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. There is consensus that humanity is facing a biodiversity crisis, with freshwater-associated biodiversity being in particularly dire state. Novel ecosystems created through human use of littoral resources, such as gravel pit lakes, can provide substitute habitats for conservation of freshwater biodiversity. However, many of these lakes are managed for recreational fisheries and may exhibit generally high recreational use intensity, which may negatively impact aquatic biodiversity.

2. To examine the possible impact of recreational fisheries on a range of aquatic and riparian taxa (plants, amphibians, dragonflies, damselflies, waterfowl, songbirds) the biodiversity in gravel pits managed (N = 16) and unmanaged (N = 10) by recreational fisheries was compared, while controlling for other environmental variables.

3. The average species richness and conservation value of all taxa examined was similar among both lake types, with the exception of amphibians whose conservation value was found to be larger in unmanaged lakes. With the exception of submerged macrophytes – a taxon found to be particularly species rich and extensively developed in managed lakes - no faunal breaks in any of the taxa were revealed when examining the pooled species inventory of managed and unmanaged lakes.

4. Variation in species richness and conservation value among lakes was strongly driven by available vegetated and woody habitat, lake morphology and location in the landscape, and not by the presence of recreational fishers or general recreational use intensity. Collectively, there were limited evidence found that anglers and recreational fisheries management constitute a relevant stressor to aquatic and riparian biodiversity in gravel pits of the study region.

Keywords

amphibians, birds, disturbance, fishing, littoral, recreation, reservoir, taxon richness, vegetation

1. Introduction

Globally, biodiversity is in steep decline, creating a biodiversity crisis of unprecedented scale (IPBES, 2019; WWF, 2018). The numbers of endangered species are constantly rising (Butchart et al., 2010; WWF, 2018), with an estimated 1 million species currently threatened by extinction (IPBES, 2019). The current species extinction rates are about 1000 times higher than the calculated background extinction rate (Pimm et al., 2014). The biodiversity decline is particularly prevalent in freshwaters compared to marine and terrestrial environments (Sala et al., 2000; WWF, 2018). From 1970 to today, freshwater biodiversity has on average declined by 83% in abundance across thousands of populations (WWF, 2018). Although manifold reasons contribute to the freshwater biodiversity crisis (Reid et al., 2019), habitat alteration and fragmentation, pollution, overexploitation, invasive species and climate change constitute key drivers (Dudgeon et al., 2006; IPBES, 2019).

Artificially created aquatic habitats, such as gravel pit lakes or ponds, can play an important role in maintaining and increasing native biodiversity by providing refuges and secondary habitat for rare or endangered species across a range of taxa (Damnjanović et al., 2018; Santoul, Gaujard, Angélibert, Mastrorillo, & Céréghino, 2009). Artificial lake ecosystems are often relatively recent in origin (< 100 years of age; Schurig, 1972; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2016) and created by mining of sand, clay, gravel and other littoral resources (Saulnier-Talbot & Lavoie, 2018). More than one billion tons of sand, gravel and other earthen materials were excavated in more than 24,500 quarries and pits within the EU-28 in 2017 alone (UEPG, 2017). The resulting numerous man-made lakes (for simplicity henceforth referred to as gravel pit lakes) have become common elements in many cultural landscapes across the industrialized world (Blanchette & Lund, 2016).

Lakes, including gravel pit lakes, provide a bundle of ecosystem services to humans (Reynaud & Lanzanova, 2017). These include provisioning services, such as fish yield, as well as a range of cultural ecosystem services, in particular recreation (Venohr et al., 2018). Lakes also generate intrinsic benefits associated with the presence of threatened aquatic biodiversity (Reynaud & Lanzanova, 2017). Although the benefits of water-based recreation can be substantial (Venohr et al., 2018), recreation can also negatively impact on the biodiversity of freshwater ecosystems (Liddle & Scorgie, 1980). For example, human activities on the shoreline can alter habitats, which can lead to a loss of plant biodiversity through trampling (O'Toole, Hanson, & Cooke, 2009). Shoreline development, e.g., habitat simplification through the construction of beaches or other recreation sites, can also reduce littoral and riparian habitat quality and negatively affect associated taxa (Spyra & Strzelec, 2019). Water-based recreation has also been found to negatively impact on birds and other wildlife through fear reactions to humans (Dear, Guay, Robinson, & Weston, 2015; Frid & Dill, 2002), dogs (Randler, 2006) or pleasure boating (McFadden, Herrera, & Navedo, 2017; Wolter & Arlinghaus, 2003). Management and conservation of gravel pit lakes and other artificial waterbodies benefits from jointly considering the well-being aquatic recreation produces to humans, while balancing these benefits with the possible negative impacts that aquatic recreation can induce on aquatic and riparian biodiversity (Lemmens et al., 2013; Lemmens, Mergeay, Van Wichelen, De Meester, & Declerck, 2015).

Most gravel pit lakes in central Europe are used by recreational fisheries. Anglers are not only users but in some regions of the world also managers of fish populations and habitats of freshwater ecosystems (Arlinghaus, Alós, et al., 2017; Daedlow, Beard, & Arlinghaus, 2011). This particularly applies to Germany, where organizations of anglers, usually angling clubs and associations, are leaseholders or owners of fishing rights, and in this position are also legally entitled to manage fish stocks in gravel pit lakes (Arlinghaus, Alós, et al., 2017; Arlinghaus et al., 2015). Angler activities, both in terms of exploitation and habitat management, are mainly directed at fish stocks, e.g., through practices such as fish stocking and harvesting. Therefore, key impacts of recreational fisheries can be expected at the fish stock level (Matern et al., 2019). Angler-induced changes to fish biomass, fish size or fish community composition can have knock-on effects on submerged macrophytes (e.g., due to stocking of benthivorous fish, Bajer et al., 2016), amphibians (e.g., due to stocking of large predators, Hecnar & M'Closkey, 1997; Miró, Sabás, & Ventura, 2018) and invertebrates, such as dragonflies (Knorp & Dorn, 2016; Miller & Crowl, 2006). In addition, anglers may modify littoral habitats through angling site constructions (Dustin & Vondracek, 2017), thereby affecting plants (O'Toole et al., 2009), dragonflies (Z. Müller et al., 2003) or birds (Kaufmann, Hughes, Whittier, Bryce, & Paulsen, 2014). Certain angler types also contribute to eutrophication through ground-baiting (Niesar, Arlinghaus, Rennert, & Mehner, 2004), thereby possibly affecting aquatic macrophytes (Stefanidis, Sarika, & Papastegiadou, 2019), and they may disturb wildlife and birds due to extended human presence in littoral zones (Knight, Anderson, & Marr, 1991; Wichmann, 2010). Lost fishing gear can also have lethal effects on birds (Franson et al., 2003; Heath, Dahlgren, Simon, & Brooks, 2017), for example when lost leads are ingested (Franson et al., 2003; Scheuhammer & Norris, 1996). Therefore, anglers can both be seen as stewards of aquatic ecosystems as well as a potential threat to certain aquatic taxa depending on the local angling intensity and other conditions.

In Germany, recreational fisheries are regularly constrained or even banned from a use of waterbodies, including gravel pits (Landkreis Lüneburg, 2018; H. Müller, 2012), while other recreational uses were not constrained. This is commonly justified by angling particularly disturbs taxa and habitats of conservation concern (Erlinger, 1981; Reichholf, 1988). There is evidence that the recreational fisheries use of newly created gravel pit lakes was already banned during the process of licensing the sand or gravel extraction, i.e. well before the gravel pit lake even started being excavated (H. Müller, 2012). To empirically examine the ecological justification of such actions, a space-for-time substitution design was used, studying the biodiversity in gravel pits that are used and managed by recreational fisheries compared with the biodiversity in similar gravel pits that are not used and managed by recreational fisheries. This study was not meant to reveal the specific pathways by which anglers may impact on different taxa, rather to examine the aggregate impact of recreational fisheries on biodiversity in gravel pit lakes. Specifically, there was a major interest in estimating the additive effect of the presence of recreational fisheries on the species richness, faunal composition and conservation value across a range of aquatic and riparian taxa commonly debated in conservation conflicts. It was hypothesized that recreational fisheries will not affect the species richness and conservation value of all taxa that are not directly targeted by anglers (Odonata, amphibians, submerged and riparian vegetation, waterfowl and songbirds). This was used as null hypothesis when testing for statistical differences between managed and not managed gravel pit lakes. It was further hypothesized that some disturbance-sensitive taxa of songbirds, waterfowl or dragonflies may be absent in intensively used lakes, thereby affecting the species richness and conservation value of these taxa in lakes with substantial recreational use.

2. Methods

Study area and lake selection

This study was conducted in Lower Saxony, in the German lowlands (Figure 1). Lower Saxony is populated by 8 million people corresponding to a population density of 167 inhabitants per km^2. The total area of the state is 47,710 km^2, of which more than 50% constitute of agricultural land, in total 27,753 km^2, and 10,245 km^2 of managed forests (Landesamt für Statistik Niedersachsen (LSN), 2018). Natural lentic water bodies are scarce. Out of a total of 35,048 ha of standing water surface in Lower Saxony, artificial lakes (mainly ponds and gravel pit lakes) form 73% by surface and more than 99% of the number of lentic waterbodies in the region (Manfrin et al., unpublished data).

In Germany, fishing rights are tight to the owner of the water body. If not already owned they are typically leased by local angling clubs. However, there are still gravel pits were the fishing right is neither used nor leased by the owner. To compare the biodiversity present in angler-managed and unmanaged lakes, first a sample of intensively managed gravel pits was selected in Lower Saxony that fulfilled the following criteria: (1) fishing rights and associated management duties must be in the hand of local angling clubs for a period of at least ten years, (2) angling clubs must be willing to accept intensive biological sampling over the course of many years and (3) all angling clubs must be united in the same umbrella association to facilitate planning and communication. It was partnered with the Angler Association of Lower Saxony (AVN) and all the associated angling clubs were used as a sample frame to identify managed lakes. The final set of lakes was identified through a key informant (a fisheries biologist) of the AVN who helped identifying cooperating angling clubs. To that end, all angling clubs of the AVN membership were asked for their interest in contributing lakes to a multi-year study on the ecology of gravel pit lakes. From the set of angling clubs principally interested in the study and thereby willing to allow the research team to grant repeated access to assess biodiversity, a random sample was drawn and a structured questionnaire sent to identify which type of lakes and rivers were under the management regime. The final club and lake selection was constrained to a set of clubs having at least one gravel pit as private property because particularly intensive recreational use and management was expected in these systems. Through this approach N = 16 managed lakes were selected as study sites (Table 1, Figure 1). Then local informants of residents and anglers of each of the 16 lakes were used to identify gravel pits not managed by anglers in direct or close vicinity to the managed lakes, thereby creating a paired design. After having identified too few lakes by this, governmental offices were asked for helping in identifying unmanaged gravel pit lakes comparable to the already chosen managed lakes. As the number of unmanaged lakes is substantially smaller than the number of managed lakes in Lower Saxony and due to logistical constraints in effectively sampling a large number of lakes during the same time period over multiple year, N = 10 unmanaged lakes were identified and included in the study (Table 1, Figure 1). The lakes were chosen as to most closely as possible match each other's environmental conditions, both in terms of location in the landscape, age, productivity and vegetation. The lakes were confined to being small and ranging from 1 ha to 20 ha of surface area, they had no recent dredging in the last ten years happening and the lakes where scattered across Lower Saxony to cover all conditions (Figure 1). In a subset of these lakes, Matern et al. (2019) revealed identical fish biomasses and abundances in both lakes types, but a substantially larger local fish species richness and a significantly larger presence of game fishes (particularly piscivorous fish and large-bodied cyprinids such as carp, *Cyprinus carpio*) in angler-managed lakes. These data already suggested that angler-managed lakes were indeed more intensively managed in terms of fish biodiversity metrics. This was a major precondition of the study design to isolate the impact of recreational fisheries on biodiversity while controlling for possible confounding environmental variables.

Land use

Several indicators of land use and spatial arrangement were assessed for each lake to control for these variables when comparing managed and unmanaged lakes and their biodiversity inventory. To that end, distances of each lake to nearby cities, villages, lakes, canals and rivers were calculated in google maps (© 2017), and the shares of different land use categories within a distance of 100 m around each lake shoreline (buffer zone) were 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, 2006). The categories of the ATKIS®-objects were pooled to classes of (1) urban land use (all anthropogenic infrastructures like buildings, streets, railroad tracks etc.), (2) agricultural land use (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 surface (e.g., lakes, rivers, canals) and (7) other land use (not fitting in previous classes like succession areas, grass land, boulder sites etc.). With this classification it was tried to account for the general land use effects on the studied aquatic and riparian taxa.

Recreational use intensity

Several indicators of recreational use intensity were assessed, enumerating the type and number of recreationists during each site visit (between six and nine visits per lake, see below) as well as using indirect measures of use intensity. The indirect measures encompassed measures of accessibility and litter as follows: every lake was walked around with a measuring wheel (NESTLE-Cross-country measuring wheel – Model No. 12015001, with 2 m circumference and 0.1% accuracy), measuring the distances of all trails and paths at the lake. This was summed and then normalized to shoreline length. Angling sites and open spaces along the shoreline were counted, and all litter encountered was assigned to one of two categories, (1) angling related (e.g., lead weight, nylon line, artificial bait) or (2) not angling related (e.g., plastic packaging, beer bottles, cigarettes), and counted. It was assumed that more intensively used lakes also receive larger amount of litter and are easily accessible through paths and trampled sites (O'Toole et al. 2009).

Morphology

Every lake was mapped with a SIMRAD NSS7 evo2 echo sounder paired with a Lawrence TotalScan transducer. The equipment was mounted on a boat driving at 3 – 4 km/h along the lake on transects 25 – 45 m apart from each other depending on lake size and lake depth. The echo sounding data was stored in the Lawrence format .slg2 and processed by BioBase (Navico). The post-processed raw data (depth and gps-position per ping) were used to calculate depth contour maps using ordinary kriging with the gstat-package in R (Gräler, Pebesma, & Heuvelink, 2016). The contour maps were used to extract maximum depth and to calculate the relative depth ratio (Damnjanović et al., 2018). Shoreline length and lake area were estimated in QGIS 3.4.1, and used to calculate the shoreline development factor (Osgood, 2005).

Water chemistry and nutrient levels

In spring during overturn (complete mixing of holomictic lakes), epilimnic water samples were taken for analyzing total phosphorus concentrations (TP), total organic carbon (TOC), ammonium and nitrate concentrations (NH_4, NO_3) and chlorophyll a (Chl-a) as a measure of algal biomass. The TP was determined using the ammonium molybdate spectrometric 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 Chl-a was enumerated using high performance liquid chromatography (HPLC) (Mantoura & Llewellyn, 1983; Wright, 1991). The lake's conductivity and pH were measured with a WTW Multi 350i sensor probe (WTW GmbH, Weilheim, Germany). Additionally, water turbidity was assessed using a standard Secchi-disk.

Littoral and riparian habitat assessment

As measures of littoral and riparian habitat quality, the riparian vegetation and dead wood was assessed using a plot design evenly spaced throughout the shoreline following Kaufmann & Whittier (1997). Transects were placed perpendicular to and along the shore line with a 15 x 15 meter riparian plot at the shore (Figure 2). The positions of the plots were randomly distributed along the shoreline, but had at least 50 meter distance to each other. Each littoral transect was 4 meter wide and at maximum 10 meter long or shorter if the maximum sampling depth of 3 meter was reached. In each transect all dead wood structure was counted and assigned to one of two categories: (1) simple dead wood (bulk diameter < 5 cm and length < 50 cm, no and 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), Newbrey et al. (2005) and Mallory et al. (2000). Also, the length and bulk diameters were measured for all dead wood structures; additionally width and height was measured for coarse woody structure. From these measurements, the volume for each dead wood structure was calculated using the formula for a cylinder as reference for simple dead wood and the formula for an ellipsoid as reference for coarse woody structure. Riparian habitats (e.g., trees, tall herbs, reed) were evaluated in the plots at the shore following the protocol of Kaufmann & Whittier (1997) where "0" means absent, "1" means sparse (<10% coverage), "2" means moderate (10-39% coverage), "3" means dominant (40-75% coverage), and "4" means very dominant (>75% coverage) in the plot.

Submerged macrophytes

All lakes were sampled for the extension of submerged macrophytes and macrophyte diversity between late June and late August, following the sampling protocol of Schaumburg et al. (2014). Every lake was scuba dived and snorkeled along transects extending from the shoreline (depth = 0m) towards the lake center perpendicular to the shoreline until the deepest point of macrophyte growth was reached. The position of the first sampled transect was randomly chosen and all other transects were then spaced evenly along the shoreline at distances of 80 m – 150 m depending on lake size. This summed up to totals between four and 20 transects per lake. Along each transect, in every depth stratum (0-1 m, 1-2 m, 2-4 m, 4-6 m) the dominance of each macrophyte species was estimated according to the ordinal Kohler scale: "0 – absent", "1 – very rare", "2 – rare", "3 – widespread", "4 – common", "5 – very common" (Kohler, 1978; Van de Weyer, 2003). No macrophytes were found in areas deeper than 6 m. The species were identified under water or, if not possible, samples were taken into laboratory and identified under binoculars following Van de Weyer & Schmitt (2011). Macrophyte dominance of each species was transformed into percent coverage for each transect (Van der Maarel, 1979). The average coverage per stratum was extrapolated to its respective total lake area from contour maps. Afterwards, 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 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 feet around the lake searching for calling adults. Each observation (adult or eggs) was marked with a GPS (Garmin Oregon 600), identified in the field or photographed for later identification following Schlüpmann (2005), and 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 regional species pool was estimated from the Red List of Lower Saxony in combination with their expected distribution (BfN, 2012; Kühnel, Geiger, Laufer, Podloucky, & Schlüpmann, 2009).

Odonata

Dragonflies and damselflies were sampled once per lake between early- and mid-summer. At each lake the whole shoreline was intensively searched during the mid-day. Sitting or flushing imagines 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 in combination with their expected habitat preferences (Altmüller & Clausnitzer, 2010; Hein, 2018).

Waterfowl and songbirds

Waterfowl were identified following Dierschke (2016), counted and protocoled at every visit of each lake (between six and nine visits per lake). Songbirds were sampled once per lake between early- and mid-summer using 2-minutes audio-recordings (ZOOM Handy Recorder H2, Surround 4-Channel setting, 44.1kHz sampling frequency, 16 bit quantification) at sampling points distributed along the shoreline, placed 200 m apart around the whole shoreline, assuming each sampling point covers a radius of 100 m. Sampling points were marked with GPS. The audio-records were later analyzed in the lab, and singing species were identified using reference audio samples from two websites (www.deutsche-vogelstimmen.de; www.vogelstimmen-wehr.de) and a smart phone application (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, excluding birds with not matching habitat preferences (i.e., waders; Dierschke, 2016; Krüger & Nipkow, 2015).

Riparian vegetation

All lakes were sampled for riparian vegetation in May. At each lake, four transects were sampled, one at each cardinal direction of the lake. Each transect was 100 m long and contained five evenly spaced (20 m distance) 1 m^2-plots. Trees (>3 m high) were identified (using Spohn, Golte-Bechtle, & Spohn, 2015) and counted along each transect. If species were not obvious, an application for smart phones called Pl@ntNet was used (Goëau et al., 2014). Herbs were identified following the same keys (Goëau et al., 2014; Spohn et al., 2015) as far as possible in each plot. Abundance classes ("r" = 1 individual in plot, "+" = 2 – 5 individuals in plot but < 5 % coverage, "1" = 6 – 50 individuals in plot but < 5 % coverage, "2m" = > 50 individuals in plot but < 5 % coverage, "2a" = 5 – 15 % coverage, "2b" = 16 – 25 % coverage, "3" = 26 – 50 % coverage, "4" = 51 – 75 % coverage, "5" = 76 – 100 % coverage; Braun-Blanquet, 1964) were estimated for each species, genus or family (depending on identification accuracy, Table S9). The regional species pool was estimated from the Red Lists of Lower Saxony excluding plants with not matching ecoregions (Garve, 2004; Spohn et al., 2015).

Diversity metrics

Presence-absence data and estimated species richness by taxon was used in this study. Additionally, a taxon-specific conservation value was calculated following Oertli et al. (2002). To that end, each identified species was assigned a threat status according to its most threatened status on any of the following four lists: regional Red Lists of Lower Saxony (Altmüller & Clausnitzer, 2010; Garve, 2004; Korsch et al., 2013; Krüger & Nipkow, 2015; Podloucky & Fischer, 1994), national Red Lists of Germany (Grünberg et al., 2015; Korsch et al., 2013; Kühnel et al., 2009; Ludwig & Schnittler, 1996; Ott et al., 2015), the international Red List (IUCN, 2018) and the annex lists of the European Union (EU) Habitats Directive and the EU Birds Directive (EU, 1992; EU, 2009). For each species, the highest threat status mentioned on any of these four lists was used. The conservation value c for a species of the least threatened rank (not listed, very common, not threatened) was $c_0 = 2^0 = 1$, and every ascending threat status was given an exponentially larger conservation value (i.e., weight) $c_r = 2^r$ as shown in Table 2. The final taxon-specific conservation value (CV) for each lake was calculated by taxon as the sum of all values (c) for every observed species ($s_1, s_2, s_3, \dots, s_n$) divided by the total number of observed species (n):

$$CV = \frac{1}{n} * \sum_{s_{i=1}}^{s_n} \mathrm{c}_{s_i}$$

Statistical analysis

Mean/median differences among lake types (managed or unmanaged gravel pits) were calculated for all individual environmental variables and taxon-specific biodiversity variables (species richness and conservation value) with Student's t-tests (variance homogeneity) or Welch-F-test (variance heterogeneity) when the error term was normally distributed (Shapiro-Wilk-test), otherwise a Mann-Whitney-U-test assessing median differences was used. These tests were carried out in R (stats-package, R Core Team, 2013) and p-values were afterwards Sidak-corrected (Šidák, 1967) to control for multiple comparisons. To estimate faunal breaks and species turn over rates, the pooled species inventory by lake type (managed and unmanaged) was used and two indices were calculated: (1) the Sørensen index (Sørensen, 1948) as a measure of community similarity and (2) the richness-based species exchange ratio SER_r (Hillebrand et al., 2018) as a measure of species turnover. The Sørensen index ranges from 0 (no species in common) 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 the two lake types. The SER_r also ranges from 0 (all species the same) to 1 (no species in common) and is calculated as $\frac{b+c}{a+b+c}$. Following Matthews (1986), faunal breaks among lake types were assumed to occur when the Sørensen index was < 0.5, and the species exchange among lake types was considered to be substantial when the SER_r index was > 0.5.

As different environmental variables and the diversity metrics of the different taxa could co-vary, further multivariate tests of differences among lake types in terms of the environment as well as taxon-specific biodiversity were conducted using Redundancy Analysis (RDA; Legendre & Legendre, 2012), carried out after first conducting standard Principal Component Analyses (PCA) without rotations as a dimension reduction tool (PCA; Mardia, Kent, & Bibby, 1979). Environmental variables forming PCA were considered correlated, the loadings identified and interpreted as class of environmental variables (e.g., morphology, productivity, land use) and PC axes scores were used in further analyses. The environmental predictors of species richness and conservation value across different taxa were subsequently evaluated with a forward selection process (Blanchet, Legendre, & Borcard, 2008) in a RDA using PC scores after removing highly correlated variables using the variance inflation factor (VIF; Neter, Kutner, Nachtsheim, & Wasserman, 1996). The models were first run with only the environmental predictors and without the factor "management". These models were compared to models including "management" as additional predictor variable. Data for PCA and RDA was scaled and centered (z-transformation), and the amount of variance explained by variables in the best models was expressed using the adjusted coefficient of multiple determination (R^2_a; Ezekiel, 1930).

Significance was assessed using a 5 % rejection level ($p < 0.05$). Because the sample size of lakes was moderate, p-values of $0.05 \leq p < 0.10$ were also interpreted as a trend.

3. Results

Environmental variables of managed and unmanaged gravel pit lakes

The studied lakes were overwhelmingly small (mean ± SD, area 6.7 ± 5.1 ha, range 0.9 – 19.6 ha), shallow (maximum depth 9.7 ± 5.1 m, range 1.6 – 24.1 m) and mesotrophic (TP 26.3 ± 30.4 µg/l, range 8 - 160 µg/l) with moderate visibility (Secchi depth 2.4 ± 1.4 m, range 0.5 – 5.5 m). The land use in a 100 m buffer around the lake was characterized by low degree of forestation (mean percentage of forests in buffer zone of 16 ± 21 %, range 0 – 68 %) and high degree of agricultural land use (mean percentage of agricultural land use in buffer zone of 27 ± 22 %, range 2.4 – 79 %). Lakes were closely situated to human settlements (mean distance to the next village 618.3 ± 523.1 m, range 20 – 1810 m) and were on average a few m away from other water bodies (mean distance to next lake, river, or canal 55.8 ± 84.7 m, range 1 – 305 m). Most of the lakes were regularly used by recreational angling (legal only in managed lakes) and other recreational activities and were generally accessible through paths, parking lots and trails. An overview of all environmental variables and their values across lakes is provided in the supplementary Tables S1-S4.

The multivariate RDA revealed the lack of significant differences among managed and unmanaged lakes in all variables representing morphology ($R^2_{adj.} = -0.005$, $F = 0.86$, $p = 0.470$, Figure 3a), 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 ($R^2_{adj.} = 0.033$, $F = 1.85$, $p = 0.135$, Figure 3b, see the full PCA results behind the dimension reduction of the environmental variables in Tables S7, S8). It also revealed that the habitat structure differed significantly among managed and unmanaged lakes along the first principal component axis (Dim 1) representing a vegetation gradient (Table S7), with managed lakes being more vegetated in both the riparian and the littoral zone than unmanaged ones (Figure 3c, $R^2_{adj.} = 0.056$, $F = 2.48$, $p = 0.022$). The strongest separation of both lakes types, however, was revealed in relation to the first PC axis representing the intensity of recreational use by both angling and non-angling recreational activities and general accessibility through trails around the lake; here, managed lakes exhibited a substantially greater recreational use intensity and greater accessibility to humans than unmanaged lakes (Figure 3d, $R^2_{adj.} = 0.16$, $F = 5.76$, $p < 0.001$). Note that there was less differentiation among lake types along the second PC axis of the recreational variables, which represented an index of accessibility difficulty (Table S8, Figure 3d). Note also that the PC of recreational variables did not cleanly separate lakes with high angler use from lakes with high use of other recreationists: lakes with plenty of anglers were also regularly used by plenty other recreationists (Table S8). Finally, although unmanaged lakes were not managed by recreational fisheries, a small degree of illegal fishing was also detected at some unmanaged lakes (Table S4, for full set of univariate results see supplementary Table S5, S6).

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

In total 60 species of submerged macrophytes, 191 species of herbs, 44 species of trees, 3 species of amphibians, 33 species of Odonata, 36 species of songbirds and 34 species of waterfowl were detected across the pool of lakes (Supplement, Table S9). This species inventory represented a substantial fraction of the regional species pool of trees (59%), Odonata (56%), submerged macrophytes (48%) and waterfowl (45%). By contrast, only one third or less of the regional species pool of herbal species (12%), songbirds (33%) and amphibians (38%) was detected.

Variation in local species richness and presence of endangered taxa among lakes was large, yet the frequency of threatened species showed rather similar patterns in managed or unmanaged lakes (Supplement, Figures S1, S2). Most managed and unmanaged lakes hosted at least a few threatened species (Figures S1, S2). Unique species were found in all taxa (except for amphibians) in each of the two lake types (Table 3). Managed lakes hosted more unique species within most taxa than unmanaged lakes, while unmanaged lakes had more unique Odonata. Overwhelmingly, common species were detected, particularly among amphibians (Table S9). Only few species non-native to Lower Saxony or Germany were found (Table S9), all together 4 submerged macrophyte species (e.g., *Elodea nuttallii* [Planch.] H. St. John, which is invasive), 3 riparian tree species, 2 waterfowl species (e.g., *Alopochen aegyptiaca* L., which is invasive) and 1 dragonfly species.

The average taxon-specific species richness (alpha-diversity) was statistically similar in managed and unmanaged lakes across all taxa (Table 4). Similarly, the taxon-specific conservation value of each taxon was, on average, similar among managed and unmanaged lakes with one exception: unmanaged lakes hosted amphibian species of higher average conservation value. However, the overall species richness was particularly low for this taxon compared to the other taxa (Table 4).

When examining the pooled species inventories, no evidence for faunal breaks among managed and unmanaged lakes were identified using the Sørensen index (all indices ≥ 0.5; Table 3) except for submerged macrophytes that were particularly species rich in managed lakes (Table 4). Similarly, there was no evidence for substantial species turnover (SER_r), with the exception of submerged macrophytes, where almost 70% of the species pool was different between the two management types (Table 3).

Environmental correlates of species richness and conservation value in gravel pit lakes and the role of management

There was no joint variation in species richness and conservation value across all taxa and lakes indicating taxon-specific responses to lake conditions (Figures 4, 5, a complete visualization is plotted in supplementary Figures S3, S4). In relation to species richness across taxa, the first PCA axis represented covariance of amphibian, songbirds and riparian herb species diversity, collectively representing riparian diversity (Table S11). It was along this axis, where managed and unmanaged lakes varied close to significance, if the model included only the factor management. The unmanged lakes showed a non-significant trend (RDA, $R^2_{adj.}$ = 0.043, F = 2.12, p = 0.051) for hosting larger riparian diversity (Figure 4). The second PCA axis represented high species richness of aquatic diversity in relation to submerged macrophytes and Odonata, and no differentiation among managed and unmanaged lakes (Figure 4). The third PC axis was related to the diversity of riparian tree species and the forth mainly to waterfowl diversity, and again no relevant separation among lake types was revealed (Figure S3, Table S11).

High conservation value of macrophytes and waterfowl correlated with lakes offering a low conservation value for amphibians (first PC axis, Figure 5, Table S12). Along this first PC axis managed and unmanaged lakes differentiated the most: in a model with only management as environmental variable, managed lakes revealed a significantly higher conservation value of waterfowl, Odonata and submerged macrophytes and a lower conservation value of amphibians (Figure 5, $R^2_{adj.}$ = 0.068, F = 2.83, p = 0.008). The second PC axis was mainly represented by a high conservation value of songbirds and to a lesser degree waterfowl, and the third axis represented the conservation value of riparian plants, but lakes did not differentiate along the second and third axes (Figure 5, Table S12, Figure S4).

All environmental indicators subsumed by PC-scores into predictors of environmental classes (Tables S7, S8) had acceptable inflation factors (Table S10) and were thus used for RDA analysis of species richness and conservation value across the different taxa. The RDA-based forward model selection retained several environmental class variables as correlates of species richness across taxa (Table 5Table 6). Woody habitat was negatively correlated with the riparian species richness and positively with tree diversity (along the first axis, Figure 4, Table S11), and vegetated habitat was positively correlated with species richness of submerged macrophytes and Odonata (second axis, Figure 4, Table S11). The lake steepness (which correlated with smaller lake sizes and low shoreline development factor; Table S7) was negatively correlated with waterfowl species richness (Figure 4, Table S11). Agricultural extension (Table S8) was positively associated with species richness of submerged macrophytes and Odonata (second axis, Figure 4, Table S11). The recreational use intensity did not correlate with species diversity (Table 5Table 6). After accounting for these environmental variables, management was no longer close to significant in explaining species diversity across taxa and dropped out of the best-fitting RDA (Table 6). The best model explained more than 42 % of the total variance in the multivariate species richness, which is a lot more than management alone (about 8 % explained variance).

In terms of variation in conservation value across all taxa, the best model explained only 15.6 % of total variance (management alone explained 10.5 %), and the RDA analysis indicated that the general recreational use intensity of a lake positively correlated with the first PC axis: lakes with greater recreational use intensity also hosted a larger conservation value of aquatic taxa (submerged macrophytes, Odonata and waterfowl) and lower conservation value of amphibians (Figure 5, Table S12). The extension of woody habitat negatively correlated with the conservation value of songbirds, which mainly represented the second axis (Table S12). Managed and unmanaged lakes strongly differed in the recreational use intensity, but in contrast to expectations this environmental factor was positively associated with the conservation value of all taxa except amphibians (Figure 5, Table S12). When entering management as an additional explanatory factor in the RDA, it was retained as the only variable for explaining conservation value, and all other environmental predictors dropped out (Table 6). This is most likely because management correlates significantly and strongly with the recreational use intensity (RDA: $R^2_{adj.} = 0.16$, $F = 5.76$, $p < 0.001$; Figure 3d, Table S8) and as a categorical variable the factor management absorbs more of the variance than the quantitative recreational use intensity index.

4. Discussion

Biodiversity potential of gravel pits

This comparative study revealed that gravel pit lakes managed and used by anglers as well as unmanaged lakes constitute a highly suitable environment hosting a substantial species diversity and fraction of the regional species' pools of several aquatic and riparian taxa, in particular submerged macrophytes, tree species, Odonata and waterfowl. This finding supports related work revealing gravel pits as suitable habitats for multiple plant, vertebrate and invertebrate taxa, some of which have a very high conservation value (Damnjanović et al., 2018; Völkl, 2010). Yet, only small fractions of the regional species' pools for herbal species, amphibians and songbirds were found. Gravel pits are relatively steeply-sloped with small fractions of littoral areas, disconnected from rivers, placed in agricultural landscapes and close to anthropogenic infrastructure (Blanchette & Lund, 2016). Also, they have unique colonization and succession histories (Köppel, 1995). Because gravel pit lakes are limited in certain habitat features and due to their special origin, they are suitable only for a fraction of a regional species pool that typically inhabits lakes and lake shores.

Differences in the environment among managed and unmanaged lakes

Our studied lakes were similar in the majority of the environmental factors examined except the recreational use intensity and the extension of vegetation, particularly of submerged macrophytes. The latter were, surprisingly perhaps, more prevalent in managed gravel pit lakes. Managed lakes were found to have more developed tracks, parking places and other facilities that attract anglers. However, these features also appeared to attract other recreational users as seen in the first PC axes ("recreational use intensity", Figure 3d). Thus, angler-managed lakes were more accessible to recreationists in general, and while the angler presence was - as expected by design - more pronounced in managed lakes, also other recreational activities were more frequently observed at managed lakes. Unmanaged lakes were also visited by non-angling recreationists (e.g., walkers), yet at a lower intensity. Importantly, in contrast to the expectations of this study, the combined index of recreational use intensity correlated positively with the conservation value of aquatic taxa (submerged macrophytes, Odonata and waterfowl) and there was no relation of recreational use intensity and species richness. Thus, although it could not isolate the impact of recreational fisheries use from other recreational uses, this study does not support negative effects of aquatic recreation on the metrics that were assessed.

In light of previous work, lakes managed by anglers were expected to be heavily modified along the shoreline to accommodate angling sites and access to anglers (Dustin & Vondracek, 2017; O'Toole et al., 2009). Although indeed higher accessibility in angler-managed lakes was recorded (in particular the extension of trails), at the lake-level the degree of aquatic and riparian vegetation was found to be significantly larger in angler-managed systems compared to unmanaged lakes. These data show that good accessibility does not equal diminished riparian or littoral habitat quality. In fact, anglers have an interest to maintain access to lakes to be able to fish, but there is also an interest in developing habitat suitable for their targets, which can then indirectly support other biodiversity as well. The littoral zone belongs to the most productive habitats of lakes (Winfield, 2004), and many angler-targeted fish depend on underwater and riparian vegetation for spawning and refuge (Lewin, Mehner, Ritterbusch, & Brämick, 2014; Lewin, Okun, & Mehner, 2004). In addition, crowding is a severe constraint that reduces angler satisfaction (Beardmore, Hunt, Haider, Dorow, & Arlinghaus, 2015). 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 maintains or even improves aquatic and riparian vegetation.

Differences in biodiversity among managed and unmanaged lakes

The only taxon where faunal breaks and a substantial turnover was observed among managed and unmanaged lakes were submerged macrophytes, but surprisingly the extension, diversity and conservation value of submerged macrophytes was higher in managed compared to unmanaged lakes. Submerged macrophytes are thought to be strongly affected by popular fisheries-management actions, particularly by stocking of benthivorous fish such as common carp (Bajer et al., 2016; Miller & Crowl, 2006). Matern et al. (2019) studied some of the lakes that were examined in this study revealing that managed and unmanaged lakes hosted similar biomasses and abundances of fishes. However, given the gears that were used (electrofishing and gill nets) it is likely that Matern et al. (2019) underestimated the abundance and biomass of common carp and other large benthivorous fish (Ravn et al., 2019). These species can thus be expected to be substantially more abundant in managed gravel pit lakes. Bajer et al. (2016) reported a substantial reduction of species richness and extension of macrophytes in North American lakes, and Vilizzi, Tarkan, & Copp (2015) conducted a meta-analysis showing that carp-induced impacts on submerged macrophytes are most likely at biomasses well beyond 200 kg/ha. It is highly unlikely that the lakes that were studied here offered such carp biomasses as most lakes were mesotrophic, and these systems rarely can support more than 200-500 kg of fish per hectare in total (Barthelmes, 1981). Although no absolute biomass data of carp or other species in these studied lakes are available by now, the fact that submerged macrophytes were more diverse and more extended in the angler-managed lakes suggests that co-existence of carp and other fish with a species rich macrophyte community, also in terms of threatened stonewort species (*Chara sp., Nitella sp.*), in recreationally managed lakes is possible. This is in contrast to the common assumption expressed by some aquatic conservation botanists that angler-managed lakes have less macrophytes (Van de Weyer, Meis, & Krautkrämer, 2015). One reason might be the "intermediate disturbance effect" (Connell, 1978) that leads to better conditions, especially for pioneer species, than extremely disturbed or stable systems would generate. Another reason might be that the carp biomasses necessary to exert substantial impacts on plant species richness were simply not achieved, because either of the insufficient productivity of the lakes studied or many carp are quickly removed by anglers after stocking (Arlinghaus, Hühn, et al., 2017).

In terms of average alpha diversity, no statistical differences were found in species richness and conservation value for most of taxa that were examined (submerged macrophytes, Odonata, herbs, trees, waterfowl, songbirds) among managed and unmanaged lakes. The only exception was amphibians whose conservation value was significantly greater in unmanaged compared to managed lakes. One reason could be that managed gravel pit lakes host a greater diversity of predatory fishes with rather large gapes (Matern et al., 2019), in turn the predation pressure on tadpoles and even adult amphibians (e.g., through pike, *Esox lucius*) is likely greater in managed compared to unmanaged lakes. However, the general amphibian diversity was very low across all lakes. Typically only 1 to 3 species were detected. This is likely the result of the specific habitat conditions in gravel pit lakes that render these systems a suboptimal habitat for amphibians. Both managed and unmanaged lakes host fish (Matern et al., 2019), are rather steeply sloped and located in agricultural and urbanized landscapes with little forest canopy. Other studies showed that amphibian species richness in lakes is promoted by littoral vegetation (Hecnar & M'Closkey, 1998; Shulse, Semlitsch, Trauth, & Williams, 2010), but also habitat heterogeneity and shallow lakes promote species richness (Atauri & de Lucio, 2001; Porej & Hetherington, 2005). All of these conditions are key preferences for the life-cycle and recruitment of amphibians (Trochet et al., 2014), indicating that alternative habitats might be more important targets for amphibian conservation (e.g., temporarily drained ponds or small kettle ponds) than gravel pit lakes (Porej & Hetherington, 2005; Werneke, Kosmac, van de Weyer, Gertzen, & Mutz, 2018).

Previous work has repeatedly shown or implicated strong reductions in bird biodiversity through human disturbances via recreation at lakes, including anglers (Lozano & Malo, 2013; Reichholf, 1970). However, similar species richness and conservation value of both waterfowl and riparian songbirds were found in managed and unmanaged lakes. In fact this study was unable to reject the key hypothesis of no differences in aquatic and riparian biodiversity (here: species richness and conservation value) in and at angler-managed lakes compared to unmanaged ones. Therefore, we conclude that with few exceptions (in particular amphibians, this study, and fish, Matern et al., 2019) managed and unmanaged lakes host a species inventory, including birds, of largely similar richness and conservation value. However, it has to be noted that gravel pits as a specific kind of stagnant, small, artificial waterbodies principally can serve only parts of the total species inventory with corresponding habitat preferences.

Environmental determinants of biodiversity in gravel pit lakes

The multivariate analyses showed that the different taxa did not vary uniformly in terms of richness and conservation value among lakes. For example, lakes that offer high richness for amphibians (dimension 1 of PCA, Table S11) may not be offering high richness for riparian trees (dimension 3 of PCA, Table S11) and lakes offering high richness for submerged macrophytes (dimension 2 of PCA, Table S11) may not necessarily offer high richness for waterfowl (dimension 4 of PCA, Table S11). This finding disagrees with a related study from managed shallow ponds by Lemmens et al. (2013). These authors examined strictly aquatic taxa with corresponding trophic requirements (zooplankton, macrophytes, benthic invertebrates), revealing uniform responses in species richness across taxa and ponds. Given that both aquatic and riparian taxa were examined, the lack of uniform responses can be explained by taxa-specific habitat requirements and trophic responses that differ among species that depend purely on in-lake conditions (e.g., submerged macrophytes) compared to those that are more strongly governed by habitat connectivity and land use practices (e.g., amphibians). Also, bigger lakes in a wider regional range were sampled, where Lemmens et al. (2013) did their study in a spatial constrained setting with very small artificial lakes (< 2.5 ha).

This analysis indicated that the variation in species richness is most strongly governed by available habitat and habitat quality (in particular related to vegetation and woody habitat), the morphology (area, shoreline development and slope steepness) of a lake and the surrounding land use (represented by degree of agriculture). By contrast, species richness across taxa was not a significant function of recreational fisheries management when considering a set of environmental variables. Thus, a sustainable use of gravel pit lakes by anglers is not a significant constraint to the establishment of a water type specific species rich aquatic and riparian community. Mosaics of different habitats (reeds, overhanging trees etc.) constitute highly suitable habitat for a range of taxa (Kaufmann et al., 2014), and relatedly it was also found that managed lakes hosting a stronger vegetation gradient offered higher species richness of submerged macrophytes and Odonata. By contrast, extended woody habitat both in water and particularly in the riparian zone was correlated with increased tree diversity, but reduced riparian diversity of herb species, amphibians and songbirds as well as reduced conservation value of songbirds. Perhaps, the regular shoreline development activities by anglers create disturbances (Dustin & Vondracek, 2017; O'Toole et al., 2009) that regularly interrupt the successions of tree stands thereby reducing the shading effects of the riparian zone (Balandier et al., 2008; Monk & Gabrielson, 1985), in turn creating diverse habitats of herb and reed habitats important for a range of species (Paracuellos, 2006; Shulse et al., 2010). This work suggests that anglers can substantially advance riparian biodiversity by properly managing lake shorelines and thereby contributing to the biodiversity value of the lakes they predominantly manage for fish diversity and abundance only. Alternatively viewed, the traditional fisheries-management actions do seemingly not constrain the establishment of a diverse community of species that does not differ in average richness to unmanaged lakes. Hence, constraining or even banning recreational fisheries from gravel pits seems unsupported in regard to the underlying justification of possible impacts on species richness and conservation value.

The relationship between woody habitat and the richness of riparian vegetation that was found can be explained by the shading effect of trees (at the shore or fallen in the water) on herbal vegetation (Balandier et al., 2008; Monk & Gabrielson, 1985), which leads to less vegetation cover and therefore to reduced species richness following species-area-relationships (Brown, 1995). It is obvious that with more submerged macrophyte coverage more submerged macrophyte species can be expected to occur and also the Odonata species benefit from more vegetated littoral habitats (Foote & Rice Hornung, 2005; Remsburg & Turner, 2009). Macrophyte and Odonata species richness were also positively correlated with the extension of agriculture in proximity. More agriculture is often associated with higher nutrient loads, in run-offs as well as the groundwater (Lawniczak et al., 2016). Although, no effect of the productivity variables could be seen, this might have impacted submerged macrophytes by altering species composition. For example, Stefanidis et al. (2019) found positive effects of high nitrate nitrogen (> 1 mg/L) and phosphate (> 0.1 mg/L) concentrations on species richness in greek lakes. The agricultural index was also correlated with the degree of excavation (Figure 3b, Table S8). Dragonflies often use secondary habitats like excavation sites as step-stones for distribution and colonization (Buczyński, 1999), which could explain the positive effect of these land use elements on Odonata species richness in the studied systems.

The songbird diversity (and their conservation value) responded negatively to an index of extension of woody habitat. Most studies dealing with songbirds focus on terrestrial habitats, finding that habitat heterogeneity and forests promote species richness in this taxon (Atauri & de Lucio, 2001; Tellería, Santos, Sánchez, & Galarza, 1992). Only few studies look at riparian songbirds, revealing positive effects of reed and tall herbaceous structure and/or intermediate forests (e.g., shrubs) when considering a smaller spatial scale such as ours (Paracuellos, 2006). This essential habitat will be negatively affected by extensive woody habitat (i.e., large trees; Balandier et al., 2008; Monk & Gabrielson, 1985), possibly explaining the correlations of this study. The species richness of waterfowl was strongly governed by the lake area and the steepness of the shoreline, which can be interpreted as larger and shallower lakes having a higher richness of waterfowl species than smaller and deeper lakes, confirming earlier findings (Elmberg, Nummi, Poysa, & Sjoberg, 2006; Paszkowski & Tonn, 2000).

Collectively, this data do not support assumptions of substantial negative impacts of recreational fisheries management on the species richness and conservation value of waterfowl and songbirds present at gravel pit lakes when benchmarked against unmanaged reference systems of similar ecology and origin. It is important to note that whole-lake metrics were examined and not the abundances of specific taxa or breeding successes. Also, this work constitutes a comparative approach where lakes were not randomly allocated to either angler managed or controls. Therefore, it cannot conclusively be stated that recreational fishing will not impact bird populations. However, the study by Cryer, Linley, Ward, Stratford, & Randerson (1987) conducted in artificial lakes revealed only distributional changes of waterfowl to the presence of anglers, and no changes to abundance. Similarly negligible effects of anglers on birds were reported by Somers, Heisler, Doucette, Kjoss, & Brigham (2015). Specific for gravel pit lakes, Bell et al. (2018) failed to find evidence for recreational use impacts on community structure of waterfowl, but selected species, in particular diving waterfowl, responded through reduced abundance to the presence of anglers and other recreationists. Yet, other environmental factors related to habitat quality and size of the ecosystem were typically more important than the use of the shoreline by anglers, and management of shorelines benefited grazing waterfowl by opening up sites among the terrestrial and aquatic habitats (Bell et al. 2018). Thus, the often-cited assumption that anglers alter species diversity of birds (Reichholf, 1970, 1988) does not necessarily hold, and here no impacts at the species presence levels were detected compared to unmanaged lakes.

Compared to the among-lake variation in species richness, the conservation value of the detected species was much more random and less clearly correlated with overarching environmental factors, which might have resulted from the weighting factor assigned to the species classified as threatened. In this study the number of threatened species was overall low. But threatened and rare species might have very specific habitat requirements (Lindenmayer, 1989; Magurran & Henderson, 2003) and are also more likely missed in field surveys (Yoccoz, Nichols, & Boulinier, 2001; Zhang et al., 2014). Importantly, when accounting for environmental factors, fisheries management dropped out as a relevant predictor of species richness, and management was positively, rather than negatively, associated with the conservation value of aquatic taxa that were examined (submerged macrophytes, Odonata and waterfowl). This indicates that fisheries management and the associated recreational use is not per se a constraint for the establishment of a substantial species inventory of aquatic and riparian taxa.

Limitations

Our study has a number of limitations. The first relates to the fact that a space-for-time replication design was used that lends itself to a correlational study that has to be interpreted in light of the gradients that have been able to be sampled. Obviously, environmental variables differing from the ones that were observed may lead to different conclusions (e.g., higher recreational use intensity than present in the studied landscape). Secondly, all the lakes of this study were situated in agricultural environments and this study lacked any lakes without any form of recreational use. This background disturbance (Liley, Underhill-Day, Panter, Marsh, & Roberts, 2015), either through recreation or other human-induced disturbances (e.g., noise from railways or roads), may have affected the species pool to be sampled independent of the studies variables of interest. There is also the possibility for sampling effects, especially for seasonal and migratory taxa (e.g., Odonata, amphibians, waterfowl), and rare species were likely to be missed (Yoccoz et al., 2001). We think, however, that a possible bias in the sampling would not affect the conclusions by being a systematic effect affecting both lake types. Finally, the recreational use that was measured was directly captured mainly during weekdays when the field visits at the lakes were done. Thus, high intensity phases during the weekends might have been undersampled. But, as further surrogates in multivariate indexes of recreational use were used (e.g., litter, angling sites, trails etc.), we consider a robust dimension of recreational use to be identified. However, this index integrated both anglers and non-anglers such that this study ultimately cannot conclusively disentangle the isolated effect of angling-induced disturbances from other recreational impacts in angler-managed lakes.

Conclusions

This study shows that the presence of anglers and actions associated with recreational fisheries management, even if it is affecting the fish communities via adding piscivorous and other highly demanded species to gravel pits (see Matern et al., 2019), is not a constraint to the establishment of a rich biodiversity of aquatic and riparian taxa traditionally not considered from a fisheries perspective. The different taxa that were investigated did not respond uniformly to the presence of fisheries-management and were driven by a set of overarching habitat- and other environmental factors unrelated to recreational fisheries management. Thus, when judged on the metrics used in this work (species richness and conservation value of the species pool) co-existence of recreational fisheries and aquatic and riparian biodiversity of high conservation value and richness is possible under the specific ecological conditions offered by gravel pit lakes in agricultural landscapes. When examined as a whole, given the negligible differences in both species diversity and conservation value across most taxa in managed and unmanaged lakes and in light of the lack of faunal breaks observed for most of the taxa that were studied, this study does not support the idea that selectively constraining recreational fishing from gravel pit lakes will offer substantial conservation gains, as long as other recreational uses continue to be present and lakes are situated in disturbed cultural landscapes. Instead, we recommend specifically considering the location of specific lakes in the landscape when deciding about local and lake-specific conservation actions (Lemmens et al., 2015; Werneke et al., 2018). We also propose to work together with anglers and attempt to create and maintain a mosaic of different habitat types in the riparian zone of lakes, thereby fostering the co-existence of people and nature for the benefit of all. By contrast, selective bans of anglers from gravel pit lakes with the aim to foster species richness and conservation value of selected taxa is not supported under the conditions offered by gravel pit lakes in Lower Saxony. These results likely hold for many other states in highly populated states. While gravel pits are suitable habitats for a range of species, effective amphibian conservation seems impossible in these systems. Instead, fish free ponds and other temporary waters maybe needed to effectively address the current crisis in amphibian diversity (Scheffer et al., 2006; Werneke et al., 2018).

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Tables

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

Lake name	Lake type	Management interventions	Recreationists identified during on-site visits	Trophic state	End of mining
Chodhemster Kolk	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1971
Collrunge	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1982
Donner Kiesgrube 3	Managed	recreational fisheries, regular stocking	Anglers	Eutrophic	2000
Kiesteich Brelingen	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1999
Kolshorner Teich	Managed	recreational fisheries, regular stocking	Anglers, horses	Mesotrophic	1980
Linner See	Managed	recreational fisheries, regular stocking	Anglers	Mesotrophic	2000
Meitzer See	Managed	recreational fisheries, regular stocking	Anglers, dog walkers, swimmers	Oligotrophic	2006
Neumanns Kuhle	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Polytrophic	1970
Plockhorst	Managed	recreational fisheries, regular stocking	Anglers, dog walkers, horses	Eutrophic	1998
Saalsdorf	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1995
Schleptruper See	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1965
Stedorfer Baggersee	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Eutrophic	1983
Steinwedeler Teich	Managed	recreational fisheries, regular stocking	Anglers, dog walkers, cyclists	Mesotrophic	1978
Wahle	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1990
Weidekampsee	Managed	recreational fisheries, regular stocking	Anglers	Mesotrophic	1994
Wiesedermeer	Managed	recreational fisheries, regular stocking	Anglers, dog walkers	Mesotrophic	1990
Bülstedt	Unmanaged	Nature conservation	Birdwatchers	Polytrophic	1991
Lohmoor	Unmanaged	Nature conservation	Birdwatchers	Eutrophic	1991
Goldbeck	Unmanaged	Private (no management)	Owner/friends, horses, swimmers, anglers	Eutrophic	1992
Handorf	Unmanaged	Private (no management)	Horses, dogs (commercial)	Eutrophic	2004
Hänigsen	Unmanaged	Private (no management)	Swimmers, dog walkers, anglers, campfires, dumping ground	Mesotrophic	2011
Hopels	Unmanaged	Angling club, not stocked or managed at time of assessment	Swimmers, dog walkers	Mesotrophic	1998
Pfütze	Unmanaged	Private (no management)	Dog walkers, canoes, swimmers, cyclists	Mesotrophic	2000
Schwicheldt	Unmanaged	Private (no management)	Owner/hunter, dog walkers	Mesotrophic	2007
Heeßel	Unmanaged	Business property (no management)	No	Eutrophic	1963
Xella	Unmanaged	Business property; endangered crayfish (*Astacus astacus*) breeding	No (restricted access)	Mesotrophic	1975

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

IUCN Red List category	EU Directives	Red List categories of Germany and Lower Saxony	Rank r	Weight c
EX – extinct EW – extinct in the wild		0 – extinct	5	32
CR – critically endangered	Annex I (Birds) Annex IV (Habitats)	1 – critically endangered 2 – endangered	4	16
EN – endangered	Annex II (Habitats)	3 – vulnerable G – intermediate	3	8
VU – vulnerable		R – rare	2	4
NT – near threatened	Annex V (Habitats)	V – near threatened	1	2
LC – least concern DD – data deficient	Annex II and III (Birds)	* – least concern - – data deficient	0	1

Table 3: Overview about unique species species of different taxa found at managed and unmanaged gravel pits in Lower Saxony, Germany. Full details of the species inventory are in Table S9.

Taxon	Species number found only in …			Sørensen index (similarity)	SER_r index (dissimilarity)
	…managed lakes	…unmanaged lakes	…one lake (any type)		
submerged macrophytes	28	9	31	0.48	0.68
riparian herbs	55	27	57	0.73	0.43
riparian trees	6	4	8	0.86	0.25
amphibians	0	0	0	1.00	0.00
Odonata	5	8	7	0.76	0.38
waterfowl	10	5	6	0.69	0.47
songbirds	9	4	12	0.74	0.42

Table 4: Comparison of species richness 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 (range) managed (N = 16)	unmanaged (N = 10)	test	Statistics statistic	p-value
species richness	submerged macrophytes	8.8 ± 4.4 (3-17)	5.9 ± 4.3 (0-14)	t-test	t = 1.63	0.710
	riparian herbs	41.8 ± 12.5 (15-57)	50 ± 10.7 (30-64)	t-test	t = -1.73	0.638
	riparian trees	12.8 ± 2.1 (9-17)	12.6 ± 5.3 (3-24)	Welch-test	t = 0.08	1.000
	amphibians	1.6 ± 0.5 (1-2)	2.2 ± 0.8 (1-3)	U-test	W = 43	0.299
	amphibians reproducing	1 ± 0.6 (0-2)	1.4 ± 0.8 (0-3)	U-test	W = 59	0.922
	Odonata	7.9 ± 2.8 (2-12)	9 ± 4.3 (4-18)	t-test	t = -0.77	0.997
	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	0.995
	songbirds	9.2 ± 2.8 (5-14)	11.3 ± 3 (7-17)	t-test	t = -1.81	0.577
	waterfowl	9.5 ± 2.8 (3-13)	9.1 ± 3.5 (2-13)	t-test	t = 0.32	1.000
threatened species	submerged macrophytes	2.2 ± 1.8 (0-5)	1.4 ± 1.6 (0-5)	U-test	W = 100.5	0.949
	riparian herbs	1.6 ± 0.7 (0-3)	2.2 ± 1 (1-4)	U-test	W = 55.5	0.823
	riparian trees	0.6 ± 0.6 (0-2)	0.2 ± 0.4 (0-1)	U-test	W = 105	0.714
	amphibians (only when reproducing)	0.2 ± 0.4 (0-2)	0.5 ± 0.7 (0-2)	U-test	W = 61.5	0.893
	Odonata	0.8 ± 0.8 (0-2)	1.3 ± 1.2 (0-4)	U-test	W = 61.5	0.967
	damselflies	0.3 ± 0.5 (0-1)	0.1 ± 0.3 (0-1)	U-test	W = 92	0.985
	dragonflies	0.6 ± 0.7 (0-2)	1.2 ± 1.2 (0-4)	U-test	W = 54.5	0.780
	songbirds	0.4 ± 0.5 (0-1)	0.5 ± 0.5 (0-1)	U-test	W = 70	0.999
	waterfowl	1.6 ± 1.3 (0-4)	1.1 ± 1.1 (0-3)	U-test	W = 98.5	0.969
conservation value	submerged macrophytes	5.6 ± 2.2 (1.2-10.9)	3.5 ± 1.9 (1-6.2)	t-test	t = 2.38	0.232
	riparian vegetation	1.6 ± 0.4 (0.7-2.6)	1.4 ± 0.2 (1-1.7)	t-test	t = 1.72	0.643
	riparian herbs	1.7 ± 0.7 (0.3-3.4)	1.4 ± 0.3 (0.8-1.8)	Welch-test	t = 1.48	0.812
	riparian trees	1.7 ± 0.3 (1-2.3)	1.3 ± 0.4 (1-1.9)	U-test	W = 122	0.245
	amphibians	**1.3 ± 0.3 (1-1.5)**	**1.6 ± 0.3 (1-2)**	**U-test**	**W = 30.5**	**0.048**
	Odonata	1.8 ± 0.8 (1-3.7)	1.7 ± 1 (1-3.9)	U-test	W = 91.5	1.000
	damselflies	1.4 ± 0.6 (1-2.8)	1.2 ± 0.2 (1-1.7)	U-test	W = 87	1.000
	dragonflies	2.1 ± 1.6 (1-6)	2.3 ± 1.9 (1-6.5)	U-test	W = 75	1.000
	songbirds	1.6 ± 0.5 (1-2.7)	1.6 ± 0.2 (1.2-1.9)	Welch-test	t = 0.06	1.000
	waterfowl	3.1 ± 1.7 (1.1-6.6)	2.7 ± 1.1 (1.2-3.9)	t-test	t = 0.68	0.999

Table 5: ANOVA results of forward selection of RDA models explaining species richness and conservation value (management not used as predictor variable). Variables are ordered by their R^2_{adj}-value. **Significant variables (p < 0.05) are bolded**, *statistical trends (p < 0.1) are italic*.

Modelling step	Variable	Variance explained	R^2_{adj}	F-statistic	p-value
full model (without management) for **species richness**	**woody_habitat**	**0.96**	**0.130**	**5.23**	**< 0.001**
	agricultural_extension	**0.52**	**0.041**	**2.83**	**0.017**
	age	**0.51**	**0.039**	**2.77**	**0.020**
	lake_steepness	**0.46**	**0.038**	**2.49**	**0.031**
	acidity	0.16	0.032	0.86	0.532
	vegetated_habitat	**0.48**	**0.030**	**2.63**	**0.025**
	nitrogen	0.21	0.018	1.12	0.352
	lake_shallowness	*0.39*	*0.017*	*2.14*	*0.061*
	conductivity	0.31	0.017	1.67	0.140
	non_accessibility	*0.38*	*0.006*	*2.07*	*0.069*
	trophic state	0.19	0.005	1.06	0.396
	general_recreational_use_intensity	0.30	-0.011	1.64	0.156
	wetland	0.04	-0.011	0.20	0.980
	distance_to_next_river	0.16	-0.016	0.88	0.523
	rural	0.15	-0.022	0.81	0.576
	forest_extension	0.15	-0.027	0.80	0.582
best model for **species richness**	**woody_habitat**	**1.16**	**0.311**	**5.99**	**< 0.001**
	agricultural_extension	**0.69**		**3.59**	**0.003**
	lake_steepness	**0.60**		**3.11**	**0.008**
	vegetated_habitat	**0.50**		**2.60**	**0.021**
full model (without management) for **conservation value**	*woody_habitat*	*0.60*	*0.040*	*2.14*	*0.063*
	general_recreational_use_intensity	0.19	0.039	0.67	0.683
	forest_extension	0.33	0.029	1.19	0.323
	lake_shallowness	0.45	0.026	1.60	0.163
	non_accessibility	0.43	0.022	1.54	0.180
	nitrogen	0.20	0.015	0.71	0.627
	distance_to_next_river	0.43	0.013	1.54	0.180
	age	0.22	0.007	0.77	0.605
	acidity	0.32	0.003	1.16	0.335
	agricultural_extension	0.35	-0.001	1.24	0.297
	vegetated_habitat	0.21	-0.012	0.75	0.623
	conductivity	0.26	-0.013	0.91	0.479
	rural	0.27	-0.014	0.97	0.452
	trophic_state	0.09	-0.017	0.32	0.926
	wetland	0.06	-0.026	0.20	0.979
	lake_steepness	0.03	-0.037	0.12	0.996
best model for **conservation value**	**woody_habitat**	**0.55**	**0.083**	**2.14**	**0.047**
	general_recreational_use_intensity	**0.54**		**2.12**	**0.049**

Table 6: ANOVA results of forward selection of RDA models explaining species richness and conservation value (management included as predictor variable). Variables are ordered by their R^2_{adj}-value. **Significant variables (p < 0.05) are bolded**, *statistical trends (p < 0.1) are italic*.

Modelling step	Variable	Variance explained	R^2_{adj}	F-statistic	p-value
full model for species richness	**woody_habitat**	**0.85**	**0.130**	**4.90**	**0.001**
	management	**0.57**	**0.043**	**3.26**	**0.009**
	agricultural_extension	**0.40**	**0.041**	**2.31**	**0.044**
	age	*0.40*	*0.039*	*2.31*	*0.050*
	lake_steepness	**0.42**	**0.038**	**2.43**	**0.036**
	acidity	0.16	0.032	0.92	0.488
	vegetated_habitat	*0.39*	*0.030*	*2.24*	*0.055*
	nitrogen	0.28	0.018	1.59	0.165
	lake_shallowness	*0.37*	*0.017*	*2.13*	*0.067*
	conductivity	*0.34*	*0.017*	*1.96*	*0.092*
	non_accessibility	*0.38*	*0.006*	*2.17*	*0.062*
	trophic state	0.20	0.005	1.13	0.357
	general_recreational_use_intensity	*0.38*	*-0.011*	*2.17*	*0.059*
	wetland	0.05	-0.011	0.30	0.943
	distance_to_next_river	0.08	-0.016	0.46	0.843
	rural	0.18	-0.022	1.03	0.414
	forest_extension	0.15	-0.027	0.86	0.528
best model for species richness	**woody_habitat**	**1.16**	**0.311**	**5.99**	**< 0.001**
	agricultural_extension	**0.69**		**3.59**	**0.002**
	lake_steepness	**0.60**		**3.11**	**0.006**
	vegetated_habitat	**0.50**		**2.60**	**0.019**
full model for conservation value	**management**	**0.73**	**0.068**	**2.75**	**0.018**
	woody_habitat	0.37	0.040	1.38	0.240
	general_recreational_use_intensity	0.47	0.039	1.75	0.121
	forest_extension	0.36	0.029	1.34	0.255
	lake_shallowness	0.43	0.026	1.61	0.163
	non_accessibility	0.42	0.022	1.56	0.177
	nitrogen	0.14	0.015	0.52	0.787
	distance_to_next_river	0.35	0.013	1.32	0.260
	age	0.19	0.007	0.73	0.630
	acidity	0.30	0.003	1.14	0.361
	agricultural_extension	0.22	-0.001	0.84	0.556
	vegetated_habitat	0.11	-0.012	0.43	0.867
	conductivity	0.28	-0.013	1.05	0.403
	rural	0.30	-0.014	1.11	0.366
	trophic_state	0.09	-0.017	0.33	0.918
	wetland	0.05	-0.026	0.19	0.982
	lake_steepness	0.03	-0.037	0.10	0.998
best model for conservation value	**management**	**0.73**	**0.068**	**2.83**	**0.008**

Figure legends

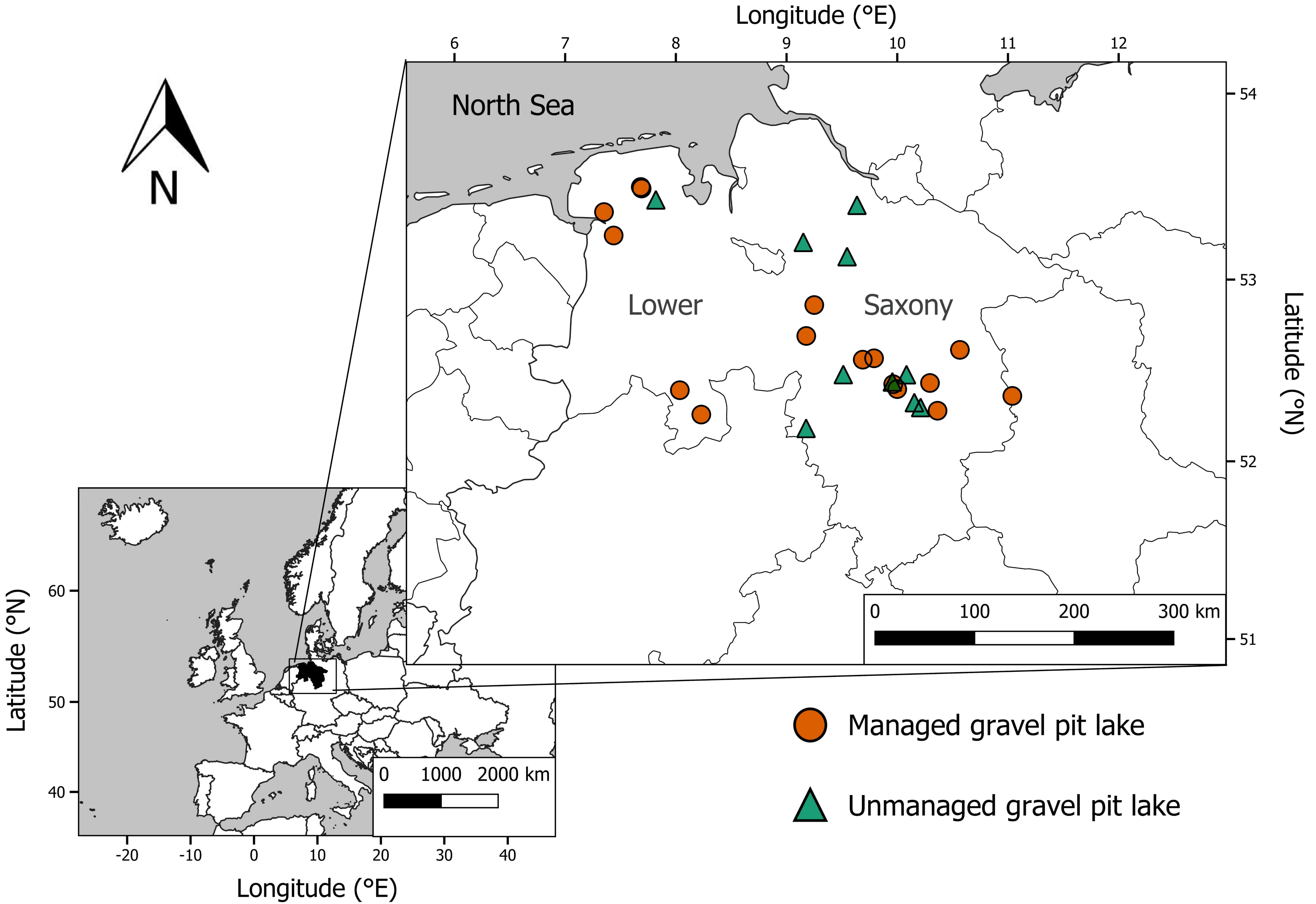
Figure 1: Map of study area in Lower Saxony (Germany).

Figure 2: Habitat assessment plot, modified after Kaufmann & Whittier (1997) and Newbrey et al. (2005).

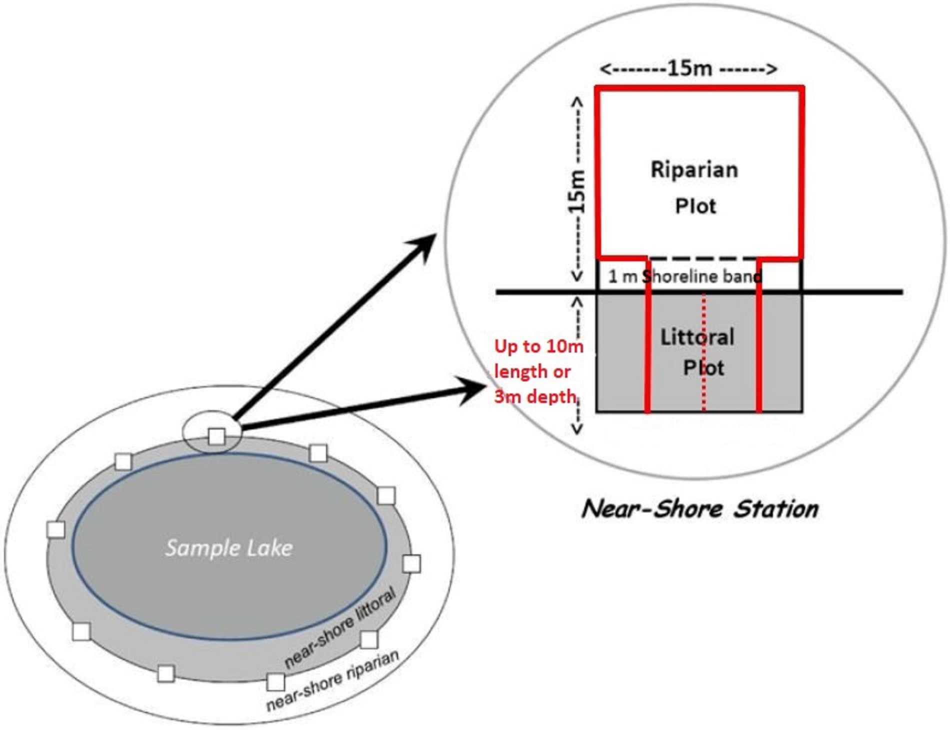
Figure 3: Principal component analysis (PCA) by category of environmental variables visualized for (a) morphology, (b) land use, (c) habitat structure, and (d) recreational use intensity. Percentages in brackets show the proportional variance explained by each axis. See Tables S7, S8 for details on PCA-results. The abbreviations used are shown in Tables S5, S6. 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. Differences are highly significant when confidence levels do not overlap.

Figure 4: Principal component analysis (PCA) of species richness plotted for the first two axes. Percentages in brackets show the proportional variance explained by each axis. Names of selected explanatory variables are shown in Tables S5, S6. Numbers reflect the different lakes (Table 1). The centroids of management types and the explanatory variables from redundancy analysis (RDA, slashed purple lines) are plotted as supplementary variables to not influence the ordination. The 95% confidence-level around centroids are plotted to visualize differences between lake types.

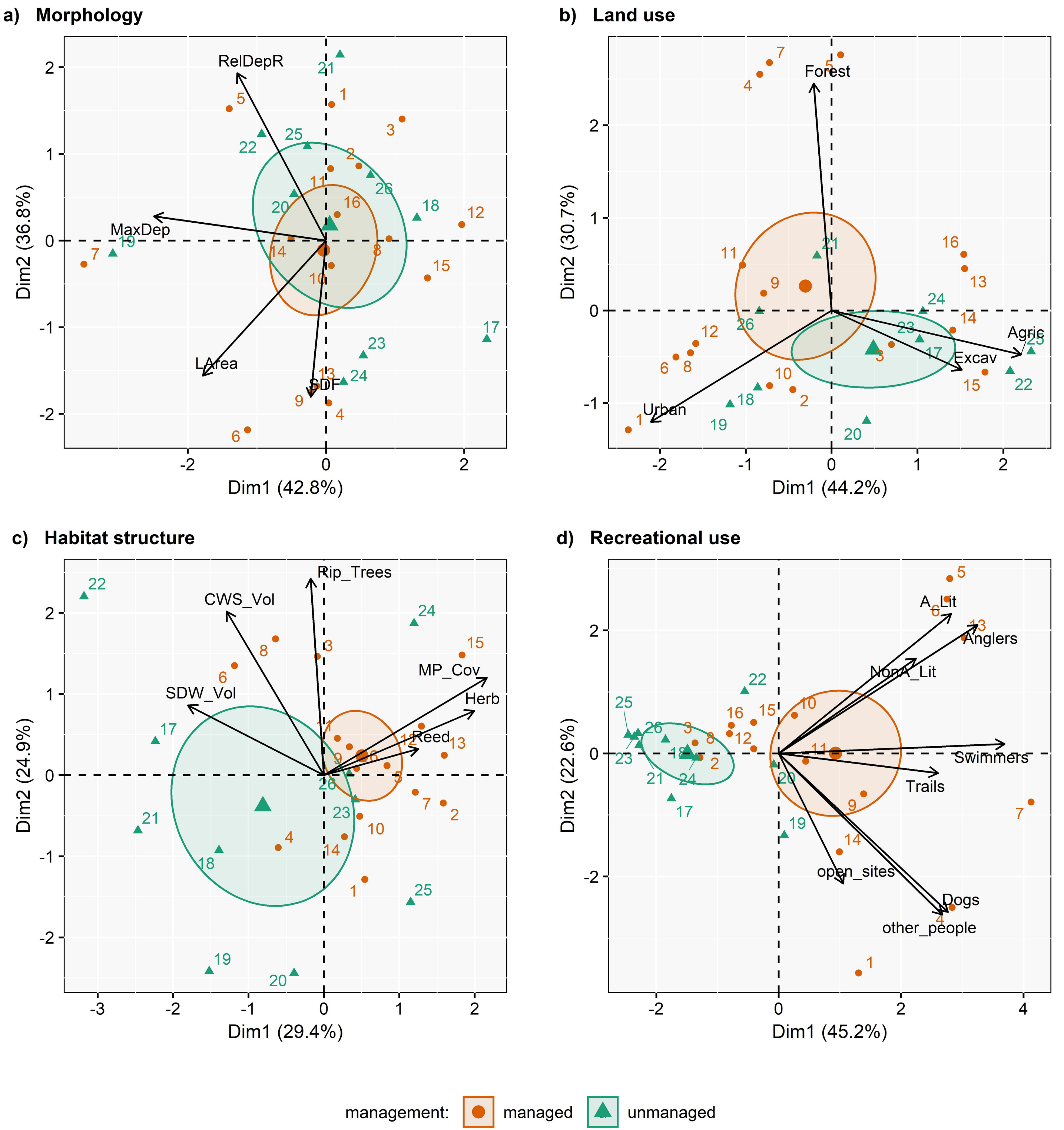
Figure 5: Principal component analysis (PCA) of conservation value plotted for the first two axes. Percentages in brackets show the proportional variance explained by each axis. Names of selected explanatory variables are shown in Tables S5, S6. Numbers reflect the different lakes, see Table 1. The centroids of management types and the explanatory variables from redundancy analysis (RDA, slashed purple lines) are plotted as supplementary variables to not influence the ordination. The 95% confidence-level around centroids are plotted to visualize differences between lake types.

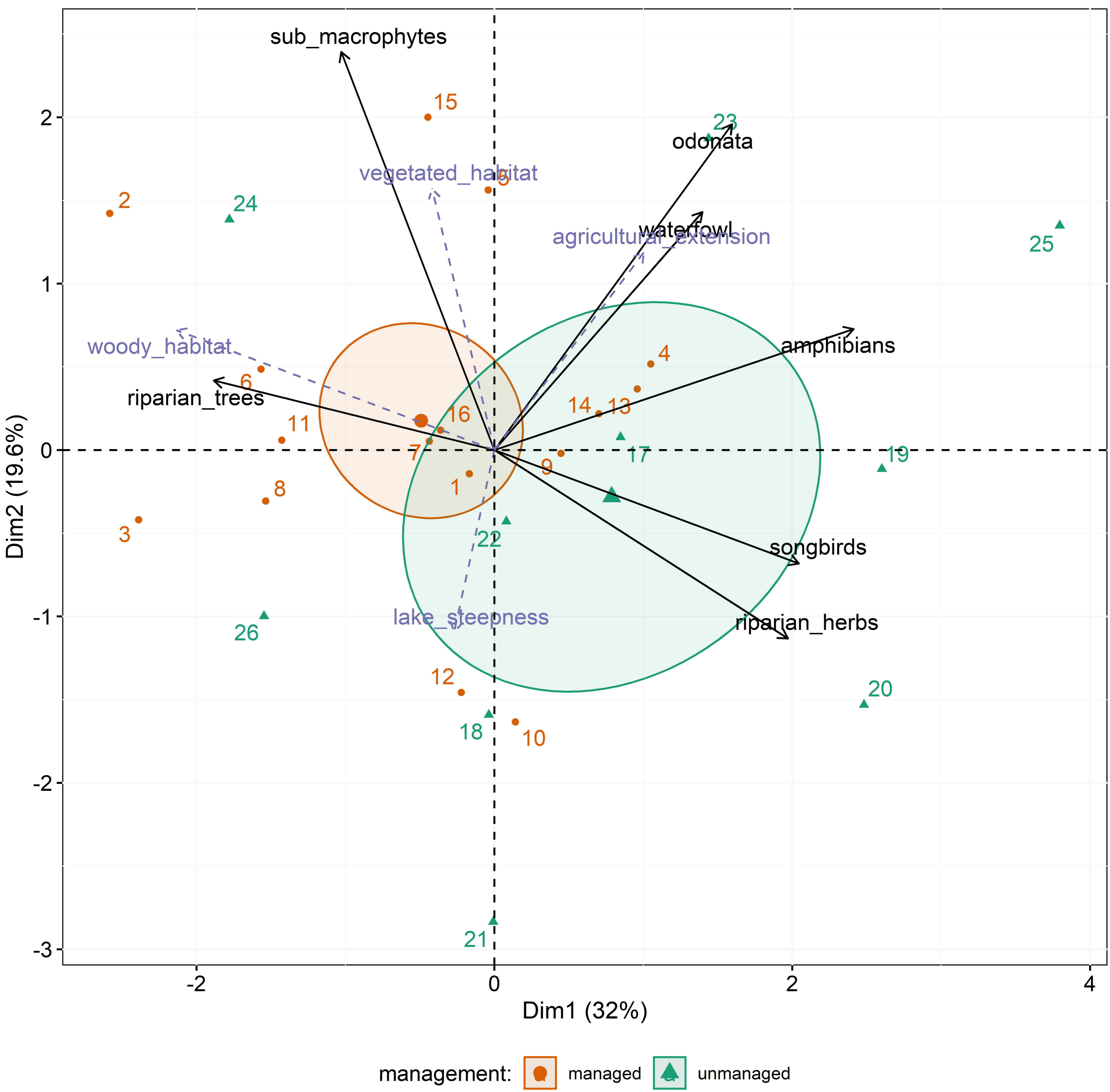


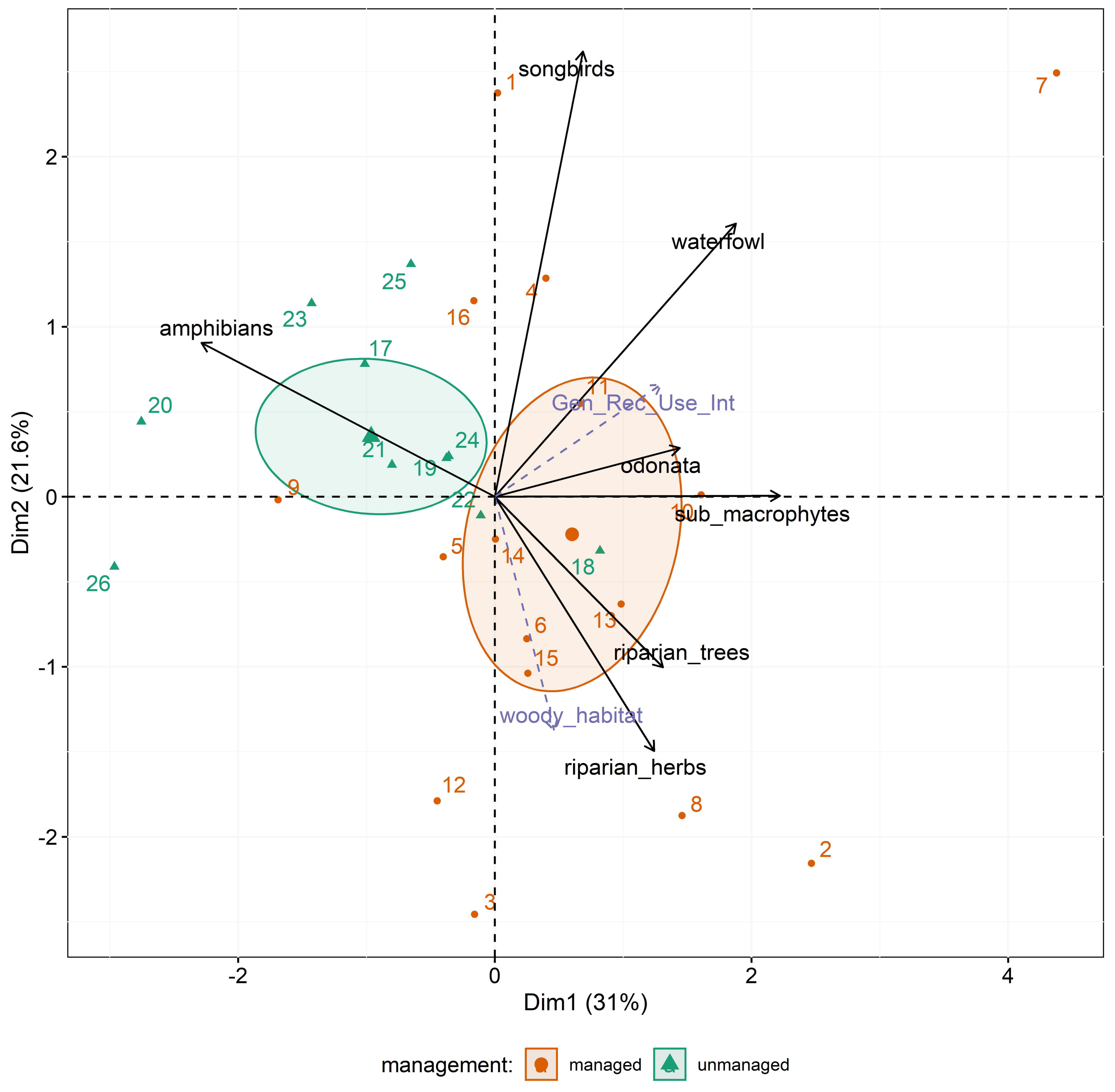
Longitude (°E)
6
7
8
9
10
11
12
54
53
52
51
Latitude (°N)
N
North Sea
Lower
Saxony
0
100
200
300 km
60
50
40
Latitude (°N)
-20
-10
0
10
20
30
40
Longitude (°E)
0
1000
2000 km
Managed gravel pit lake
Unmanaged gravel pit lake



<-------15m ------>
15m
Riparian
Plot
1 m Shoreline band
Littoral
Plot
Up to 10m
length or
3m depth
Sample Lake
near-shore littoral
near-shore riparian
Near-Shore Station


a) Morphology
b) Land use
c) Habitat structure
d) Recreational use
RelDepR
MaxDep
LArea
SDF
Dim1 (42.8%)
Dim2 (36.8%)
Forest
Agric
Excav
Urban
Dim1 (44.2%)
Dim2 (30.7%)
Rip_Trees
CWS_Vol
SDW_Vol
MP_Cov
Herb
Reed
Dim1 (29.4%)
Dim2 (24.9%)
A_Lit
Anglers
NonA_Lit
Swimmers
Trails
open_sites
Dogs
other_people
Dim1 (45.2%)
Dim2 (22.6%)
management:
managed
unmanaged


sub_macrophytes
odonata
vegetated_habitat
waterfowl
agricultural_extension
woody_habitat
riparian_trees
amphibians
songbirds
riparian_herbs
lake_steepness
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
-3
-2
-1
0
1
2
-2
0
2
4
Dim2 (19.6%)
Dim1 (32%)
management:
managed
unmanaged



songbirds
waterfowl
amphibians
Gen_Rec_Use_Int
odonata
sub_macrophytes
riparian_trees
woody_habitat
riparian_herbs
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
Dim2 (21.6%)
Dim1 (31%)
2
1
0
-1
-2
-2
0
2
4
management:
managed
unmanaged