open sites, paths and trails and number of anglers observed (Table 4). By
contrast, the average recreational use intensity of managed and unmanaged lakes by non-angling
recreationists (e.g., swimmers) did not statistically differ when analyzed by univariate statistics on a
variable-by-variable level (Table 4). However, when all indicator variables of the recreational use,
both angling and non-angling, were combined in a multivariate RDA analysis as a function of lake
type, managed lakes separated from unmanaged lakes along PC axis 1. This axis represented
differences in recreational use intensity by both anglers and other recreationists (particularly
swimmers) and extension of trails and paths (Figure 3, $R^2_{adj.}$ = 0.16, F = 5.76, P < 0.001). Note that
there was no differentiation among lake types along the second PC axis of the recreational variables
(Figure 3), which represented shoreline (in)accessibility.

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

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

Based on the pooled species inventories (gamma diversity), unique species (i.e. species present in
only one lake or only one lake type) were found in all taxonomic groups except amphibians (Table 5).

414 Managed lakes hosted more unique species within most taxonomic groups than unmanaged lakes,

415 while unmanaged lakes had more unique Odonata. No faunal or floral breaks were detected

416 between managed and unmanaged lakes using the Sørensen index (all indices ≥ 0.5; Table 5). The

417 average taxon-specific species richness (alpha-diversity), the Simpson diversity index, the average

418 number of threatened species and the average taxon-specific conservation value were statistically

419 similar in managed and unmanaged lakes across all taxonomic groups when analyzed using

420 univariate statistics (Table **6**).

421 *Environmental correlates of among-lake variation in species richness*

422 Across lakes, species richness of amphibians, Odonata, songbirds and riparian vascular plant species

423 covaried along the first axis (Figure 4), collectively representing riparian diversity (for full PCA results,

424 see Table S8). The second PCA axis represented mainly submerged macrophytes (Figure 4). The third

425 axis was related to the diversity of riparian tree species and the forth mainly to waterfowl diversity

426 (Figure 5). Therefore, lakes offering high riparian species richness were not necessarily rich in

427 biodiversity of submerged macrophytes, waterfowl or trees. The RDA analysis to explain the among-

428 lake variation in species richness as a function of lake type alone revealed no influence of this factor

429 on among-lake richness across several taxa (RDA, $R^2_{adj.}$ = 0.028, F = 1.73, *P* = 0.114).

430 All environmental variables subsumed by PC-scores into environmental predictors and lake age had

431 acceptable inflation factors (VIF < 5, maximum: 4.98, supplement Table S7) and were used along with

432 catchment association and lake type in the full RDA analysis to explain among-lake species richness

433 jointly across all taxa. The RDA-based forward model selection retained a few environmental

434 variables as key correlates of species richness of multiple taxa across lakes, but lake type dropped

435 from the best model (Table 7). Therefore, among lake variation in richness across several aquatic and

436 riparian taxa was solely explained by environmental factors unrelated to either lake type or

437 recreation-related variables. Specifically, the coverage of woody habitat along the littoral was

438 negatively correlated with riparian species richness and positively correlated with tree diversity along

439 the first axis in Figure 4. The extent of agricultural land use (representing also more rural conditions,

440 supplementary Table S6) was positively associated with riparian species richness (Figure 4). Lake

441 steepness (representing also small lake size and low shoreline development factor, supplementary

442 Table S5) was negatively correlated with waterfowl species richness (Figure 5). All other

443 environmental variables, including lake age and catchment were not significant (Table 7). The best

444 model explained 36 % of the total variance in the multivariate species richness. In this model, neither

445 lake type nor any of the recreational use variables explained variation in species richness of a range

446 of aquatic and riparian taxa among lakes.

4. Discussion

In line with initial expectations no differences in species richness, Simpson diversity and conservation

value were found across all examined taxa among managed and unmanaged gravel pit lakes, and a

similar species pool was found to be present in both lake types. Collectively, this study did not reveal

that recreational-fisheries management (through impacts on fish communities) or the presence of

anglers (through disturbance effects on shoreline habitat and wildlife or lethal impacts through lost

fishing gear) significantly constrains the development of diverse communities of amphibians, birds,

submerged macrophytes, terrestrial plants and Odonata relative to those expected at lakes that are

not managed for recreational fisheries. Instead, the best predictors of the variation in species

richness among lakes were found to be related to land use variables, the extent of woody habitat at

the lake shores and the lake morphology (size and steepness). Therefore, this study suggests that for

the taxonomic groups and lake types that were examined broader environmental factors and land

use, and not the presence of recreational fisheries and its management of fish stocks and littoral

zones, shape taxonomic diversity of plants, birds, amphibians, and dragonflies.

Biodiversity potential of gravel pit lakes

Gravel pit lakes in Lower Saxony, Germany, were found to host a substantial species diversity and

fraction of the regional species' pools of aquatic and riparian taxa, in particular trees, Odonata and

waterfowl. This finding supports related work in other areas of Europe (Damnjanović et al., 2018;

Oertli, 2018; Spyra & Strzelec, 2019). Yet, only small fractions of the regional species' pools were

detected for vascular plant species, submerged macrophytes, songbirds and amphibians. In particular

amphibians are considered very sensitive to predation from fish (Hecnar & M'Closkey, 1997) and

none of our study lakes were free of fish (Matern et al., 2019). Many amphibian species depend on

shallow water and best develop in small, temporary waters (Shulse, Semlitsch, Trauth, & Williams,

2010). The gravel pits of this study were also relatively steeply-sloped with small fractions of littoral

areas, disconnected from rivers, placed in agricultural landscapes and close to anthropogenic

infrastructure. All of these factors are negative for amphibian diversity and can explain the low

species richness detected for this taxon (Shulse et al., 2010). Importantly, the results of this study

indicate that management by recreational fisheries and the substantially different fish communities

in managed and unmanaged lakes can be excluded as an additional stressor.

Environmental differences among managed and unmanaged lakes

The gravel pit lakes studied were similar in the majority of the environmental factors examined

(including age) except the coverage of submerged macrophytes, which was more prevalent in

managed gravel pit lakes compared to unmanaged ones. Submerged macrophytes have been

reported to be strongly affected by stocking of benthivorous fishes, such as common carp (Bajer et

al., 2016; Miller & Crowl, 2006). However, in a subset of the same gravel pit lakes presented here, Matern et al. (2019) found similar biomasses of fishes in managed and unmanaged lakes, with carps and breams being present in both lake types. Due to the sampling gear used by Matern et al. (2019), the authors likely underestimated the abundance and biomass of common carp and other large benthivorous fish (Ravn et al., 2019). Although no absolute biomass data of carp or other species in the study lakes are available, the fact that submerged macrophytes were more diverse and more developed in the angler-managed lakes suggests that co-existence of carp and other game fish with a species rich submerged macrophyte community, also in terms of threatened stonewort species (*Chara sp., Nitella sp.*), is possible. This disagrees with expectations expressed elsewhere that managing lakes with benthivorous fish necessarily harms submerged macrophytes (Van de Weyer, Meis, & Krautkrämer, 2015). Instead, the more developed submerged macrophytes in managed lakes revealed here suggests that critical biomass thresholds for benthivorous fish after which macrophytes often vanish or strongly decline (about 100 kg/ha; Vilizzi, Tarkan, & Copp, 2015) might not have been reached in the study lakes. Alternatively, the transferability of typical mesocosm studies that have reported substantial impacts of carp on macrophytes to occur after reaching about 100 kg/ha may not hold under conditions in the wild (Arlinghaus, Hühn, et al., 2017).

Lake shorelines managed by anglers were previously reported to be heavily modified to accommodate angling sites and access to anglers (O'Toole et al., 2009). At the same time, crowding is a severe constraint that reduces angler satisfaction (Beardmore, Hunt, Haider, Dorow, & Arlinghaus, 2015). Although improved accessibility in angler-managed lakes was supported in this study, the amount of aquatic and riparian vegetation was significantly larger in angler-managed systems compared to unmanaged lakes. This indicates that maintaining accessibility of lakeshores to anglers does not necessarily mean degraded riparian or littoral habitat quality. Anglers have an interest to maintain access to lakes to be able to fish, but there is also an interest in developing suitable habitats for fish (Meyerhoff et al., 2019) and maintaining sites that promise solitude during the experience (Beardmore et al., 2015), which indirectly may also support biodiversity. We speculate the regular shoreline development activities by anglers and angling clubs to maintain access to angling sites may create "disturbances" (O'Toole et al., 2009), that regularly interrupt the succession of tree stands, thereby reducing the shading effects in the littoral zone (Monk & Gabrielson, 1985), thereby promoting growth of submerged macrophytes (Holtmann, Kerler, Wolfgart, Schmidt, & Fartmann, 2019). The littoral zone is the most productive habitat of lakes (Winfield, 2004), and most fish species depend on submerged macrophytes and other structures for spawning, foraging and refuge (Lewin, Mehner, Ritterbusch, & Brämick, 2014). Therefore, although anglers regularly engage in shoreline development activities and angling site maintenance, the data of this study suggest they do so to a degree that may maintain or even foster aquatic and riparian vegetation.

Differences in recreational use of managed and unmanaged lakes

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

Differences in biodiversity among managed and unmanaged lakes

Across all taxa that were examined, no statistical differences were found in species richness, number
of threatened species, conservation value and Simpson diversity between managed and unmanaged
lakes. This result was unexpected. Recreational-fisheries management can affect aquatic and riparian
biodiversity through various pathways, first through supporting and enhancing fish stocks that exert
predation pressure (e.g., on tadpoles and Odonata larvae; Hecnar & M'Closkey, 1997; Knorp & Dorn,
2016), second through indirect fish-based effects (e.g., uprooting macrophytes through benthivorous
feeding; Bajer et al., 2016), third through direct removal or damage of submerged and terrestrial
plants during angling activities (O'Toole et al., 2009), which may have knock-on effects on dragonflies
(Z. Müller et al., 2003), and fourth through activity-based disturbance effects or lethal impacts
through lost fishing sinkers in particular on birds (Cryer et al., 1987; Sears, 1988). This study design
was not tailored towards directly measuring disturbance effects on particular species; instead it was
designed to examine a range of taxonomic richness indices in aggregate for communities present at
gravel pit lakes that are subjected to recreational fisheries compared to ecologically similar lakes that
do not. When judged against these aggregate biodiversity metrics, the study presented here does not
support the idea that recreational-fisheries management and angler presence has important impacts
that modify species inventories to a degree that strongly depart from situations expected at
unmanaged lakes without anglers. Previous work has reported relevant reductions in bird
biodiversity from lakes exposed to human disturbances due to recreation including angling (Bell et
al., 1997). However, similar species richness and conservation value of both waterfowl and riparian

songbirds in managed and unmanaged lakes were found in the present work. This does not exclude

the possibility that for example the breeding success of specific disturbance-sensitive taxa might

have been impaired in angler-managed lakes (Park, Park, Sung, & Park, 2006; Reichholf, 1988). But if

such effects were present, they were not strong enough to substantially alter species richness, not to

be confused with species identity. Overall, against the chosen metrics, the findings supported the

initial hypothesis of no impacts from recreational fishing on non-targeted taxa in gravel pits situated

in agricultural landscapes.

Environmental determinants of aquatic and riparian biodiversity in gravel pit lakes

The species richness of different taxa did not uniformly vary among lakes, in contrast to a study of

managed shallow ponds by Lemmens et al. (2013). While examining strictly aquatic taxa

(zooplankton, submerged and emerged aquatic macrophytes, benthic invertebrates), Lemmens et al.

(2013) revealed uniform responses in species richness across taxa and ponds in their study. The much

broader trophic and habitat requirements of aquatic and riparian taxa examined here resulted in

significantly more variable biotic responses. For example, lakes rich in riparian biodiversity were not

necessarily rich in submerged macrophytes and waterfowl biodiversity. The reason was that the

aquatic and riparian biodiversity responded to many variables beyond those measured within the

lake. The multivariate analyses revealed that variation in species richness across multiple taxa was

driven by structural variables such as habitat quality, lake morphometry (surface area and steepness)

and land use in a buffer zone around the lake, but not by recreational use intensity or the presence

of recreational-fisheries management activities. Thus, environmental factors unrelated to

recreational fishing seem to overwhelm any specific impacts of angling, at least for the taxonomic

diversity metrics and the taxa examined here.

Mosaics of different habitats (reeds, overhanging trees etc.) along the shoreline support species

richness and diversity for most taxa (Kaufmann, Hughes, Whittier, Bryce, & Paulsen, 2014), and the

presence of endangered biodiversity increase the recreational value of gravel pit lakes as perceived

by anglers (Meyerhoff et al., 2019). Extended woody habitat both in water and particularly in the

riparian zone was correlated with increased tree diversity, but reduced riparian species richness of

vascular plants, amphibians, Odonata and songbirds. This might be explained by the shading effect of

trees on non-woody vegetation (Monk & Gabrielson, 1985). Odonata, songbirds and amphibian

species benefited from more vegetated littoral habitats, in agreement with previous work

(Paracuellos, 2006; Remsburg & Turner, 2009; Shulse et al., 2010). The species richness of waterfowl

was strongly governed by lake surface area and steepness of the littoral, with larger and shallower

lakes having a higher waterfowl species richness, confirming earlier findings by Paszkowski & Tonn

(2000). The three dominant waterfowl species (occurring on 85 % or more of sampled lakes) were

either omnivorous (mallard, *Anas platyrhynchos*, L.) or herbivorous-invertivorous (common coot,

Fulica atra, L., and tufted duck, *Aythya fuligula*, L.). In addition, 77 % of the lakes were used by grey

goose (*Anser anser*, L.), which feeds on terrestrial plants. Thus, it can be concluded that the dominant waterfowl detected at the studied lakes benefit from submerged macrophytes or riparian plants, both found to be more abundant at managed lakes.

Collectively, the presented data does not support substantial negative impacts of recreational fisheries management on the species richness and community diversity of waterfowl and songbirds present at gravel pit lakes. In a related study from Welsh reservoirs Cryer et al. (1987) observed only distributional changes of waterfowl to the presence of anglers and no changes in abundance. Similarly negligible effects of anglers on piscivorous birds at Canadian natural lakes were reported by Somers, Heisler, Doucette, Kjoss, & Brigham (2015). Specifically for gravel pit lakes, Bell et al. (1997) failed to find evidence for impacts of recreational fishing on the community structure of waterfowl, although in particular diving waterfowl reduced their abundance during presence of anglers and other recreationists. In that study, similar to the presented one, habitat quality and lake size were more important for waterfowl diversity than the bank use by anglers, and their shoreline management rather supported grazing waterfowl by opening up sites (Bell et al., 1997). This does not mean that recreational fishing will not impact bird populations at all as for example the breeding success of certain disturbance sensitive species might still be impaired (Park et al., 2006; Reichholf, 1988). However, this study was not designed to examine the breeding success of particular species and rather focused on aggregate diversity metrics. Against these, this study did not reveal any significant disturbance effects caused by recreational fisheries.

Limitations

The strength of the study design is the focus on multiple taxa, which is rare in the recreational ecology literature related to freshwaters. The limitations are that it was not focused on specific species, and the sampling design does not answer whether the detected mobile species (e.g., birds or Odonata) recruited in the study lakes or only used them temporarily as feeding or resting habitat. Moreover, because of adjustments in taxa-specific sampling schemes, seasonal taxa (amphibians, Odonata) might have been underestimated in the sampling and rare species might likely been missed (Yoccoz, Nichols, & Boulinier, 2001). However, even if this is the case the conclusions presented are robust because this systematic error affected both lake types compared here.

This study used a comparative approach where lakes were not randomly allocated to either angler-managed lakes or controls. All lakes sampled were from the same geographical area and the age of the lakes and the wider environmental factors were similar; thus, the key differences among lake types related to the presence of recreational fishing. Therefore, the design would have been able to differentiate strong angling-induced biodiversity effects would they exist in reality.

A further limitation is that the design did not include entirely unused lakes where recreation whatsoever is prohibited. The present data have to be interpreted against the possibility that gravel

pits situated in reserves with strictly no human access might show higher species diversity than

revealed in the sample lakes. All the lakes were situated in agricultural environments and all were

exposed to a certain recreational use. Background disturbance (Liley, Underhill-Day, Panter, Marsh, &

Roberts, 2015) might have affected the observed species pool, affecting the detectability of species

in the study region. The conclusions of the present work are also confined to the environmental

gradients that could be observed. For example, higher angler use intensities than found in the

present work might reveal different results.

Finally, the recreational use intensity was mainly recorded during weekdays when the field visits

were done. Thus, potential high intensity phases at weekends might be unrepresented. However,

this would even strengthen our conclusions, if the real recreational use of managed lakes was well

beyond what was considered in this analysis.

Conclusions

The present study shows that recreational-fisheries management does not constrain the

establishment of a rich biodiversity of aquatic and riparian taxa in and around gravel pit lakes relative

to conditions expected at ecologically similar unmanaged lakes. Environmental variables related to

habitat quality, land use and lake morphometry rather than recreation-related drivers were key in

driving the species richness for multiple taxa across lakes. This study thus shows that co-existence of

recreational fisheries and aquatic and riparian biodiversity of high conservation value and richness is

possible, at least under the specific ecological conditions of gravel pit lakes in agricultural landscapes.

From a conservation perspective, it is suggested that recreational fishing clubs increasingly rely on

habitat enhancement activities to support both fish and other taxa present at gravel pit lakes.

Moreover, development of diverse shorelines as well as the creation of more gently sloped littoral

areas is recommended as actions to be completed during the creation of gravel pit lakes. If these

actions are taken, bans on recreational fishing, are unlikely to produce further conservation benefits

if the aim is to create high species diversity, independent of a specific species identity.

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Tables

Table 1: Descriptors of gravel pits sampled in Lower Saxony. The locations of the catchments (fourth column) are shown in Figure 1. Trophic state was determined using Riedmüller, Hoehn, & Mischke (2013). The pH values and conductivities are annual means.

No.	Lake name	Lake type	catch-ment	End of mining	Trophic state	Maximum depth [m]	Lake area [ha]	pH value	Conductivity [$\mu S*cm^{-1}$]	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[1]	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, horse riders
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, horse riders
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, horse riders
15	Weidekampsee	Managed	Weser	1994	Oligotrophic	4.3	2.9	8.0	461	Anglers, dog walkers
16	Wiesedermeer	Managed	SNST[1]	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, horse riders, swimmers
19	Handorf	Unmanaged	Weser	2004	Eutrophic	23.0	13.6	9.2	666	Horse riders, dog walkers
20	Hänigsen	Unmanaged	Weser	2011	Mesotrophic	12.3	6.2	8.6	437	Swimmers, dog walkers, anglers, campfires, dumping waste
21	Heeßel	Unmanaged	Weser	1963	Eutrophic	7.4	0.9	8.2	537	No
22	Hopels	Unmanaged	SNST[1]	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, canoeing, 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)

[1] Small North Sea Tributaries

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

Red List categories of Lower Saxony and meaning in terms of IUCN	Rank r	Weight c
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 related environmental variables, **significant ones (*P* < 0.05) are bolded**, *statistical trends (P < 0.1) are in italics*.

| Class | Environmental variable (abbreviation) | mean ± standard deviation (minimum - maximum) | | Comparison | | |
		Managed (N = 16)	Unmanaged (N = 10)	Test [*]	Statistic	*P*-value
Morphology	Maximum depth (m) (MaxDep)	9.7 ± 4.9 (2.8-23.5)	9.5 ± 6.0 (1.1-23.0)	U-test	W = 89	0.986
	Lake area (ha) (LArea)	7.4 ± 5.6 (1.0-19.5)	4.9 ± 4.2 (0.9-13.6)	U-test	W = 105	0.592
	Shoreline development factor (SDF)	1.5 ± 0.3 (1.1-2.2)	1.6 ± 0.3 (1.3-2.2)	t-test	t = -1.0	0.824
	Relative depth ratio (RelDepR)	0.04 ± 0.01 (0.02-0.07)	0.04 ± 0.02 (0.01-0.07)	t-test	t = -1.1	0.754
Trophic state	Total phosphorus ($\mu g*l^{-1}$) (TP)	25.7 ± 36.5 (8-160)	27.2 ± 20.9 (12-72)	U-test	W = 63.5	0.983
	Total organic carbon ($mg*l^{-1}$) (TOC)	6.6 ± 2.8 (2.5-13)	6.0 ± 2.5 (2.9-12.4)	U-test	W = 93	0.997
	Mean chlorophyll a ($\mu g*l^{-1}$) (CHLa)	11.6 ± 15.9 (2.05-65.3)	21.2 ± 26.1 (2.6-90.6)	U-test	W = 53	0.765
	Secchi depth (m) (Secchi)	2.6 ± 1.5 (0.5-5.5)	2.0 ± 1.1 (0.5-4.5)	t-test	t = 0.9	0.972
	Ammonium ($\mu g*l^{-1}$) (NH4)	56.9 ± 71.2 (15.0-240.0)	84.0 ± 164.8 (15.0-550.0)	U-test	W = 75	1.000
	Nitrate ($\mu g*l^{-1}$) (NO3)	283.8 ± 380.4 (5.0-1040.0)	733.0 ± 984.1 (5.0-2940.0)	U-test	W = 50	0.604
	Conductivity ($\mu S*cm^{-1}$) (Con)	450.9 ± 192.3 (136-742)	478.6 ± 279.8 (159-957)	t-test	t = -0.3	1.000
	pH Value (pH)	7.9 ± 0.5 (6.7-9)	8.1 ± 0.5 (7.5-9.2)	t-test	t = -1	0.967
Habitat structure	Volume-% of simple dead wood (SDW_Vol)	0.005 ± 0.009 (0-0.035)	0.008 ± 0.010 (0.001-0.028)	U-test	W = 65.5	0.973
	Volume-% of coarse woody structure (CWS_Vol)	1.5 ± 1.4 (0.02-5.6)	1.7 ± 2.0 (0.02-6.2)	U-test	W = 86.5	1.000
	Mean riparian tree cover on an ordinal scale from 0 to 4 (Rip_Trees)	1.0 ± 0.2 (0.4-1.5)	0.9 ± 0.3 (0.4-1.2)	t-test	t = 0.9	0.942
	Mean litoral reed cover on an ordinal scale from 0 to 4 (Reed)	1.3 ± 0.9 (0-2.5)	0.8 ± 0.7 (0-1.7)	t-test	t = 1.25	0.779
	Mean riparian vascular plants cover on an ordinal scale from 0 to 4 (Rip_Herbs)	1.7 ± 0.4 (1.1-3.0)	1.0 ± 0.7 (0.1-1.9)	U-test	W = 118	0.225
	Submerged macrophyte cover in the littoral zone in % (MP_Cov)	*39.3 ± 19.9 (12.5-82.3)*	*21.1 ± 27.5 (0-85.2)*	*U-test*	*W = 126*	*0.083*
Age	Lake age in years by 2017 (Age)	29.4 ± 12.4 (11-52)	23.8 ± 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 related environmental variables, **significant ones (*P* < 0.05) are bolded**, *statistical trends (P < 0.1) are in italics.*

| Class | Environmental variable (abbreviation) | mean ± standard deviation (minimum - maximum) | | Comparison | | |
		Managed (N = 16)	Unmanaged (N = 10)	Test [*]	Statistic	*P*-value
Land use	Excavation within 100m-buffer (%) (Excav)	4.8 ± 7.2 (0-21.3)	9.4 ± 14.6 (0-39.0)	U-test	W = 63	0.718
	Agriculture within 100m-buffer (%) (Agric)	22.8 ± 19.9 (2.4-55.9)	33.8 ± 25.4 (3.5-79.0)	U-test	W = 58	0.598
	Forest within 100m-buffer (%) (Forest)	22.0 ± 25.1 (0-72.6)	5.6 ± 6.0 (0-15.5)	U-test	W = 118	0.132
	Urban area within 100m-buffer (%) (Urban)	27.8 ± 29.2 (0-87.5)	17.4 ± 24.5 (0-59.5)	U-test	W = 99	0.767
Water	Wetland within 100m-buffer (%) (Wetland)	0.9 ± 3.6 (0-14.4)	5.1 ± 14.1 (0-45.1)	U-test	W = 61.5	0.504
	Water surface within 100m-buffer (%) (Water)	9.7 ± 12.5 (0.9-50.4)	8.7 ± 8.8 (0.5-30.1)	U-test	W = 80	1.000
	Distance to next lake (m) (DistLake)	164.1 ± 236.4 (5-850)	264.1 ± 440.6 (1-1280)	U-test	W = 87	0.999
	Distance to next river (m) (DistRiver)	5226.1 ± 9805.2 (25-29,900)	3999.5 ± 9841.6 (220-31,920)	U-test	W = 92	0.980
	Distance to next canal (m) (DistCanal)	312.4 ± 462.3 (1-1630)	224.5 ± 367.9 (5-1180)	U-test	W = 84	1.000
Human presence	Distance to next road (m) (DistRoad)	265.3 ± 314.4 (15-1010)	558.0 ± 510.1 (30-1530)	U-test	W = 50.5	0.416
	Distance to next settlement (m) (DistVille)	504.1 ± 407.8 (20-1400)	801.0 ± 673.0 (60-1810)	t-test	t = -1.4	0.530
	Distance to next city (m) (DistCity)	7135.0 ± 4087.6 (170-13,130)	5859.0 ± 4488.3 (1070-15,110)	t-test	t = 0.8	0.917
Recreational use	**Litter related to angling (pieces per m shoreline) (A_Lit)**	**0.05 ± 0.05 (0-0.20)**	**0.002 ± 0.007 (0-0.021)**	**U-test**	**W = 140.5**	**0.007**
	Litter unrelated to angling (pieces per m shoreline) (NonA_Lit)	0.70 ± 0.50 (0.02-1.48)	0.34 ± 0.71 (0-2.29)	U-test	W = 126	0.124
	Angling-sites and open spaces (% of shoreline) (open_sites)	**18.5 ± 19.8 (3.6-87.7)**	**8.4 ± 14.4 (0-48.6)**	**U-test**	**W = 133**	**0.044**
	Trails and paths per shoreline (m*m^{-1}) (Trails)	**0.9 ± 0.1 (0.6-1.1)**	**0.4 ± 0.5 (0-1.4)**	**U-test**	**W = 138**	**0.019**
	Anglers per lake per visit (Anglers)	**1.6 ± 1.6 (0-5.1)**	**0.1 ± 0.2 (0-0.8)**	**U-test**	**W = 143**	**0.006**
	Dog walkers per lake per visit (Dogs)	1.7 ± 1.9 (0-6)	0.5 ± 1.0 (0-3.3)	U-test	W = 123.5	0.154
	Swimmers per lake per visit (Swimmers)	*2.9 ± 2.6 (0-10)*	*0.7 ± 1.0 (0-3.1)*	*U-test*	*W = 129.5*	*0.075*
	Other recreationists per lake per visit (other_people)	*2.9 ± 3.2 (0.3-11.9)*	*0.9 ± 1.4 (0-3.8)*	*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)		Comparison		
		managed (N = 16)	unmanaged (N = 10)	Test [*]	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	**Woody_habitat**	**14.7%**	**0.112**	**6.63**	**< 0.001**
	Catchment	**14.8%**	**0.080**	**2.22**	**0.028**
	Acidity	**6.9%**	**0.063**	**3.12**	**0.019**
	Agricultural_extent	**9.1%**	**0.060**	**4.10**	**0.003**
	Age	3.6%	0.050	1.63	0.165
	Lake_steepness	**6.9%**	**0.043**	**3.12**	**0.015**
	Lake type	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	**Woody_habitat**	**14.7%**		**5.05**	**< 0.001**
	Agricultural_extent	**11.8%**	0.271	**4.06**	**0.001**
	Lake_steepness	**9.3%**		**3.20**	**0.004**

* 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 catchments (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 classes of related 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 cover, Herb = mean riparian vascular plants cover, Reed = mean litoral reed cover, MP_Cov = submerged macrophyte cover 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 lake 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 classes of related 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 = no. per visit, Dogs = dog walkers per visit, Swimmers = no. 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 lake 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 lake 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 lake 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.