Impact of recreational fisheries on aquatic and riparian biodiversity in artificial lake ecosystems: implications for conservation

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Abstract

There is consensus that humanity is facing a global biodiversity crisis, with freshwater-associated biodiversity being reported to be in particularly dire state. Novel ecosystems created through human use of littoral resources (e.g., sand, gravel), i.e., gravel pit lakes, can provide substitute habitats of importance to conservation of freshwater biodiversity. However, we can expect these lakes, which are often managed for and by recreational fisheries, to also exhibit generally high recreational use intensity, which may negatively impact aquatic biodiversity. Our objective was to evaluate the species inventory and conservation value of a range of aquatic and riparian taxa (plants, amphibians, dragonflies, damselflies, waterfowl, songbirds) within and associated with artificially created lake ecosystems managed by recreational fisheries. To examine the specific impact of recreational fisheries we compared the biodiversity in N = 16 gravel pits managed by recreational fisheries with N = 10 lakes that were not experiencing recreational fisheries, while controlling for a set of environmental variables. Managed and unmanaged gravel pit lakes were similar in regards to morphological and productivity-related lake variables, while differing in littoral and riparian habitat structure and recreational use intensity by anglers and other recreationists. Despite these differences, the average species richness and conservation value of all the examined taxa 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. 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, rather than being related to the presence of recreational fisheries or recreational use intensity. Collectively, we found no evidence that anglers and recreational-fisheries management constitute a relevant stressor to aquatic and riparian biodiversity.

Keywords

amphibians, biodiversity, birds, conservation, macrophytes, management, novel ecosystems, odonata, recreational fishing, waterfowl

1. Introduction

Globally, biodiversity is in steep decline, creating a biodiversity crisis of unprecedented scale (Brooks et al., 2006; Ceballos, García, & Ehrlich, 2010; IPBES, 2019; WWF, 2018). The numbers of endangered species are constantly rising (Butchart et al., 2010; WWF, 2018), with an estimated number of at least 1 million species threatened by extinction (IPBES, 2019). The current species extinction rates are estimated to be 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 (Abell, 2002; Freyhof & Brooks, 2011; Sala et al., 2000; WWF, 2018). From 1970 to today, freshwater biodiversity has declined by 83% in abundances across thousands of populations (WWF, 2018). Analysis of European red lists has shown that more than a third (37%) of freshwater fishes are threatened (Freyhof & Brooks, 2011). This compares with 44% of freshwater molluscs, 23% of amphibians, 19% of reptiles, 15% of mammals and dragonflies, 13% of birds, 9% of butterflies and 7% of the aquatic plants present in Europe (Freyhof & Brooks, 2011). Although manifold reasons contribute to the freshwater biodiversity crisis (Reid et al., 2019), habitat alteration and fragmentation (e.g., due to damming or land use changes), pollution, overexploitation, invasive species and climate change are key threats (Dudgeon et al., 2006; IPBES, 2019).

Freshwater-associated species respond to aquatic environmental variables as well as those associated with riparian habitat quality and land use. The specific drivers vary by species and taxon. For example, the diversity of submerged macrophytes is strongly governed by nutrient inputs (which is fundamentally related to land use and hydrology at catchment scales) and in-water chemical variables, sediments and water turbidity (which affects light penetration) (Hilt et al., 2018; Stefanidis, Sarika, & Papastegiadou, 2019). However, submerged macrophytes can also be negatively affected by benthivorous fish (Bajer et al., 2016) and herbivory, e.g. by crayfish (Carreira, Dias, & Rebelo, 2014; Roessink, Gylstra, Heuts, Specken, & Ottburg, 2017; van der Wal et al., 2013) and waterfowl (Wood, Stillman, Clarke, Daunt, & O'Hare, 2012). By contrast, amphibian species diversity is more strongly dependent on habitat fragmentation and loss affecting migration corridors in terrestrial ecosystems (Gonçalves, Honrado, Vicente, & Civantos, 2016; Shulse, Semlitsch, Trauth, & Williams, 2010; Trochet et al., 2019); hence this taxon will be strongly influenced by land use developments, urbanization, settlements and loss of temporary waters (Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018). Additionally amphibians and in particular tadpoles are sensitive to fish predation (Shulse et al., 2010) and are affected by littoral habitat structure and water depth (Porej & Hetherington, 2005). Similarly, the diversity of dragonflies and damselflies is controlled by the spatial arrangement of water bodies in a landscape, and littoral habitat homogenization and loss of vegetation and other structures (e.g., woody habitat) (Clausnitzer et al., 2009; Elo, Penttinen, & Kotiaho, 2015; Goertzen & Suhling, 2018; Koch, Wagner, Sahlén, & Tsubaki, 2014) as well as fish predation during the larval aquatic stages (Knorp & Dorn, 2016; Morin, 1984a, 1984b) also play an important role in driving local species diversity. Key threats to bird populations associated with freshwater ecosystems encompass land use changes, climate shifts, pollution, loss of forage bases, mortality increases through pets (e.g., cats; see Bonnaud, Berger, Bourgeois, Legrand, & Vidal, 2012) and humans (e.g., hunting), but birds are also sensitive to non-lethal disturbances caused by humans due to proximity to urban areas and after exposure to intensive outdoor recreation (BirdLife International, 2015; Wahl *et al.*, 2015). Given the complexity of taxon-specific environmental drivers on freshwater biodiversity, it is difficult to identify a common set of key environmental factors to inform effective conservation management across taxa at individual water bodies.

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 (Biggs, von Fumetti, & Kelly-Quinn, 2017; Damnjanović et al., 2018; De Meester et al., 2005; Lemmens et al., 2013; Lenda, Skórka, Moroń, Rosin, & Tryjanowski, 2012; Santoul, Gaujard, Angélibert, Mastrorillo, & Céréghino, 2009; Scheffer et al., 2006; Völkl, 2010). Artificial lake ecosystems are often relatively recent in origin (< 100 years of age, Gee, 1978; Schurig, 1972; R. M. Wright, 1990; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2016), created by mining of sand, clay, gravel and other resources (Saulnier-Talbot & Lavoie, 2018; Søndergaard, Lauridsen, Johansson, & Jeppesen, 2018). More than one billion tons of sand, gravel and other littoral resources were excavated in more than 24,500 quarries and pits within the EU-28 in 2017 alone (Delvoie, Zhao, Michel, & Courard, 2019; UEPG, 2017). Germany is the largest producer of sands in Europe, generating 256 million tons in 2,733 quarries and pits in 2017 (Delvoie, Zhao, Michel, & Courard, 2019; UEPG, 2017). The resulting numerous man-made "pit lakes" (for simplicity henceforth referred to as gravel pit lakes) have become common landscape elements in many cultural landscapes across the industrialized world (Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Søndergaard et al., 2018). For example, in the study area of the research present in this paper (Lower Saxony in Germany), gravel pits today constitute the dominant lentic habitat, constituting about 95% (in numbers) and 70% (in terms of area) of all water bodies larger than 1 ha (Manfrin et al., unpublished data). Accordingly, gravel pit lakes have become important for both biodiversity conservation and recreation (Emmrich, Schälicke, Hühn, Lewin, & Arlinghaus, 2014; Matern et al., in press).

Lakes, including gravel pit lakes, provide a bundle of ecosystem services to humans (Reynaud & Lanzanova, 2017). These include provisioning services, such as fish yield, drinking water supply as well as a range of cultural ecosystem services, in particular recreation (Venohr et al., 2018) and intrinsic benefits associated with the presence of threatened aquatic biodiversity (Holmlund & Hammer, 1999; 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 (Larson, Reed, Merenlender, & Crooks, 2016; Liddle & Scorgie, 1980). For example, human activities on the shoreline can alter habitats, which can lead to a loss of plant biodiversity through trampling effects (Bonanno, Leopold, & Hilaire, 1998; Manning, 1979; O'Toole, Hanson, & Cooke, 2009; Seer, Irmler, & Schrautzer, 2015). Shoreline development, e.g., habitat simplification through the construction of beaches or other recreation sites, can reduce littoral and riparian habitat quality and affect macroinvertebrate abundance and biodiversity (Brauns, Garcia, Walz, & Pusch, 2007; Spyra & Strzelec, 2019). Water-based recreation can negatively impact on birds and other wildlife through fear reactions in response to human presence (Dear, Guay, Robinson, & Weston, 2015; Frid & Dill, 2002; Lozano & Malo, 2013), presence of dogs (Lee, Marsden, Tatum-hume, & Brightsmith, 2017; Randler, 2006) or intensive pleasure boating (McFadden, Herrera, & Navedo, 2017; Wolter & Arlinghaus, 2003). Moreover, the use of gravel pit lakes through fisheries can modify the fish community (Lewin, Arlinghaus, & Mehner, 2006; Matern et al., in press), and short term increases of the biomass of stocked fish as well as natural fish predation can affect survival of tadpoles (Miró, Sabás, & Ventura, 2018; Shulse et al., 2010) or aquatic stages of invertebrates such as damselflies (Knorp & Dorn, 2016; Morin, 1984b). Certain species that are commonly stocked by anglers, such as common carp (*Cyprinus carpio*), may also modify the habitat for aquatic vegetation through suspension of sediments via benthivory and reduce species richness (Bajer et al., 2016). Recreational activities, such as pleasure boating, diving or angling, can also constitute vectors of the spread of non-native and potentially invasive species, hitchhiking via attachment to boats (Ros, Vazquez-Luis, & Guerra-Garcia, 2013) or recreational gear (Bacela-Spychalska, Grabowski, Rewicz, Konopacka, & Wattier, 2013). Non-native fishes may also be introduced through deliberate or unintentional introductions via the common fisheries-management practice of fish stocking (Johnson, Arlinghaus, & Martinez, 2009; Zhao et al., 2016). 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 are at the same time stewards, and in some regions of the world also managers of fish populations and habitats of freshwater ecosystems (Arlinghaus et al., 2019, 2017; Daedlow, Beard, & Arlinghaus, 2011; Matern et al., in press). 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 pits (Arlinghaus et al., 2017, 2015; Emmrich et al., 2014; Matern et al., in press). Angler activities, both in terms of exploitation and fisheries and habitat management, are mainly directed at fish stocks, e.g., through practices as fish stocking and fish harvesting. Therefore, key impacts of recreational fisheries can be expected at the fish stock level (Matern et al., in press). Angler-induced changes to fish biomass, fish size or fish community composition can have knock-on effects on submerged macroyphtes (Bajer et al., 2016), amphibians (Hecnar & M'Closkey, 1997; Miró et al., 2018) and invertebrates such as dragonflies (Knorp & Dorn, 2016). In addition, anglers may modify littoral habitats through angling site constructions (O'Toole et al., 2009), thereby affecting plants (O'Toole et al., 2009), dragonflies (Z. Müller et al., 2003) or birds (Kaufmann, Hughes, Whittier, Bryce, & Paulsen, 2014). Certain anglers also contribute to eutrophication through ground-baiting (Niesar, Arlinghaus, Rennert, & Mehner, 2004), thereby possibly affecting macrophytes, and they may disturb wildlife and birds due to extended human presence in littoral zones (Burger & Gochfeld, 1998; Frid & Dill, 2002; Knight, Anderson, & Marr, 1991; Le Corre, Gélinaud, & Brigand, 2009; Reichholf, 1988; Wichmann, 2010; Yalden, 1992). Lost fishing gear can also have lethal effects on birds (Franson et al., 2003; Heath, Dahlgren, Simon, & Brooks, 2017), for example when lost fishing leads are ingested by birds (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.

Calls have been raised to either foster the presence of recreational fishers as stewards and managers of aquatic ecosystems (Danylchuk & Cooke, 2011; Fujitani, McFall, Randler, & Arlinghaus, 2017) or to spatio-temporally constrain or even ban recreational fisheries on selected waters or sites because anglers can be seen as a long-lasting, non-natural disturbance to aquatic ecosystems that may negatively affect natural processes and reduce local biodiversity, in particular bird populations (Bauer, Stark, & Frenzel, 1992; D. V Bell & Austin, 1985; Cooke, 1974; Erlinger, 1981; J. L. Newbrey, Bozek, & Niemuth, 2005; Park, Park, Sung, & Park, 2006; Reichholf, 1988; Wichmann, 2010). From a scientific perspective, spatial or temporal constraints on popular activities, such as recreational fishing, for the sake of conservation shall be informed by objective data that document relevant biodiversity impacts at the scale of entire ecosystems (Stock et al., 1994). However, much research on the biodiversity impacts of recreational fisheries is directed at single taxa (e.g., birds), tends to be focused on selected sites rather than entire ecosystems (e.g., Bauer et al., 1992; Erlinger, 1981; Reichholf, 1970; Wichmann, 2010), interprets biodiversity impacts of recreation without appropriately considering alternative non-recreation based impact sources (e.g., land use change; see Reichholf, 1988), suffers from lack of replication and controls (e.g., Cooke, 1974) or focuses on individual-level endpoints (e.g., flight initiation distance) that are not necessarily scaled up to population and species presence (e.g., de Boer & Longamane, 1996). However, it is the latter impacts at higher levels of biological organization (e.g., populations, species diversity) that are crucially important from a legal conservation perspective to justify management interventions and constraints on popular activities such as recreational fishing. For example, the German Nature Conservation Law specifies in its clause 33 that human disturbances are prohibited in Natura-2000 conservation areas designed within the EU Habitats Directive (EU, 1992) when they are considered of having a substantial ("erheblich") impact on conservation goals that relate to the presence of selected endangered species or sensitive habitats as specified in the appendices of the Directive. This clause can be interpreted that conservation action is warranted when listed species substantially change in abundance or species composition (e.g., recreation-induced faunal breaks) or even go extinct (e.g., Fernández-Juricic, 2002) due to human interference. However, German nature conservation authorities regularly regulate and even entirely ban recreational fisheries in national conservation areas in the absence of local-level evidence for substantial impacts of recreational fishing on aquatic biodiversity or habitats, and these decisions and initiatives are fueling intensive conflicts with anglers and hunters on local scales (Arlinghaus, 2005).

Our objectives were to inform an ongoing conservation debate about the biodiversity impacts of recreational fisheries using gravel pit lakes as model system. In Germany, recreational fisheries are regularly constrained or even banned from a use of selected waterbodies (Landkreis Lüneburg, 2018; Landkreis Nienburg/Weser, 2018; H. Müller, 2012) based on the assumption that a fisheries use constitute a lasting disturbance for selected taxa and habitats that is of concern from a conservation perspective (Bauer et al., 1992; D. V Bell & Austin, 1985; Erlinger, 1981; Park et al., 2006; Reichholf, 1988; Wichmann, 2010). Similarly, there is evidence that the use of recreational fisheries in gravel pits sometimes prohibited a priori during environmental impact assessments associated with approval processes to mine sand and gravel, based on the assumption that not using the gravel pit in construction in the future via angling is beneficial to nature conservation (H. Müller, 2012). To examine empirical data supporting these actions, we used a space-for-time substitution design studying the biodiversity in gravel pits that are both used and managed by recreational fisheries compared with the biodiversity in similarly structured lakes that are not used and managed by recreational fisheries. Our study was not meant to reveal the specific pathways by which anglers may impact on different taxa. Rather our work was meant to showcase the aggregate impact of recreational fisheries on biodiversity in gravel pit lakes. Specifically, we were interested 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. This research aim was chosen in light of the observation that recreational fisheries are often selectively constrained from selected conservation sites without necessarily constraining other recreational uses (Cooke, 1974; Landkreis Lüneburg, 2018; Landkreis Nienburg/Weser, 2018). We tested the null hypothesis that recreational fisheries do not affect the species richness and conservation value across multiple taxa (odonata, amphibians, submerged and riparian vegetation, waterfowl and songbirds). Rejecting this statistical hypothesis would provide support for our research hypotheses that recreationally used lakes would show reduced taxonomic richness and conservation value in disturbance-sensitive taxa such as birds, waterfowl or dragonflies.

2. Methods

Study area and lake selection

This study was conducted in Lower Saxony, Germany. Lower Saxony borders the North Sea (Figure 1) and has a total population of almost 8 million people at a population density of 167 inhabitants per km^2. It has a total area of 47,710 km^2, of which more than 50% of the land or in total 27,753 km^2 are constituted of agricultural land and 10,245 km^2 are composed of managed forests (Landesamt für Statistik Niedersachsen (LSN), 2018). The lowlands of Lower Saxony are intensively used for agriculture. Natural lentic water bodies are scarce. Out of a total of 35,048 hectares of standing water surface in Lower Saxony, artificial lakes (mainly ponds and gravel pit lakes) form 73% by surface; artificial lakes account for more than 99% of the lentic waterbodies Lower Saxony by number (Manfrin et al., unpublished data).

Our sample design was geared towards identifying intensively used gravel pit lakes of a water surface of 20 ha or smaller to control for area-species diversity relationships and thereby being better able to examine the specific impact of recreational fisheries. To identify angler-managed gravel pit lakes, we approached the Angler Association of Lower Saxony, the largest umbrella association of angling clubs in Lower Saxony. We contacted about 320 angling clubs of the association, asking for angling clubs who were interested in participating in a biodiversity study in gravel pits that were owned (and not only leased) by angling clubs. We focused on owned lakes, assuming these lakes would receive particularly high levels of use and shoreline development activities compared to just leased systems. It is reasonable to assume this is the case because humans would invest more intensively in development of a lake when it is owned, rather than only leased. We first selected N = 16 angler-managed lakes randomly from the angling clubs fulfilling our search criteria (Figure 1). Subsequently, we used local informants to identify gravel pits not managed by anglers in the least possible distance to a focal angler-managed lake, thereby creating a design that attempted to control for systematic land use and other differences unrelated to recreation activity. As the vast majority of lakes in Lower Saxony are run by angling clubs, the total set of unmanaged lakes was substantially smaller. We finally managed to identify 10 unmanaged lakes. Both managed and unmanaged lakes were distributed widely across Lower Saxony (Figure 1), with no obvious clustering of any of the two lake types. The key difference among the angler-managed and unmanaged lakes was the absence of legal recreational fisheries and any planned recreational fisheries activity at the unmanaged lakes. As uncontrolled recreation by both illegal anglers and other recreationists might still occur in all lake types, we assessed each lake for recreational use, but the underlying assumption was that angler-managed lakes would also be more attractive to other recreationists (e.g., walkers) as anglers develop shorelines, built parking lots, trails etc.

All angler-managed lakes were in private property by angler clubs and received regular angling activity as well as fisheries-management actions such as fish stocking (Table 1). By contrast, the unmanaged lakes were owned by private people or companies that neither fish nor engage in fish stocking (Table 1). All managed lakes, and a subset of 7 unmanaged lakes were assessed by electrofishing and gill-netting for their fish communities, revealing identical fish biomasses and abundances in both lakes types, but a substantially larger local species richness and a significantly larger presence of game fishes (particularly piscivorous fish and large-bodied cyprinids such as carp) in angler-managed lakes (Matern et al., in press). Thus, it can be expected that the predation pressure by gape-limited fish on large bodied prey (e.g., tadpoles, large larvae of dragonflies) would be stronger in angler-managed lakes as the fish community in unmanaged lakes encompassed mainly small-bodied zooplanktivorous fishes (Matern et al., in press) strongly constrained in their gape.

We assessed the environmental variables (including recreational intensity) and local biodiversity of a range of taxa (odonata, amphibians, waterfowl, songbirds and aquatic and riparian vegetation) in 20 lakes (16 managed and 4 unmanaged) from 2016 to 2017, while 6 unmanaged lakes were sampled in 2018. All lake-specific environmental factors (e.g., morphology, trophic state etc.) can be found in the supplementary material (Table S1 to S3).

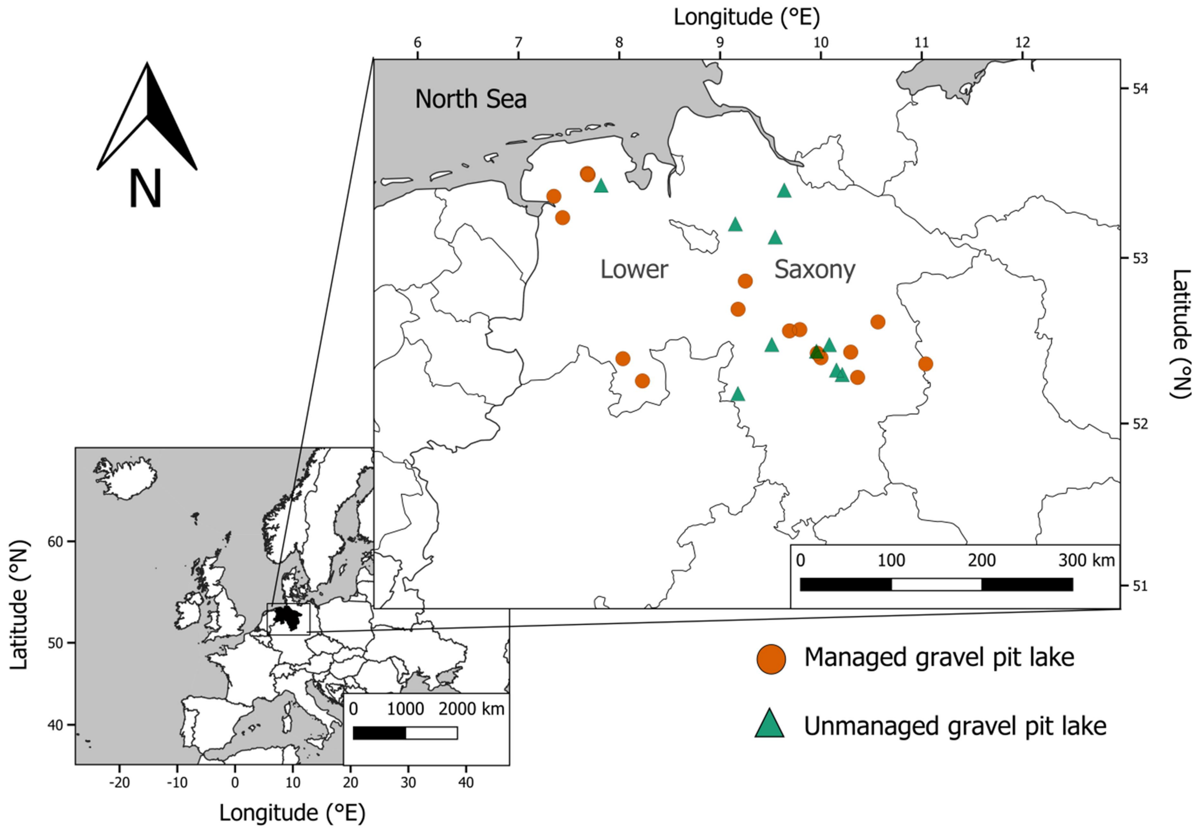
Land use

We assessed several indicators of land use and spatial arrangement for each lake. To that end, distances of each lake to next cities, villages, lakes, rivers etc. 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). We pooled categories of ATKIS®-objects 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, channels) and (7) other land use (not fitting in previous classes like succession areas, grass land, boulder sites etc.). With this classification we tried to account for all impacts on and habitat needs of our studied taxa.

Recreational use intensity

We assessed several indicators of recreational use intensity, enumerating the type and number of recreationists during each site visit (between 6 and 9 visits per lake) 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 2m circumference and 0.1% accuracy), measuring the distances of all trails and paths at the lake. This was summed up and then put in relation to the 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, too.

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



Morphology

Every lake was mapped with a SIMRAD NSS7 evo2 echo sounder together with a Lawrence TotalScan transducer. These were mounted on a boat with an electric motor, 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; Pebesma, 2004; R Core Team, 2013). The contour maps were used to extract maximum depth and also used for the calculation of the relative depth ratio (see Damnjanović et al., 2018). Shoreline length and lake area were estimated in QGIS 3.4.1, and the shoreline development factor (Osgood, 2005) was calculated with this data.

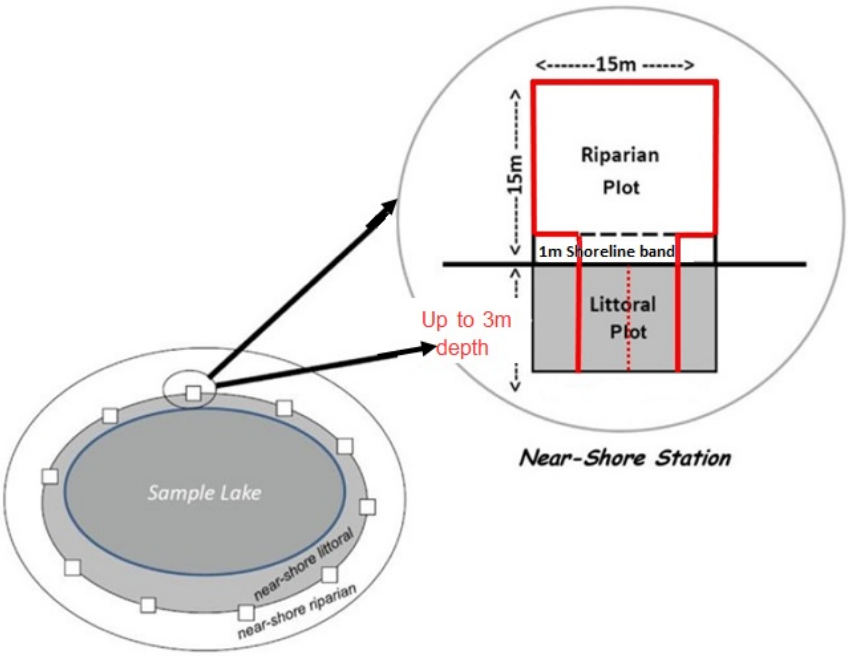
Water chemistry and nutrient levels

In spring during overturn, 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 was 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; S. W. Wright, 1991). The lake's conductivity and pH were measured with a WTW Multi 350i sensor (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 woody habitat was assessed using a plot design evenly spaced throughout the shoreline following Kaufmann & Whittier (1997). To that end, transects (= macrophyte transects, see next section) were placed perpendicular to and along the shore line with a 15 x 15 meter riparian plot at the shore (see Figure 2). 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, length and bulk diameter was measured for all dead wood structure, 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 (10-40% coverage), "3" means dominant (40-75% coverage), and "4" means very dominant (>75% coverage) in the plot.

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



Submerged macrophytes

All lakes were sampled for submerged macrophyte extension and 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 among 80 – 150 m depending on lake size. This summed up to 4 – 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 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 for littoral zone was calculated using the extrapolated coverage from strata between 0 and 3 meter 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 EU habitat directive (Garve, 2004; Korsch, Doege, Raabe, & van de Weyer, 2013; LÖBF NRW, 2004).

Table 1: Descriptors of gravel pits 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 dredging**
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

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 images 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 6 and 9 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 (Krüger & Nipkow, 2015).

Riparian vegetation

All lakes were sampled for riparian vegetation in May. At each lake, 4 transects were sampled, one at each cardinal direction of the lake. Each transect was 100 m long and contained 5 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 and 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; see Braun-Blanquet, 1964) were estimated for each species, genus or family (depending on identification accuracy, see Table S7). 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 EU habitat directive (Garve, 2004; LÖBF NRW, 2004).

Diversity metrics

We used presence-absence data and estimated species richness by taxon. 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 4 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 ($s_1, s_2, s_3, \ldots, s_n$) divided by the total number of observed species (n):

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

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

Statistical analysis

Mean/median differences among lake types (managed or unmanaged gravel pits) were calculated for all 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 variances were normally distributed (Shapiro-Wilk-test), otherwise a Mann-Whitney-U-test was used. P-values were Sidak-corrected (Šidák, 1967) due to multiple comparisons. To estimate faunal breaks and turn over rates, the pooled species inventory by lake type 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 (here: no species in common) to 1 (here: 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 (here: all species the same) to 1 (here: no species in common) and is calculated as $\frac{b+c}{a+b+c}$. Following Matthews (1986), we interpreted faunal breaks among lake types when the Sørensen index was < 0.5, and we considered the species exchange among lake types to be substantial when the SER_r index was > 0.5. We also estimated species accumulation curves visualized using the vegan-package in R (Oksanen et al., 2013; R Core Team, 2013). The species assemblages of each taxon expected for increasing numbers of lakes (species accumulation curves, see Gotelli & Colwell, 2001) for each lake type were compared among lake types using the chi squared (X^2) test developed by Mao & Li (2009). These analyses were performed in R using the vegan-package (Oksanen et al., 2013; R Core Team, 2013).

As different environmental variables and the diversity metrics of the different taxa could co-vary, we further conducted multivariate tests of differences among lake types in terms of the environment as well as taxon-specific biodiversity using Redundancy Analysis (RDA; Legendre & Legendre, 2012), carried out after first conducting standard Principal Component Analyses with no rotations applied (PCA; Mardia, Kent, & Bibby, 1979). Environmental predictors of species richness and conservation value were evaluated with a forward selection process in a RDA (Blanchet, Legendre, & Borcard, 2008) after removing highly correlated variables using the variance inflation factor (VIF; Neter, Kutner, Nachtsheim, & Wasserman, 1996). Data for PCAs and RDAs was scaled and centered (z-transformation) and the amount of variance explained by variables was expressed using the adjusted coefficient of multiple determination (R^2_a; Ezekiel, 1930). Significance was assessed using a 5 % rejection level ($p \leq 0.05$). Because our sample size of lakes was moderate, we also interpreted p-values of $0.05 < p \leq 0.10$ 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, Table S1). 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 %, Table S3) and high degree of agricultural land use (mean percentage of agricultural land use in buffer zone of 27 ± 22 %, range 2.4 – 79 %, Table S3). Lakes were closely situated to human settlements (mean distance to next village 618.3 ± 523.1 m, range 20 – 1810 m, Table S4) and were on average a few km away from other water bodies (mean distance to next water in general 55.8 ± 84.7 m, range 1 – 305 m, Table S3). 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 (Table S4). On average, managed and unmanaged gravel pits did not differ in individual morphological and trophic state-related variables as well as indicators of proximity to other water bodies, urbanization or human settlements (Table 3,Table 4). Both lake types were also similar in terms of the average volume of littoral dead wood, reed extension and riparian vegetation along the shoreline (Table 3). Also their age was not statistically different (Table 3). Lakes were similar in terms of the average agricultural land in a 100 buffer around the lake, but the buffer zone tend to be a bit more forested in managed lakes compared to unmanaged ones (Table 4). However, a statistical trend showed managed lakes to exhibit a greater average submerged macrophyte coverage along the littoral zone compared to unmanaged gravel pits (Table 3). Strong differences among lake types were also detected in several variables of recreational use intensity, with managed lakes attracting increased use of both anglers and non-angling related recreational activities (e.g., swimmers, dog walkers) than unmanaged lakes (Table 4). Managed lakes also exhibited a significantly greater average extension of trails (relative to shoreline length) and larger accessibility of the littoral zone to recreational activities compared to unmanaged gravel pits (Table 4).

The multivariate RDA confirmed no significant differences among managed and unmanaged lakes in the collective class of variables representing morphology ($R^2_{adj.}$ = -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) and general human influence in relation to urbanization and proximity to human settlements ($R^2_{adj.}$ = 0.025, F = 1.64, p = 0.173, for an example of overlapping lake types in the ordination in relation to human influence, see Figure 3a, all PCA results of environmental variables are in Table S5,Table S6). By contrast, the habitat structure differed among managed and unmanaged lakes along the first principal component axis (Dim 1) representing a vegetation gradient (Table S5), with managed lakes being more vegetated both in the riparian zone as well as in the littoral zone compared to unmanaged lakes (Figure 3b, $R^2_{adj.}$ = 0.056, F = 2.48, p = 0.022). There was a statistical trend of unmanaged lakes differing from managed lakes in relation to an agricultural gradient in a buffer of 100 m around the lake shoreline, with unmanaged lakes being situated in a zone of greater agricultural use and less forests ($R^2_{adj.}$ = 0.045, F = 2.19, p = 0.089, Figure 3c).

As expected, the strongest separation of both lakes types 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 S6, 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 other recreationists (Table S6). 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), yet the general recreational intensity was substantially smaller at unmanaged compared to angler-managed lakes. In fact, the recreational intensity variable was found to be the most consistent and strongest environmental differentiation among the two lake types we examined.

Table 3: Univariate comparison of managed and unmanaged gravel pit lakes for each environmental variable separately. P-values are Sidak-corrected to account for multiple comparisons within classes of environmental variables (morphology, trophic state etc.), **significant ones ($p < 0.05$) are bolded**, *statistical trends ($p < 0.1$) are italic*.

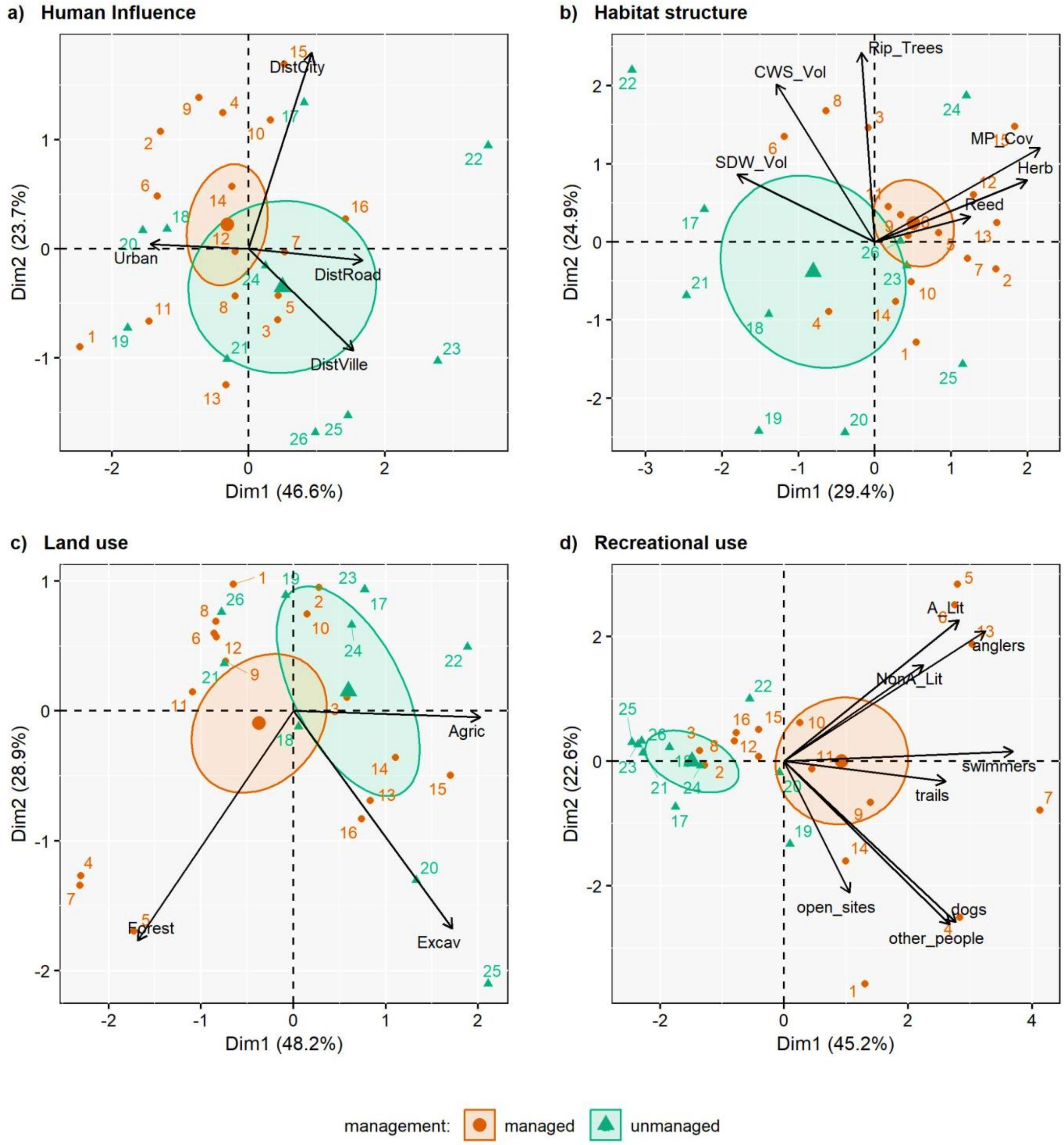
Class	Environmental variable (abbreviation)	mean ± standard deviation (range)		Statistics		
		Managed (N = 16)	Unmanaged (N = 10)	Test	Statistic	p-value
Morphology	maximum depth in m (MaxDep)	9.7 ± 4.9 (2.8-23.5)	9.5 ± 6.0 (1.1-23.0)	U-test	W = 89	0.986
	lake area in ha (LArea)	7.4 ± 5.6 (1.0-19.6)	4.9 ± 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 in µg/l (TP)	25.7 ± 36.5 (8-160)	27.2 ± 20.9 (12-72)	U-test	W = 63.5	0.983
	total organic carbon in mg/l (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 in µg/l (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 in 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 in µg/l (NH4)	56.9 ± 71.2 (15.0-240.0)	84.0 ± 164.8 (15.0-550.0)	U-test	W = 75	1.000
	nitrate in µg/l (NO3)	283.8 ± 380.4 (5.0-1040.0)	733.0 ± 984.1 (5.0-2940.0)	U-test	W = 50	0.604
	conductivity in mS/cm (Con)	0.5 ± 0.2 (0.1-0.7)	0.5 ± 0.3 (0.2-1.0)	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 coverage 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 riparian reed coverage 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 herb coverage on an ordinal scale from 0 to 4 (Herb)	1.7 ± 0.4 (1.1-3.0)	1.0 ± 0.7 (0.1-1.9)	U-test	W = 118	0.225
	submerged macrophyte coverage 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

59 Table 4: Univariate comparison of managed and unmanaged gravel pit lakes for each environmental
60 variable separately. P-values are Sidak-corrected to account for multiple comparisons within classes
61 of environmental variables (land use, recreational use etc.), **significant ones ($p < 0.05$) are bolded**,
62 *statistical trends ($p < 0.1$) are italic*.

Class	Environmental variable (abbreviation)	mean ± standard deviation (range) Managed (N = 16)	Unmanaged (N = 10)	Statistics Test	Statistic	p-value
Land use	excavation in 100m-buffer in % (Excav)	4.8 ± 7.2 (0-21.3)	9.4 ± 14.6 (0-39.0)	U-test	W = 63	0.718
	agriculture in 100m-buffer in % (Agric)	22.8 ± 19.9 (2.4-55.9)	33.8 ± 25.4 (3.5-79.0)	U-test	W = 58	0.598
	forest in 100m-buffer in % (Forest)	22.0 ± 25.1 (0-72.6)	5.6 ± 6.0 (0-15.5)	U-test	W = 118	0.132
Water	wetland in 100m-buffer in % (Wetland)	0.9 ± 3.6 (0-14.4)	5.1 ± 14.1 (0-45.1)	U-test	W = 61.5	0.504
	water surface in 100m-buffer in % (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 in m (DistLake)	164.1 ± 236.4 (5-850)	264.1 ± 440.6 (1-1280)	U-test	W = 87	0.999
	distance to next river in 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 in m (DistChannel)	312.4 ± 462.3 (1-1630)	224.5 ± 367.9 (5-1180)	U-test	W = 84	1.000
Human influence	distance to next road in m (DistRoad)	265.3 ± 314.4 (15-1010)	558.0 ± 510.1 (30-1530)	U-test	W = 50.5	0.416
	urban area in 100m-buffer in % (Urban)	27.8 ± 29.2 (0-87.5)	17.4 ± 24.5 (0-59.5)	U-test	W = 99	0.767
	distance to next village or city in 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 in 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 in No./m shore (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 in No./m shore (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 in % 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 in m/m (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 (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 (dogs)	1.7 ± 1.9 (0-6)	0.5 ± 1.0 (0-3.3)	U-test	W = 123.5	0.154
	swimmers per lake (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 (other_people)	*2.9 ± 3.2 (0.3-11.9)*	*0.9 ± 1.4 (0-3.8)*	*U-test*	*W = 128.5*	*0.087*

63

Figure 3: Principal component axes (PCA) by category of environmental variables for (a) human influence, (b) habitat structure, (c) land use, and (d) recreational intensity. Percentages in brackets show the proportional variance explained by each axis. See Table S5 & Table S6 for details on PCA-results. Abbreviations used are shown in Table 3 and Table 4. Numbers reflect the different lakes (see Table 1). The centroids of management types are plotted as supplementary variables to 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.



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

In total 34 species of waterfowl, 3 species of amphibians, 33 species of odonata, 36 species of songbirds, 60 species of macrophytes, 44 species of trees and 191 species of herbs were detected across the pool of lakes (Table S7). This species inventory represented a substantial fraction of the regional species pool in the case of odonata (56%), waterfowl (45%), submerged macrophytes (48%) and riparian tree species (59%). By contrast, we detected only around one third or less of the regional species pool in the case of songbirds (33%), amphibians (38%) and riparian herb species (12%).

Variation in local species richness and presence of endangered taxa among individual managed or unmanaged lakes was large, yet the frequency of threatened species of a lake's species pool in either managed or unmanaged lakes showed rather similar patterns (Figure 4,Figure **5**). Most managed and unmanaged lakes hosted at least a few threatened species (Figure 4,Figure **5**). We found unique species in all taxa (except for amphibians) also in single managed and/or unmanaged lakes (Table 5). Managed lakes hosted more unique species within most taxa than unmanaged lakes, while unmanaged lakes had more unique odonata species. Overwhelmingly, we detected common species, particularly among amphibians (Table S7). We found only a few non-native species (Neobiota), which are also to some degree invasive species (Kowarik, 2003). All together we found 4 submerged macrophyte species, 3 riparian tree species, 2 waterfowl species and 1 dragonfly species listed as non-native in Lower Saxony or Germany (see Table S7).

The average species richness was statistically similar in managed and unmanaged lakes (Table 6). Similarly, the taxon-specific conservation value was, on average, similar among managed and unmanaged lakes with one exception: unmanaged lakes hosted amphibian species of a higher average conservation value compared to managed lakes, but overall species richness was particularly low for this taxon compared to the other taxa (Table 6).

Table 5: Overview on unique species of different taxa found at managed and unmanaged gravel pits in Lower Saxony, Germany.

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

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 5) except for submerged macrophytes. 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 5).

Figure 4: Local species richness of different plant taxa (panels a & b: submerged macrophyte species, c & d: riparian herb species, e & f: riparian tree species), and the frequency of threatened (black) and unthreatened (grey) species at managed (panels a, c, e) and unmanaged (panels b, d, f) lakes. Also the fraction of regional species pool is indicated.

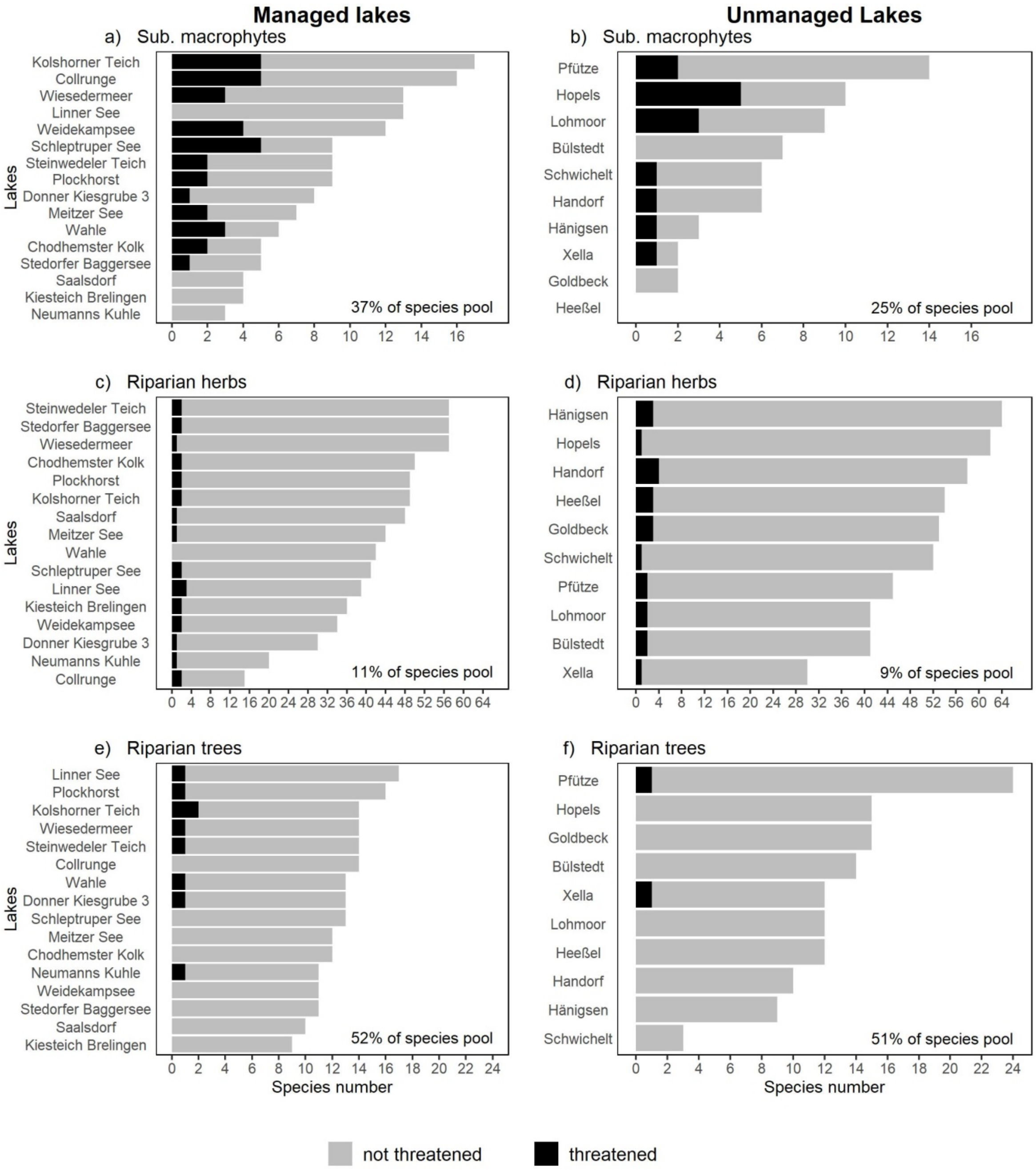


Figure 5: Local species richness of different taxa (panels a & b: amphibian species, panels c & d: odonata species, panels e & f: songbird species, panels g & h: waterfowl species), and the frequency of threatened (black) and unthreatened (grey) species at managed (panels a, c, e) and unmanaged (panels b, d, f) lakes. Also the fraction of regional species pool is indicated.

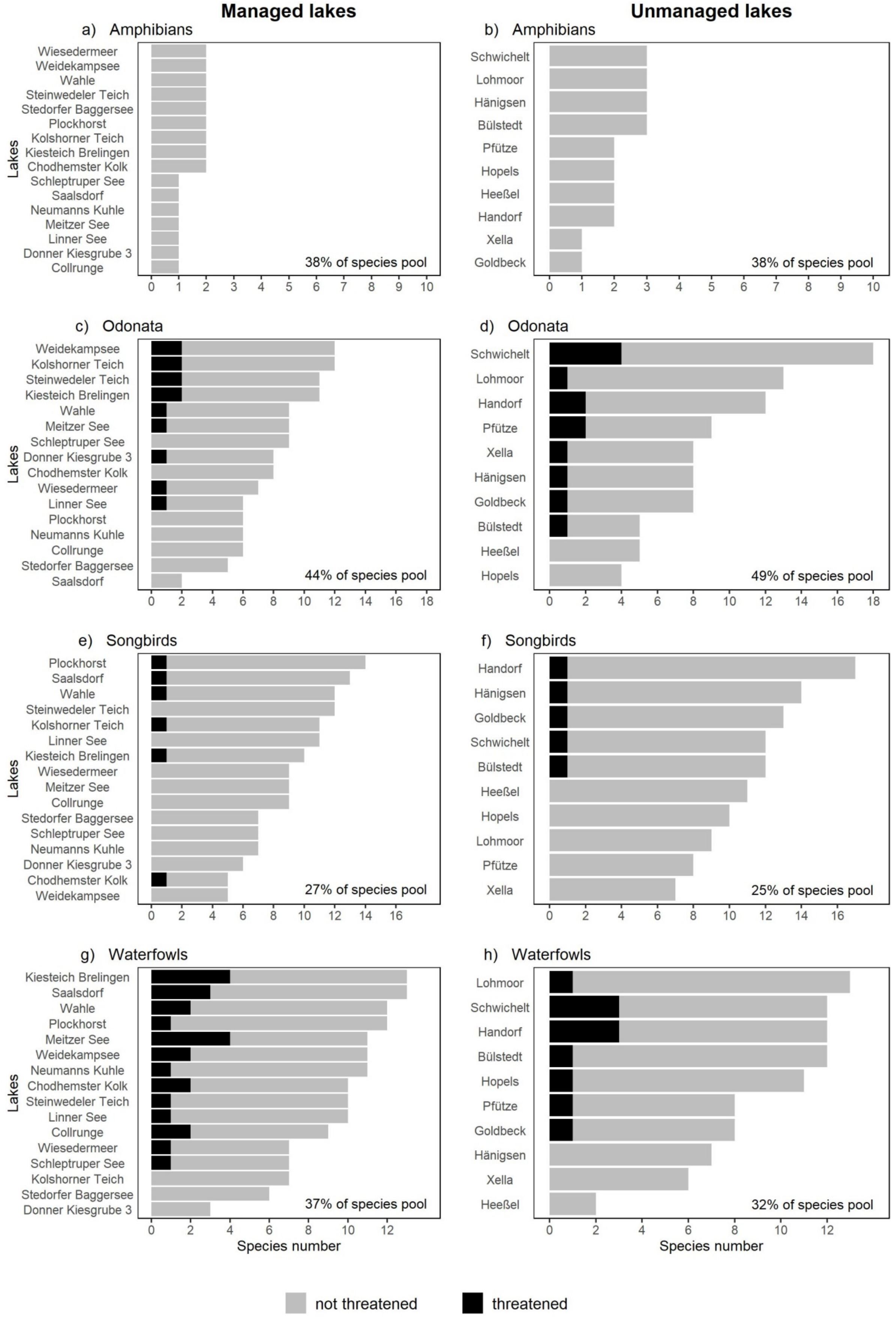


Table 6: Comparison of species richness and taxon-specific conservation values in managed and unmanaged gravel pit lakes. **Statistical differences of Sidak-corrected p-values < 0.05 are bolded**, *statistical trends (p < 0.1) are italic*.

Diversity measure	Taxa	mean ± standard deviation (range) managed (N = 16)	unmanaged (N = 10)	Statistics test	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 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

Species aggregation curves indicated that the regional species pool (i.e., gamma diversity) was not saturating in our sampling, with the exception of amphibians and to a lesser degree odonata. However, there were statistical differences in the species assemblages of managed and unmanaged lakes only in submerged macrophytes (managed lakes have a bigger regional species pool = higher gamma-diversity) and in riparian herbs (unmanaged lakes reach their regional species pool earlier = higher beta-diversity, Table 7). With the fact, that the combined curve of all sampled lakes reaches the same (amphibians) or even higher (all other taxa) regional species richness than a lake type alone, these findings indicates that the regional species pool benefits from the unique contributions of species hosted by different lakes, independent of whether they are managed or not (Figure 6,Figure 7).

Figure 6: Species accumulation curves for submerged macrophytes, riparian herbs, riparian trees, and odonata.

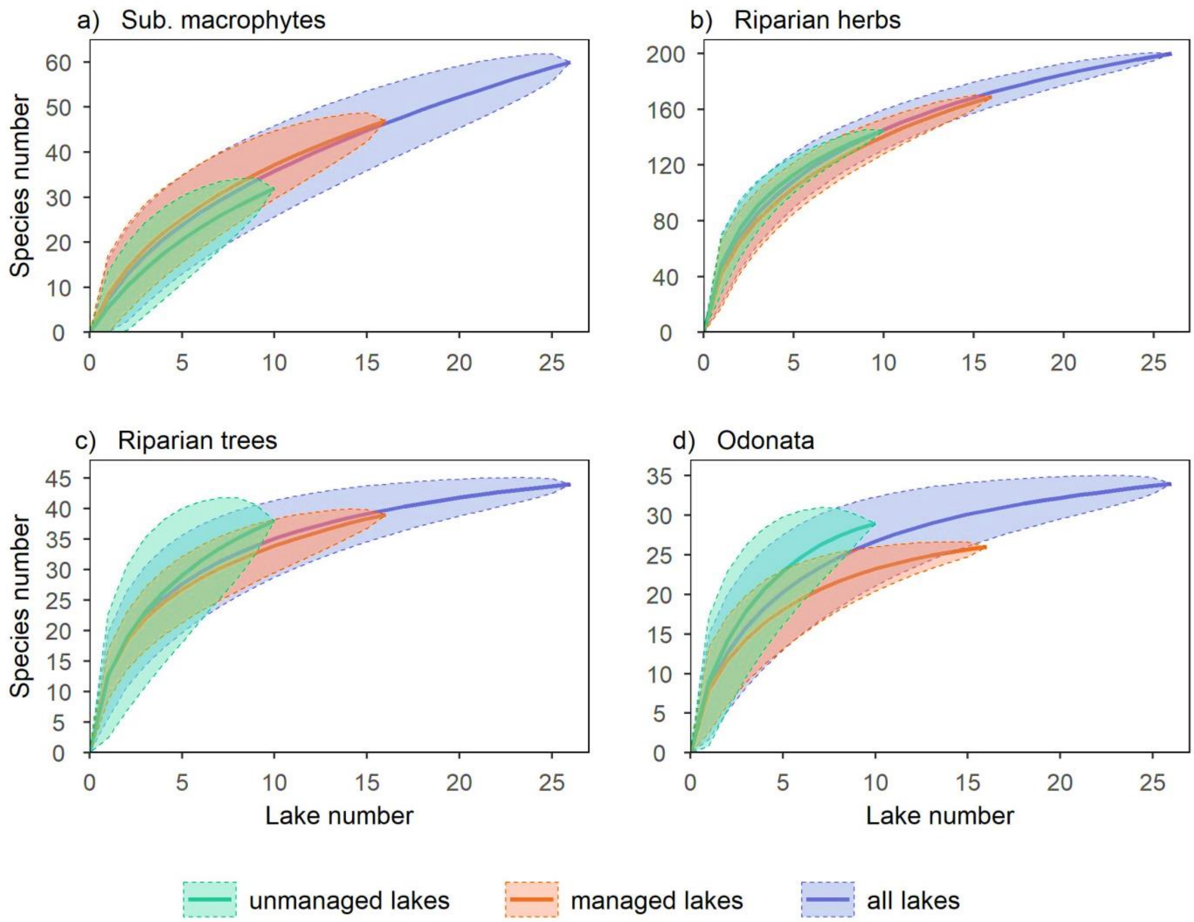
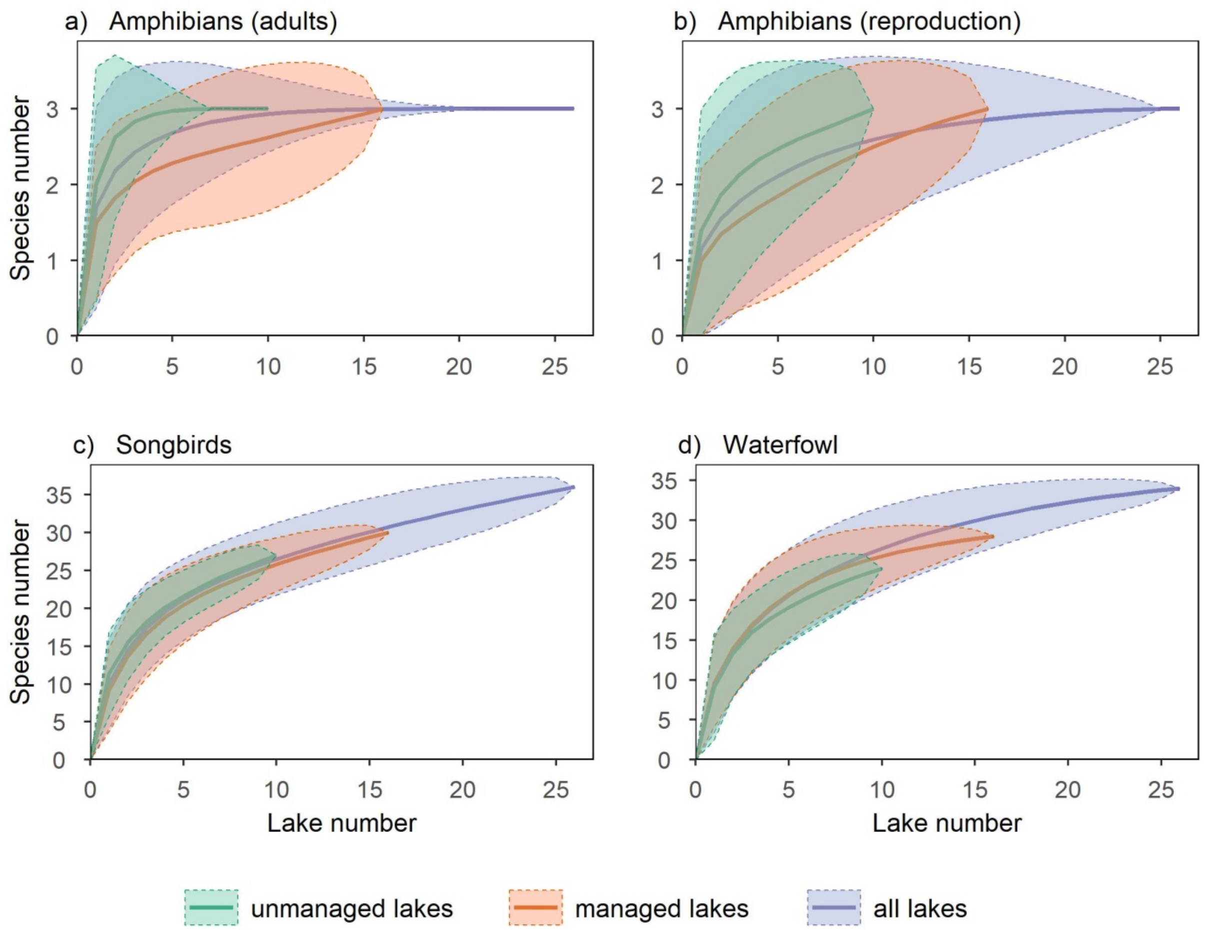


Table 7: Comparison of species assemblages of different taxa in managed and unmanaged gravel pit lakes assessed by comparing the species aggregation curves (Figure 6,Figure 7) with X^2-tests. **Statistical differences of Sidak-corrected p-values < 0.05 are bolded**, *statistical trends (p < 0.1) are italic*.

Species assemblages	T-statistic	p-value
submerged macrophytes	**121.76**	**< 0.001**
riparian herbs	**50.51**	**< 0.001**
riparian trees	10.63	0.980
amphibians (adults)	6.61	1.000
amphibians (reproduction)	12.72	0.889
odonata	15.16	0.660
songbirds	8.95	0.998
waterfowl	6.16	1.000

Figure 7: Species accumulation curves for amphibians, songbirds, and waterfowl.



Environmental correlates of species richness and conservation value in managed and unmanaged gravel pit lakes

There was no joint variation in species richness and conservation value across lakes indicating taxon-specific responses to lake conditions (Figure 8,Figure **9**). 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 S9). It was along this axis, where managed and unmanaged lakes varied close to significantly, with unmanged lakes showing a non-significant trend (RDA, $R^2_{adj.}$ = 0.043, F = 2.12, p = 0.051) for hosting larger riparian diversity (Figure 8a). 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 was revealed (Figure 8a). 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 (Table S9).

High conservation value of macrophytes and waterfowl correlated with lakes offering a low conservation value for amphibians (first PC axis, Table S10). Along this first PC axis managed and unmanaged lakes differentiated the most: managed lakes revealed a significantly higher conservation value of waterfowl, odonata and macrophytes and a lower conservation value of amphibians (Figure 9a, $R^2_{adj.}$ = 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 (Table S10, Figure 9).

All environmental indicators subsumed by PC-scores had acceptable inflation factors and were thus used for RDA analysis of species richness and conservation value (Table S8). The forward RDA-based model selection retained several significant environmental predictor variables of species richness (Table 8). Woody habitat was negatively correlated with the riparian species richness and positively with tree diversity, vegetated habitat was positively correlated with species richness of submerged macrophytes and odonata, and the lake-steepness index (which correlated with smaller lake sizes and low shoreline development indices) was negatively correlated with waterfowl species richness (Figure 8, Table S9). The rural index most strongly correlated with submerged macrophytes and odonata (Table S9). The recreational use intensity did not correlate with species diversity (Table 8). After accounting for these environmental variables, management was no longer significant in explaining species diversity across taxa and dropped out from the RDA (Table 9).

In terms of taxa-specific conservation value, 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 (i.e., submerged macrophytes, odonata and waterfowl) and lower conservation value of amphibians (Figure 9, Table S10). The woody habitat negatively correlated with the conservation value of songbirds, which mainly represented the second axis. Managed and unmanaged lakes differed strongly in the recreational use intensity, but in contrast to our hypothesis this environmental factor was positively, rather than negatively, associated with the conservation value of all taxa except amphibians (Figure 9, Table S10). When entering management as an additional explanatory factor in the RDA, it was retained as the only variable, most likely because of its correlation with the recreational use intensity (Table 9).

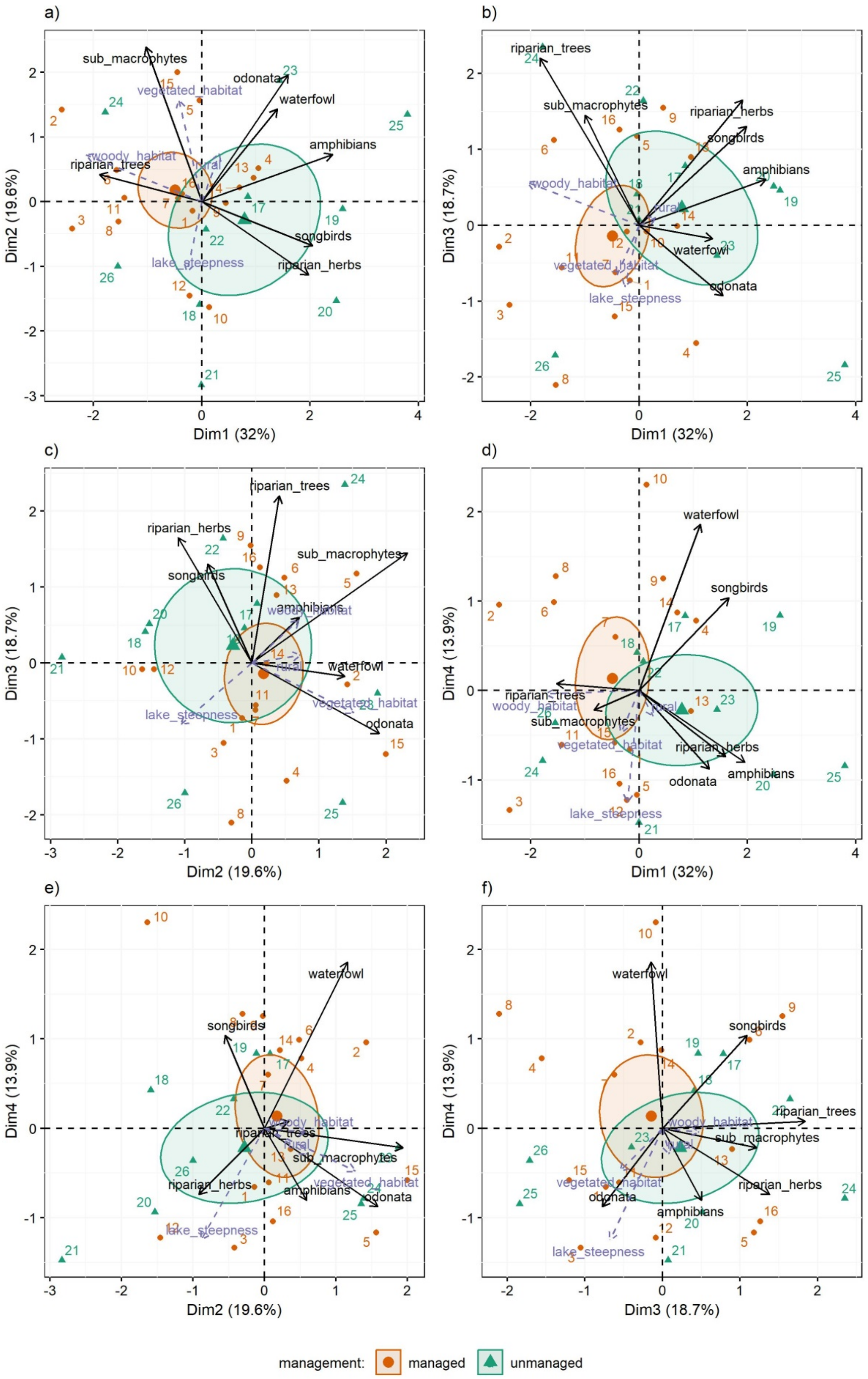
Table 8: ANOVA of forward model selection results for species richness and conservation value (management not used as predictor variable). Variables are ordered by their R^2_{adj}-value. **Significant variables (p < 0.05) are bolded**, *statistical trends (p < 0.1) are italic*.

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**	**5.03**	**< 0.001**
	Age	**0.51**	**0.039**	**2.67**	**0.022**
	lake_steepness	**0.46**	**0.038**	**2.39**	**0.038**
	acidity	0.16	0.032	0.83	0.557
	vegetated_habitat	**0.48**	**0.030**	**2.52**	**0.027**
	nitrogen	0.21	0.018	1.08	0.378
	lake_shallowness	*0.39*	*0.017*	*2.06*	*0.067*
	conductivity	0.31	0.017	1.61	0.157
	agriculture	0.33	0.009	1.72	0.123
	non_accessibility	0.34	0.006	1.78	0.116
	trophic state	0.19	0.005	1.01	0.410
	general_recreational_use_intensity	0.32	-0.011	1.66	0.141
	wetland	0.04	-0.011	0.20	0.980
	distance_to_next_river	0.17	-0.016	0.87	0.523
	rural	0.25	-0.017	1.29	0.276
best model for **species richness**	**woody_habitat**	**1.16**	**0.275**	**5.69**	**< 0.001**
	lake_steepness	**0.58**		**2.85**	**0.012**
	vegetated_habitat	**0.50**		**2.47**	**0.026**
	rural	**0.50**		**2.46**	**0.028**
full model (without management) for **conservation value**	*woody_habitat*	*0.60*	*0.040*	*2.01*	*0.083*
	general_recreational_use_intensity	0.16	0.039	0.55	0.780
	lake_shallowness	0.45	0.026	1.51	0.194
	non_accessibility	0.29	0.022	0.96	0.456
	nitrogen	0.20	0.015	0.67	0.660
	distance_to_next_river	0.43	0.013	1.46	0.211
	Age	0.22	0.007	0.73	0.643
	agriculture	0.27	0.003	0.91	0.499
	acidity	0.32	0.003	1.09	0.386
	rural	0.38	-0.010	1.28	0.278
	vegetated_habitat	0.21	-0.012	0.70	0.664
	conductivity	0.26	-0.013	0.86	0.528
	trophic_state	0.09	-0.017	0.30	0.939
	wetland	0.07	-0.026	0.23	0.971
	lake_steepness	0.03	-0.037	0.11	0.997
best model for **conservation value**	**woody_habitat**	**0.55**	**0.083**	**2.14**	**0.046**
	general_recreational_use_intensity	*0.54*		*2.12*	*0.051*

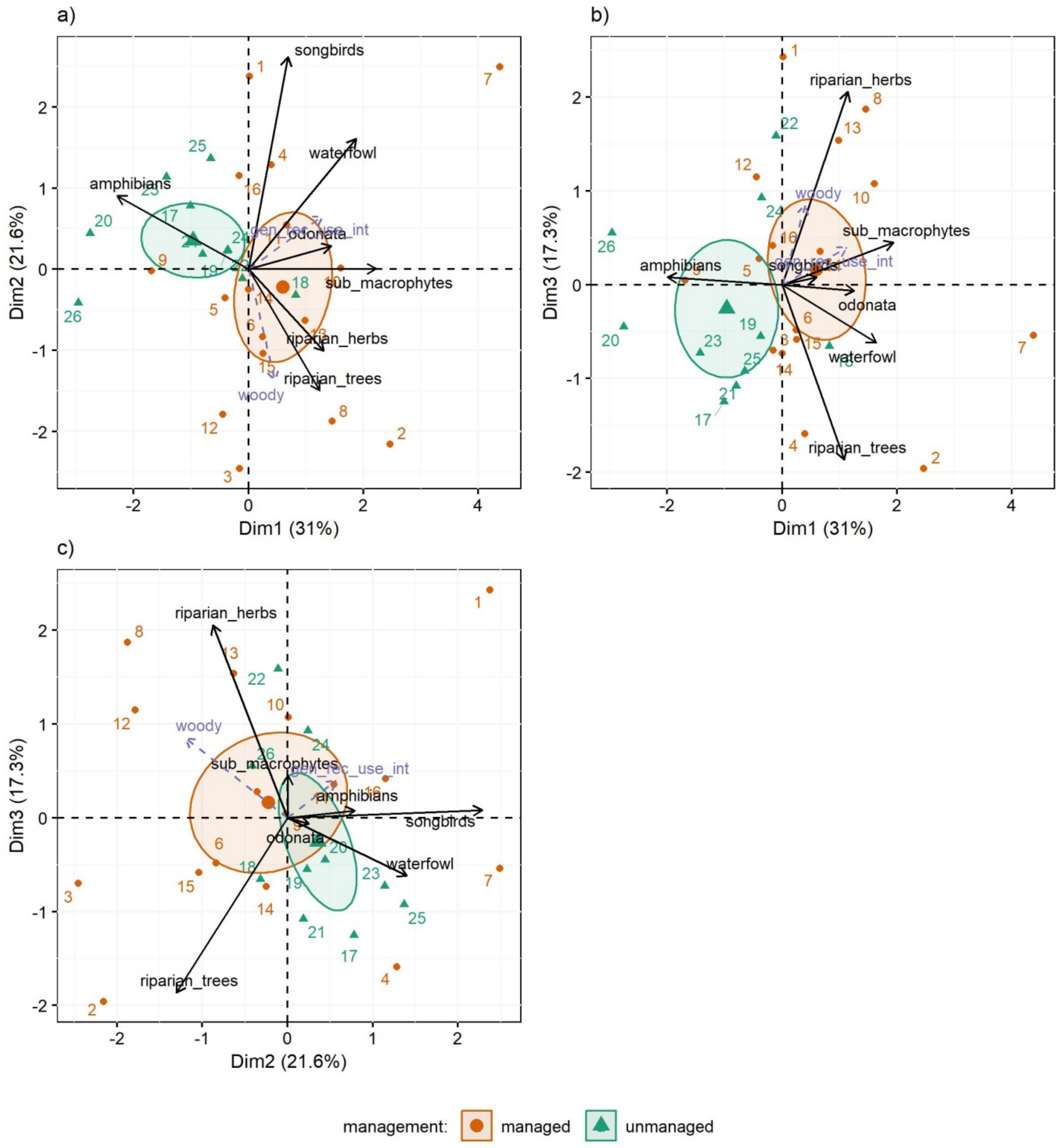
Table 9: ANOVA of forward model selection results for species richness and conservation value (management included as predictor variable). Variables are ordered by their R^2_{adj}-value. **Significant variables (p < 0.05) are bolded**, *statistical trends (p < 0.1) are italic.*

Modelling step	Variable	Variance explained	R^2_{adj}	F-statistic	p-value
full model (without management) for **species richness**	**woody_habitat**	**0.85**	**0.130**	**4.72**	**0.001**
	management	**0.57**	**0.043**	**3.14**	**0.008**
	Age	*0.40*	*0.039*	*2.23*	*0.053*
	lake_steepness	**0.42**	**0.038**	**2.34**	**0.041**
	acidity	0.16	0.032	0.89	0.510
	vegetated_habitat	*0.39*	*0.030*	*2.16*	*0.058*
	nitrogen	0.28	0.018	1.53	0.184
	lake_shallowness	*0.37*	*0.017*	*2.05*	*0.071*
	conductivity	*0.34*	*0.017*	*1.89*	*0.097*
	agriculture	0.26	0.009	1.43	0.222
	non_accessibility	*0.35*	*0.006*	*1.94*	*0.086*
	trophic state	0.20	0.005	1.09	0.376
	general_recreational_use_intensity	**0.41**	**-0.011**	**2.27**	**0.049**
	wetland	0.05	-0.011	0.28	0.951
	distance_to_next_river	0.07	-0.016	0.41	0.877
	rural	0.24	-0.017	1.35	0.247
best model for **species richness**	**woody_habitat**	**1.16**	**0.275**	**5.69**	**< 0.001**
	lake_steepness	**0.58**		**2.85**	**0.013**
	vegetated_habitat	**0.50**		**2.47**	**0.024**
	rural	**0.50**		**2.46**	**0.027**
full model (without management) for **conservation value**	**management**	**0.73**	**0.068**	**2.57**	**0.022**
	woody_habitat	0.37	0.040	1.29	0.281
	general_recreational_use_intensity	0.47	0.039	1.64	0.152
	lake_shallowness	0.43	0.026	1.50	0.194
	non_accessibility	0.28	0.022	0.98	0.443
	nitrogen	0.14	0.015	0.48	0.824
	distance_to_next_river	0.36	0.013	1.25	0.291
	Age	0.19	0.007	0.68	0.667
	agriculture	0.23	0.003	0.81	0.571
	acidity	0.30	0.003	1.06	0.404
	rural	0.34	-0.010	1.19	0.325
	vegetated_habitat	0.11	-0.012	0.40	0.885
	conductivity	0.28	-0.013	0.98	0.455
	trophic_state	0.09	-0.017	0.31	0.933
	wetland	0.05	-0.026	0.16	0.991
	lake_steepness	0.03	-0.037	0.09	0.998
best model for **conservation value**	**management**	**0.73**	**0.068**	**2.83**	**0.010**

Figure 8: Principal component analysis (PCA) of species richness plotted for the first 4 axes (a: Dim 1 & 2, b: Dim 1 & 3, c: Dim 2 & 3, d: Dim 1 & 4, e: Dim 2 & 4, f: Dim 3 & 4). Percentages in brackets show the proportional variance explained by each axis. Names of selected explanatory variables are shown in Table S5Table 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.



193 Figure 9: Principal component analysis (PCA) of conservation value plotted for the first 3 axes (a: Dim
194 1 & 2, b: Dim 1 & 3, c: Dim 2 & 3). Percentages in brackets show the proportional variance explained
195 by each axis. Names of selected explanatory variables are shown in Table S5Table S6. Numbers
196 reflect the different lakes, see Table 1. The centroids of management types and the explanatory
197 variables from redundancy analysis (RDA, slashed purple lines) are plotted as supplementary
198 variables to not influence the ordination. The 95% confidence-level around centroids are plotted to
199 visualize differences between lake types.



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4. Discussion

Our comparative study revealed that gravel pit lakes managed and used by anglers constitute a highly suitable environment for hosting a large diversity and a large fraction of regional species pool of aquatic and riparian species associated with lakes. This finding joins related work that has revealed that gravel pits are suitable habitats for multiple vertebrate and invertebrate taxa, some of which have very high conservation value (Damnjanović et al., 2018; Emmrich et al., 2014; Matern et al., in press; Søndergaard et al., 2018; Völkl, 2010). We were unable to reject our null hypothesis of no differences in aquatic and riparian biodiversity in and at angler-managed lakes compared to unmanaged ones. Therefore, we conclude that with few exceptions (in particular amphibians, this study, and fish, Emmrich et al., 2014; Matern et al., in press) managed and unmanaged lakes host a species inventory of largely similar richness and conservation value and that the regional species diversity benefits from the presence of unique species in different lakes. In fact the number of unique species across most taxa was particularly high in managed lakes. Our study provides evidence that recreational-fisheries management and the use of gravel pits by recreational anglers does not per se constitute a constraint for the establishment of a large species pool of aquatic biodiversity and in fact may foster or be positively associated with local biodiversity.

Our studied lakes were similar in the majority of the environmental factors that we examined except the recreational use intensity and the extension of vegetation, particularly submerged macrophytes, which, surprisingly perhaps, were more prevalent in managed gravel pit lakes compared to unmanaged systems. This supports our survey design because we were interested in specifically outlining the impact of the presence and management of recreational fisheries. The similarity of lake environments among the two gravel pit types resulted in the most important environmental contrast among lakes being mainly the recreational use intensity.

As expected, managed lakes were found to be more accessible to recreationists and having more developed tracks, parking places and other facilities that attracted also other recreational uses than anglers. While the angler presence was - as expected by design - more pronounced in managed lakes, also unmanaged lakes were visited by non-angling recreationists (e.g., walkers), yet at a lower intensity. Despite the significant larger recreational use, managed lakes hosted statistical similar richness and conservation value across most taxa that we examined. Importantly, the recreational use intensity was not a significant factor in explaining the variation in species richness among the lakes we studied, and in the context of the conservation value of the species that were detected the statistical analyses showed a positive, rather than a negative, relationship of recreational use intensity for the aquatic species that we examined (waterfowl, submerged macrophytes and odonata). This finding is noteworthy for two reasons. First, it indicates that the recreational use is not per se a constraint for the establishment of rare species across aquatic biodiversity. Secondly, the positive relationships of the recreational use intensity and the conservation value of selected suggests that lakes hosting rare species might be more attractive to recreationists. This can be due to two reasons. First, surveys among both the general population (Meyerhoff et al., unpublished data) and anglers (Meyerhoff, Klefoth, & Arlinghaus, in review) in our study region have shown that people value the presence of endangered species of both fish and other taxa (e.g., birds, plants) highly, increasing the attractiveness of gravel pits with increasing presence of endangered organisms (see also Fuller, Irvine, Devine-Wright, Warren, & Gaston, 2007; Rees, Rodwell, Attrill, Austen, & Mangi, 2010). Secondly, habitats suitable for the aquatic species that we examined (submerged macrophytes, odonata and waterfowl) are often also very suited to fish because all taxa depend on functional littoral and riparian habitats and good water quality (Brix, DeForest, & Adams, 2001; Lenat & Crawford, 1994; Strayer & Findlay, 2010). Therefore, lakes that host rare species of the mentioned taxa, might also host attractive fish communities (Hjalmarson, 2018), in turn drawing in both anglers and non-anglers to recreate and observe and enjoy wildlife.

In light of previous work, we expected lakes managed by anglers to be heavily modified along the shoreline to accommodate angling sites and access to anglers (Dustin & Vondracek, 2017; O'Toole et al., 2009). Although we did record higher accessibility in angler-managed lakes (in particular the extension of trials), 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 a strong interest to maintain access to lakes to be able to fish, but there is an equally high 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 for 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, our data suggest they do so to a degree that maintains or even extends aquatic and riparian vegetation. In fact, by far most of our gravel pit lakes offered angling sites in a mosaic fashion, where small patches accessible to people were interrupted by long stretches of fully vegetated shorelines. Some angler clubs also implemented protected zones where access to shorelines is prohibited to allow fish and wildlife to seek refuge. Collectively, these actions seem to produce well developed vegetation gradients that were, on average, larger in extension compared to unmanaged lakes.

Mosaics of different habitats (reeds, overhanging trees etc.) constitute highly suitable habitat for a range of taxa (Kaufmann et al., 2014), and relatedly we also found that 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 that regularly interrupt the successions of tree stands thereby reducing the shading effects of the riparian zone, in turn creating diverse habitats of herb and reed habitats important for a range of species (Coomes & Grubb, 2000; Hecnar & M'Closkey, 1998; Mabry & Dettman, 2010; Monk & Gabrielson, 1985; Paracuellos, 2006; Remsburg & Turner, 2009; Shulse et al., 2010; Whitaker & Montevecchi, 1999).

The multivariate analyses showed that the different taxa did not vary uniformly in terms of richness and conservation value among lakes, i.e., lakes that offer high richness for a particular taxon may not be offering high richness for another. This finding disagrees with a related study from managed ponds by Lemmens et al. (2013). These authors examined aquatic taxa (zooplankton, plants, macroobenthos), revealing uniform responses in species richness across taxa and lakes. Given that we examined both aquatic and riparian taxa, the lack of uniform responses can be explained by taxa-specific habitat requirements that strongly differ among species that depend purely on in-lake conditions (e.g., macrophytes) compared to those that are more strongly governed by land use practices (e.g., amphibians).

Our 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 and slope steepness of a lake and the location to human settlements (represented by degree of "rurality"). The relationship between woody habitat and riparian vegetation 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). Also, macrophyte and odonata species richness were positively correlated with vegetated habitat, but also with further distance to human infrastructures. It is obvious that with more macrophyte coverage we can expect more macrophyte species to occur. However, also the donata species profit from more vegetated littoral habitats. This finding is supported by other studies (Foote & Rice Hornung, 2005; Mabry & Dettman, 2010; Remsburg & Turner, 2009).

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 can be explained by the fact that the conservation value is driven by rare species which will have very specific habitat requirements (e.g., Lindenmayer, 1989; Magurran & Henderson, 2003) and are also more likely missed in field surveys (Bäumler, Moser, Gygax, Latour, & Wyler, 2005; Gu & Swihart, 2004; Yoccoz, Nichols, & Boulinier, 2001; Zhang et al., 2014). Importantly for our paper, however, when accounting for environmental factors fisheries management dropped out as a relevant predictor of species richness, and recreational use intensity as key differences among managed and unmanaged lakes was positively, rather than negatively, associated with the conservation value of aquatic taxa.

The only taxon where we observed faunal breaks and substantial turn over among managed and unmanaged lakes were submerged macrophytes, but to our surprise 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 the promotion of benthivorous fish such as common carp through stocking (Miller & Crowl, 2006). Submerged macrophytes can also interfere with angling activities and may then be selectively removed. We have no evidence the latter activity happened in the lakes that we examined. In relation to the impact of benthivorous fish, Matern et al. (in press) studied some of the lakes that we examined 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. (in press) underestimated the abundance and biomass of common carp and other large benthivorous fish (Ravn et al., 2019), which can be expected to be substantially more abundant in managed gravel pit lakes. Bajer, Sullivan, & Sorensen (2009) 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 we studied offered such carp biomasses as all lakes were mesotrophic, and these systems rarely can support more than 200-500 kg of fish of all species altogether (Barthelmes, 1981). Although we have no absolute biomass data of carp or other species, 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 that most angler-managed lakes should have less macrophytes (Van de Weyer, Meis, & Krautkrämer, 2015). The 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.

We found no differences in average species richness and conservation value for most of taxa we examined (macrophytes, odonata, herbs, trees, waterfowl, songbirds) among managed and unmanaged lakes. The only exception were 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, 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., in press), lakes are rather steeply sloped and they are located in agricultural and urbanized landscapes with little forest canopy. Other studies also showed that amphibian species richness is promoted by littoral vegetation (Hecnar & M'Closkey, 1998; Shulse et al., 2010), but also habitat heterogeneity and shallow lakes can 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).

Previous work has repeatedly shown or implicated strong reductions in bird biodiversity through human disturbances, including anglers (Bezzel & Reichholf, 1974; Knight & Gutzwiller, 1995; Lozano & Malo, 2013). However, we found similar species richness and conservation value of both waterfowl and riparian songbirds in managed and unmanaged lakes. The multivariate analyses showed that 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 (M. C. Bell, Delany, Millett, & Pollitt, 2018; Elmberg, Nummi, Poysa, & Sjoberg, 2006; Paszkowski & Tonn, 2000; Scheffer et al., 2006). Importantly, the recreational use intensity was positively, not negatively, associated with the conservation value of waterfowl present at gravel pits, and generally higher conservation values of waterfowl, macrophytes and odonata were revealed in angler-managed lakes. The songbird diversity and their conservation value showed no relationships to our indicators of recreational intensity and instead responded negatively to an index of extension of woody habitat, and when management was used as categorical variable there was only a non-significant trend for the riparian diversity of amphibians, herbs and songbirds to be elevated in unmanaged lakes. When considering further environmental variables, this trend vanished. 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; Sutter & Brigham, 1998; 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) if considering a smaller spatial scale such as ours (Paracuellos, 2006; Triquet, McPeek, & McComb, 1990; Whitaker & Montevecchi, 1999). This essential habitat will be negatively affected by extensive woody habitat (i.e., large trees; see Coomes & Grubb, 2000; Monk & Gabrielson, 1985), explaining the correlations of our study.

Importantly, and collectively, our data do not support any negative impact of either recreational fisheries management or recreational use intensity on the species richness and conservation value of waterfowl and songbirds present at gravel pit lakes. It is important to note that we examined whole-lake metrics and did not examine abundances or breeding successes. Also, our work constitutes a comparative approach where lakes were not randomly allocated to either angler managed or controls. Therefore, we cannot conclusively state that recreational fishing will not impact bird populations. However, also many of the already published studies on the topic of angler impacts on bird populations are inconclusive by focusing on poor metrics of impacts (e.g., only behavioural metrics, such as flight initiation distance, rather than species presence/absence; see Bötsch, Gugelmann, Tablado, & Jenni, 2018; Bötsch, Tablado, & Jenni, 2017), only representing site rather than lake-levels (Knight et al., 1991; Reichholf, 1988; Yalden, 1992), not controlling for the impact of unaccounted environmental factors (Knight et al., 1991; Reichholf, 1988; Yalden, 1992) or lacking controls entirely (Reichholf, 1970; Yalden, 1992). The study by Cryer, Linley, Ward, Stratford, & Randerson (1987) conducted in artificial lakes revealed only distributional changes of waterfowl to the presence of anglers, but no changes to abundance. Similar results of negligible effects of anglers on birds were reported by Somers, Heisler, Doucette, Kjoss, & Brigham (2015). Specific at 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). Collectively, the often-cited assumption that anglers alter species diversity of birds (Bezzel & Reichholf, 1974; Knight & Gutzwiller, 1995; Lozano & Malo, 2013), may not necessarily hold, and in the present work in gravel pits no impacts at the species presence levels were detected compared to unmanaged lakes.

Our study has a number of limitations. The first relates to the fact that we used a space-for-time replication design that lends itself to a correlational study that has to be interpreted in light of the gradients that we were able to sample. Obviously, environmental variables differing from the ones we observed may lead to different conclusions (e.g., higher recreational use intensity than present in our landscape). Secondly, all our lakes were situated in agricultural environments and we 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 our variables of interest. There is also the possibility for sampling effects, especially for seasonal and migratory taxa (e.g., odonata, amphibians, waterfowl), and we thus likely missed rare species (Yoccoz et al., 2001). We think, however, that a possible bias in the sampling would not affect our conclusions by being a systematic effect affecting both lake types. Finally, the recreational use we measured was directly captured mainly during weekdays when we did the field visits at the lakes. We might thus have undersampled high intensity phases during the weekends. However, as we used further surrogates in multivariate indexes of recreational use (e.g., litter, angling sites, trails etc.), we have identified what we consider a robust dimension of recreational use. However, this index integrated both anglers and non-anglers such that our study ultimately cannot conclusively disentangle the isolated effect of angling-induced disturbances from other recreational impacts in angler-managed lakes.

Conclusions

Our 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., in press), 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 we investigated did not respond uniformly to the presence of fisheries-management and were driven by a set of habitat- and other environmental factors unrelated to recreational use intensity. Thus, when judged on the metrics used in our 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 we studied, our 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, Kosmac, van de Weyer, Gertzen, & Mutz, 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 (Lemmens et al., 2015; Werneke et al., 2018).

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