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# Impact of water-based recreation on aquatic and riparian biodiversity of small lakes

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### ABSTRACT

Lakes offer important recreational sites for people; however, water-based recreation may interfere with conservation objectives. In this study, we examined the impact of recreational use of small stagnant water bodies (<22 ha) on several aquatic and riparian biodiversity indicators (species richness, Simpson diversity-index, and number of endangered species) across multiple taxa (waterfowl, songbirds, damselflies, dragonflies, amphibians, fishes, submerged macrophytes, riparian herbs and trees). Samples were generated from 39 gravel pit lakes in Lower Saxony, Germany. Recreational use intensity was quantified using a stratified roving creel survey design involving citizen scientists. Recreational use had little correlation with the different biodiversity indicators that we examined. Most of the variance in biodiversity was explained by non-recreation related environmental and land use variables. Yet, a consistent negative relationship between recreation and biodiversity was found for dog walking, which was negatively associated with the species richness of songbirds, fish, and riparian herbs. Other recreational effects were positive, e.g., increased human use intensity correlated positively with the species richness of fishes and riparian herbs. Moreover, lakes used exclusively by anglers hosted a larger fish species richness at the expense of amphibian richness, likely due to predation impacts by fish. The abundance of dogs was found to be more influential in terms of recreation-related impacts than human density per se, possibly because wildlife perceives dogs as a stronger threat stimulus than human presence. Experimental work is needed to substantiate the correlative evidence presented here.

# 1. Introduction

Freshwater biodiversity is important for human well-being (Lynch et al., 2023; Meyerhoff et al., 2019, 2022), but also highly threatened (Albert et al., 2021; Lynch et al., 2023; Reid et al., 2019). Habitat loss and simplification, pollution, invasive species and climate change are the main threats for aquatic biodiversity (Reid et al., 2019). Further impacts relate to fisheries exploitation (Lewin et al., 2006) and recreational use-induced disturbances of habitats and wildlife (Andrés-Abellán et al., 2005; Bright et al., 2003). Impacts by recreationists on freshwater biodiversity may include disturbance of wildlife (Frid & Dill, 2002), littering (O'Toole et al., 2009), introduction of invasive species (Matern et al., 2019)– especially if introduction of fish, spread of organisms

attached to specific gears, boats or releases from bait buckets are involved (Bacela-Spychalska et al., 2013)– and modification of shoreline habitats (Andrés-Abellán et al., 2005; O'Toole et al., 2009). The latter can be intentional through cutting of riparian vegetation and constructions to improve a water's accessibility, or unintentional through habitat modifications due to trampling (Meyer et al., 2021). Some recreational activities involve boating, which can physically change habitats via wake wash, resuspend sediments and increase turbidity in lakes and rivers (Gabel et al., 2012; Wolter & Arlinghaus, 2003). Yet, considerable debate exists about the prevalence and importance of recreationinduced impacts on freshwater and terrestrial environments (Bateman & Fleming, 2017; Birk et al., 2020; Buckley & Keto, 2022; Schafft et al., 2021).

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Gravel pit lakes are artificial water bodies that might compensate for habitat losses and biodiversity declines in lentic ecosystems (Damnjanović et al., 2019; Seelen et al., 2021). However, gravel pit lakes are also often intensively used for recreation, specifically by anglers, shoreline walkers and swimmers (Meyerhoff et al., 2019; Seelen et al., 2022). Angling use of lakes can be a particularly strong driver impacting habitat quality as well as fish and wildlife in positive and negative ways (Lewin et al., 2006; Matern et al., 2019; Skeate et al., 2022). Impacts of angling on fish populations and communities not only relate to fish harvesting, but might also comprise the introduction of new fish species into lakes (Cambray, 2003; Carpio et al., 2019; Matern et al., 2019; Zhao et al., 2016). Newly introduced fish may affect other taxa, e.g. via predation on amphibians (Hecnar & M'Closkey, 1997) and invertebrates (Knorp & Dorn, 2016) or via uprooting of macrophytes by benthivorous fish (Bajer et al., 2016; Trovillion et al., 2023). In addition, anglers have been suspected to be a particularly strong disturbance to breeding birds, due to their long stays at the water side, sometimes near sensitive habitats (Reichholf, 1988). However, a recent meta-analysis by Schafft et al. (2021) did not reveal that recreational angling had stronger impacts on waterfowl relative to other recreational uses, and Nikolaus et al. (2021) reported similar biodiversity across a range of taxa in lakes managed by anglers relative to lakes without angling use.

Other activities common in small lakes involve swimming in the summertime and shoreline walking, often with dogs. Dogs may signal stronger predation risk to wildlife than humans (Banks & Bryant, 2007), because canids are natural predators of many species and therefore also domestic dogs are typically perceived as predators (Kats & Dill, 1998; Sime, 1999). Despite domestication, dogs still maintain instincts to hunt and chase, and certain breeds are used as hunting dogs (Sime, 1999). Human-induced disturbances have been suggested to be perceived by wildlife as potential predation risks (Frid & Dill, 2002), particularly when associated with threatening interactions such as hunting (Stankowich, 2008). However, at most small lakes hunting is not an everyday activity and therefore most humans will be ultimately non-threatening to wildlife like birds. Correspondingly, habituation effects to humans have been repeatedly shown in multiple habitats and across multiple taxa (Bateman & Fleming, 2017; Bötsch et al., 2018; Stankowich, 2008), which in contrast, has not been observed for dogs (Banks & Bryant, 2007). Dog's hunting skills, off trail-use when unleashed and loud barking (Randler, 2006), together with the presence of natural canid predators like red foxes (Vulpes vulpes) may prevent habituation effects, especially in birds during the breeding season (Lafferty, 2001).

In terms of habitat impacts, all forms of human-induced lake use, particularly those that move off-trails and engage in long stays at the lake can affect immobile organisms, such as plants. Especially angling, swimming or other forms of resting like picnicking can have impacts on plant richness and affect plant community composition on lake shorelines (Bonanno et al., 1998; Meyer et al., 2021; O'Toole et al., 2009). Immobile or less mobile taxa should be more affected by human-induced disturbances than mobile taxa (Schafft et al., 2021), and similarly, disturbance-sensitive wildlife shall be more strongly impacted during specific sensitive periods (e.g., birds during breeding) than outside those periods (Lafferty, 2001). Recreational impacts should also broadly scale with human use intensity and be more pronounced for mobile taxa when induced by dogs compared to sole human disturbance (Banks & Bryant, 2007). In their meta-analysis, Schafft et al. (2021) reported fairly similar recreational effect sizes of different types of water-based recreation on a range of biodiversity indicators, but the associated variances across taxa and levels of biological organization limited generalizations. The metaanalysis showed that recreational impacts on plants and macroinvertebrates were consistently the most negative, while those on birds were the most frequently reported. The authors also identified publication bias in the literature on recreational impacts on freshwaters, with negative reporting and studies of poor methodological design dominating the disturbance literature. It was suggested to pursue local studies and thereby account for highly contextualized conditions if results shall

be used to inform conservation policies. Although the meta-analysis has shown that all recreational activities can have impacts, it also revealed that impacts are in many cases not as high as expected. Because the main threats for freshwater biodiversity are habitat loss and degraded environmental conditions (Reid et al., 2019), recreation induced impacts might be of little relevance compared to those other threats (e.g. eutrophication).

Previous observational studies have compared the aquatic and riparian biodiversity of lakes with and without recreational uses (e.g., Nikolaus et al. 2021). However, the paper by Nikolaus et al. (2021) and related studies from lentic water bodies (Banks & Rehfisch, 2005; Bell et al., 1997; Spyra & Strzelec, 2019; Völkl, 2010) were limited in their quantification of the recreational use intensity. For example, Nikolaus et al. (2021) relied on non-randomly chosen visitor counts during biodiversity assessments rather than using a stratified or random sampling design to count recreationists. However, in terms of recreational impacts the intensity of use matters (Bonanno et al., 1998; Bright et al., 2003; Gabel et al., 2012; Yalden, 1992; Murphy & Eaton, 1983), likely to a greater extent than presence or absence of specific water-based recreational activities (Schafft et al., 2021). This demands proper quantification of recreational use intensity with robust methodological designs.

Here, we used a standardized roving creel survey approach to quantify angling, swimming, boating, dog walking and general human use intensity in and at lakes to advance our understanding of how specific types of recreational activities and their intensity affect biodiversity of lake ecosystems. Our study builds on Nikolaus et al. (2021) by assessing effects of recreational activities on richness- and community-based biodiversity metrics as these perform equally or better compared to relative taxon rareness (Feld et al., 2016) and are considered advantageous for integrating ecosystem functioning independent of species identity (Buckley, 2013).

Species richness in general and the number of endangered species are highly relevant metrics in the context of nature conservation (Brummitt & Lughadha, 2003). Although, it has been observed that species richness may change due to recreational activities (Bell et al., 1997; Bonanno et al., 1998; O'Toole et al., 2009), impacts are often more pronounced at population and individual levels (Buckley, 2013; Schafft et al., 2021). Therefore, we also addressed impacts of recreation on species abundances by using the inverse Simpson diversity index (Pielou, 1969), which integrates richness and dominance into a common biodiversity metric.

We examined the following five hypotheses:

- Recreational uses of water bodies generally have lower impact on biodiversity compared to other environmental factors (e.g., morphology of lakes, land use, trophic state).
- (2) Nonmobile taxa, especially plants, show greater recreationinduced impacts than mobile taxa, especially outside of the breeding season.
- (3) Impacts on biodiversity scale with human-use intensity, independent of the recreational activity.
- (4) Walked dogs have greater impacts on biodiversity at lakes than humans.
- (5) Some recreational activities, especially angling, have positive impacts on certain biodiversity indicators, specifically fish richness.

# 2 Methods

#### 2.1 Lake selection

The study was carried out in Lower Saxony, north-western Germany (Fig. 1). We used the sample of lakes with and without recreational fisheries previously reported in Nikolaus et al. (2021) and strategically added lakes with specific, potentially outstanding recreational human



**Fig. 1.** Map of the sampling area in Lower Saxony, Germany, indicating the sites of the 39 gravel pit lakes of the 5 predefined lake use categories (Control = no use, O = no angling but other usage, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating). Number of sampled lakes is given in parenthesis.

use types (e.g., only recreational uses other than angling or highly intensive recreational uses). Lake selection ensured a large gradient of different lake types and recreational usages from basically no-use over moderate to high use intensities for different recreational activities (walking with and without dogs, swimming, angling, boating, water skiing etc.). We classified lakes into five predefined lake use categories: control lakes with no use (control), no angling but other usage (O), angling use only (A), angling and other uses combined (AO) and recreation lakes with high use intensities including angling, other activities as well as camping, boating, waterskiing or windsurfing (AOB). The sample of Nikolaus et al. (2021) consisted of 26 lakes, mainly of category AO (n = 16), but also controls (n = 5), O (n = 4) and A (n = 1). In the same region we sampled additional 13 lakes to obtain a minimum of n = 5 lakes for each lake use category in 2019, to have variability and replication within any given lake category. To assure comparability among lakes regarding environmental characteristics, additional selection criteria were lake size (0.7 - 21.1 ha), no connection to other waterbodies like rivers, and similar dredging origin, which should lead to a comparable morphology and age of the lakes (Table 1).

#### 2.2 Environmental data collection

We assessed multiple environmental variables to control for confounding factors such as lake morphology, water quality and land use in the subsequent analyses. Data were collected using the methods described by Nikolaus et al. (2021, 2022). In brief, lake age at the time of sampling was determined by inquiring with landowners about the most recent dredging activity. Lake morphology was mapped with an echo sounder and allowed to determine mean and maximum depth. The lake area and shoreline length were determined using QGIS 3.4.1. Subsequently, the shoreline development factor (SDF, Seekell et al., 2022) and relative depth ratio (RelDepR, Damnjanović et al., 2019) were estimated. Lake productivity was assessed by measuring nutrient concentrations of epilimnic water samples during the full lake circulation in spring. Specifically, total phosphorous (TP) concentration was determined using the ammonium molybdate spectrophotometric method and total organic carbon (TOC) concentration with a non-dispersive infrared detector (NDIR) after combustion. Concentrations of ammonium and nitrate were measured by spectrometric continuous flow analysis and chlorophyll a concentration quantified as mean of three samples (spring, summer, autumn) using high performance liquid chromatography (HPLC, Zwirnmann et al., 1999). In addition, turbidity was measured in spring using a Secchi disc.

Land use within a 100 m buffer around the lake shorelines was quantified as percentage cover of each of seven ATKIS<sup>®</sup>land use classes (© GeoBasis-DE/BKG 2013, AdV, 2006): agricultural land, forest, urban, mining, wetland, water bodies and other, in QGIS 3.4.1 with GRASS 7.4.2 on a 10  $\times$  10 m grid scale. Distances to the nearest water body (lentic and lotic), street, settlement, regional center and to the next parking lot were measured in Google maps 2017.

#### 2.3 Recreational use

Recreational use was first assessed as described in Nikolaus et al. (2021) during each site visit (for biodiversity sampling, details below), counted and classified into four activity types: angling use, swimming use, dog use, other use, boats and the sum of all uses. The extent of water access points was measured and litter was collected at a random set of

#### Table 1

Descriptors and predefined lake use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating) of the gravel pit lakes sampled in Lower Saxony. TP = total phosphorus.

No.	Lake name	Use category	Area (ha)	Mean depth (m)	Max depth (m)	Age (y)	TP (mg/l)	Chlorophyll a (mg/l)
1	Heeßel	Control	0.9	3.8	7.4	55	0.03	12.6
2	Kiessee Isums Klein	Control	1.1	2.9	5.1	21	0.03	20.2
3	Lohmoor	Control	4.1	2.2	7.4	28	0.07	27.6
4	Schwicheldt	Control	1.8	4.0	10.0	32	0.02	2.6
5	Tongrube Bülstedt	Control	2.4	0.6	1.1	29	0.03	90.6
6	Xella	Control	2.1	3.1	7.3	47	0.01	9.8
7	Handorf	0	13.6	9.6	23.0	47	0.06	29.2
8	Hänigsen	0	6.2	7.7	12.3	27	0.02	9.8
9	Hopels	0	5.5	6.7	14.5	37	0.01	4.8
10	Kiessee Isums Groß	0	2.8	5.2	11.3	21	0.05	5.3
11	Pfütze	0	10.6	4.3	7.3	32	0.01	5.7
12	Westerhammerich	0	16.5	7.4	17.42	35	0.01	4.9
13	Buschmühlenteich	Α	3.0	0.6	1.1	41	0.04	9.2
14	Donner Kiesgrube 3	Α	1.0	3.3	5.2	40	0.03	8.9
15	Mergelgrube	Α	0.7	1.4	2.3	38	0.02	3.6
16	Röhrs Teich	Α	6.2	2.7	4.4	61	0.44	89.8
17	Stockumersee	Α	10.4	3.9	10.3	48	0.04	31.8
18	Vereinsteich Heede	Α	1.8	1.9	3.6	41	0.05	36.4
19	Chodhemster Kolk	AO	3.2	5.6	10.1	49	0.02	4.3
20	Collrunge	AO	4.3	4.0	8.6	47	0.02	4.6
21	Goldbeck	AO	2.3	2.5	5.0	35	0.02	19.2
22	Kiesteich Brelingen	AO	8.5	3.2	8.7	37	0.02	6.5
23	Kolshorner Teich	AO	4.3	6.4	16.1	52	0.02	4.8
24	Linner See	AO	17.7	5.1	11.2	48	0.02	7.4
25	Meitzer See	AO	19.5	11.9	23.5	37	0.01	2.1
26	Neumanns Kuhle	AO	6.9	3.1	6.2	53	0.16	65.3
27	Plockhorst	AO	14.3	3.2	8.2	37	0.03	30.7
28	Saalsdorf	AO	9.0	5.3	9.2	48	0.01	15.3
29	Schleptruper See	AO	4.0	4.9	10.1	57	0.01	3.7
30	Stedorfer Baggersee	AO	1.9	1.7	2.8	36	0.02	10.2
31	Steinwedeler Teich	AO	10.4	5.3	9.1	54	0.01	5.8
32	Wahle	AO	8.1	5.9	12.1	36	0.01	7.2
33	Weidekampsee	AO	3.0	2.3	4.3	26	0.01	3.0
34	Wiesedermeer	AO	2.9	3.7	9.2	37	0.02	6.7
35	Badesee Grotegaste	AOB	10.3	7.7	17.2	40	0.02	15.7
36	Badesee Tannenhausen	AOB	19.7	6.8	18.7	79	0.03	46.7
37	Handorf II/Surfteich	AOB	21.1	13.0	21.0	49	0.01	1.5
38	Heeder See	AOB	13.0	7.0	16.0	33	0.01	2.0
39	Spadener See	AOB	19.9	11.4	21.0	49	0.01	7.2

access points and in seemingly undisturbed reference points (both n = 10). All collected litter was counted, weighed and categorized into non-specific and angling specific. The extent of trails along the shoreline was measured with a measuring wheel (2 m circumference, 0.1% accuracy; Cross-country measuring wheel, model 12015001; NESTLE, Dornstetten, Germany) and the number of parking lots was counted.

In addition to this non-randomized assessment, we performed a standardized, citizen science-based visitor count at all 39 lakes in 2019 using a roving creel approach and a stratified random sample design described in Malvestuto (1983) and Pollock (1994). The roving creel approach has originally been developed for assessing angling effort (Pollock, 1994) and comprised a stratified design (by weekend and weekdays) with twelve fixed dates (Appendix Table A1) as primary sampling units. These twelve dates were randomly allocated within two seasons, the breeding season (1 April - 15 June, according to the Lower Saxony's law on forest and landscape management, NWaldLG §33, Abs.1, 1b) and mid-summer season (16 June - 31 August), with 6 dates each. Within these two seasons the days were evenly allocated to weekdays and weekend days. To cover the full daylight length (morning and the full afternoon) and still have a maximum number of days to be sampled we conducted the counts in two time shifts, serving as secondary sampling units (Malvestuto, 1983; Pollock, 1994). These two time shifts, morning (10 am - 2 pm) and afternoon (2 pm - 6 pm) were sampled randomly in a stratified fashion within each sampling day, to ensure an equal amount of each shift within each day type as described in Pollock (1994). Information from the secondary sampling unit was used to raise the daily effort in each sampling day as per Pollock (1994).

To assess the total number of users, we chose instantaneous counts (Hoenig et al., 1993), using four counts within each time shift, with each count being approximately one hour apart from the next (e.g. at 10 am, 11 am, 12 am and 1 pm). With this approach it was possible that one clerk could conduct counts at multiple lakes, if located nearby. At a specific timepoint (or within a few minutes, if the lake and its direct surroundings was not completely visible from one location, example provided in Fig. A1) each recreational activity of a given category (e.g. walker, mobile angler, stationary angler, dogs on leash, dogs unleashed, sunbathing people, people swimming in the water, etc.) occurring at the lake or its shoreline was counted by trained citizen scientists as roving clerks. In addition, at the end of the fourth instantaneous count on each sampling day the name of the counter(s), weather conditions, temperature and location(s) during the counts were protocolled. The research team was always available (via phone) during sampling days of the standardized visitor counts in case of unexpected events or questions from the trained citizen scientists. We tested the design of the standardized visitor counts with simultaneous counts of two persons at the same lake at the same time with multiple counts at 5 randomly selected lakes and validated our approach by comparing the results. Counts of the two counters were highly correlated (Spearman rank correlation; angling  $\rho = 0.98$ , swimming  $\rho = 0.82$ , boats  $\rho = 0.94$ , dog  $\rho = 0.9$ , Pearson correlation: human use r = 0.99). Therefore, we considered the counts by the citizen scientists to be unbiased.

As some citizen scientists failed to provide reliable counts, seven lakes (especially control lakes) lacked standardized visitor counts. To not loose samples for subsequent analyses, we predicted the use intensities for the lakes with the data from non-standardized counts during our on-site visits, given reasonable correlations between the standardized and non-standardized counts in the other lakes (Spearman rank correlation; angling  $\rho = 0.69$ , swimming  $\rho = 0.49$ , other use  $\rho =$ 0.76, dog  $\rho = 0.62$ , human use  $\rho = 0.72$ ). Although different recreational activities were differentiated during the standardized visitor counts, multiple categories needed to be combined to match the activities quantified during the non-standardized visitor counts: angling use, swimming use, dog use, other use and sum of all uses. Thereby, we were able to infer recreational intensity from the non-standardized observations also for the seven lakes that lacked a standardized visitor count. The following five categories were aggregated: (1) anglers = mobile anglers (e.g., spin fishers) + stationary anglers, (2) swimmers = bathers in water + bathers on land + divers, (3) humans = strollers + joggers + horse riders + bikers + campers + humans on boats (angling + nonangling) + water-skiers (in action + waiting) + windsurfers + anglers (mobile + stationary) + swimmers (in water + on shore + diving), (4)dogs = dogs leashed + dogs unleashed (not taking humans into account), (5) boats = canoes + pedal boats + paddle boats + sailboats + motor boats + model boats + dinghies + surfboards (SUPs) + waterskies/wakeboards/kneeboards (in action) + wind surfers. As boating was only permitted at the lakes with the standardized visitor counts, this category was not considered in regression models to infer human use intensity in lakes lacking standardized counts (details in Appendix).

#### 2.4 Biodiversity data collection

We investigated species richness, Simpson diversity index and the number of endangered species, across multiple taxa ranging from nonmobile (plants), predation-sensitive (amphibians) to mobile taxa (fish and birds). Particularly, we assessed waterfowl and songbirds as these taxa are prominent in conservation conflicts associated with recreation. Fish were included as angling and associated stocking might directly and indirectly affect fish species richness and density (Matern et al., 2019, 2022). Lake biodiversity data were collected using the same methods outlined in Nikolaus et al. (2021, 2022) and comprised birds (waterfowl and songbirds), Odonata (dragonflies and damselflies), amphibians, fishes, aquatic macrophytes, and riparian vegetation (herbs and trees). Waterfowl species were identified (Svensson, Mullarney, & Zetterström,

2017; Dierschke, 2016) and counted during each on site visit (four to nine visits per lake) using binoculars. Songbird species were acoustically and visually identified once in summer using two-minute audio recordings every 200 m along the shoreline in the morning (Fig. 2). Damselflies and dragonflies (Odonata) were visually identified along the shoreline during noon of each day and if necessary temporarily captured with a butterfly net. Amphibians were assessed in spring by visual inspection from boat along the whole shoreline during the day and acoustically during the night. In addition, floating funnel traps (47 cm  $\times$ 23 cm  $\times$  23 cm) were placed every 200 m overnight, and caught amphibians were identified and released the next morning. Fish were sampled by littoral electrofishing and multi-mesh gill-nets as described in Matern et al. (2019). Submerged macrophytes were assessed by snorkeling along transects perpendicular to the shoreline every 100 m (every 200 m for one lake >20 ha). Riparian vegetation was assessed along four 100 m long transects parallel to the shoreline, with each transect comprising five evenly spaced (20 m distance) 1 m<sup>2</sup> plots. Trees taller than 2 m were identified and counted along these transects, and herbs were assessed within the  $1 \text{ m}^2$  plots.

The presence and absence of species was determined to quantify species richness within each taxonomic group. Abundances of each species were used to calculate the inverse Simpson diversity index (Pielou, 1969), also called "dominance index", which provides the probability that two randomly taken individuals from a sample belong to the same species. This index reflects the extent to which an assemblage is dominated by a single or few species. As additional conservation-related measure, we quantified the number of endangered species within each taxonomic group according to the red lists of Germany (https://www.ro te-liste-zentrum.de and Freyhof (2009) for fishes). For fish, the Simpson index calculation was based on effort-corrected, species-specific abundances (catch per unit effort, CPUE, i.e. number of individuals per 50 m) from the electrofishing surveys. For estimating fish species richness and number of endangered species, data from multi-mesh gill-nets (as number of individuals per 100 m<sup>2</sup> net area) was considered, too. We additionally estimated the biomass of fish per lake using the total biomass per unit effort (BPUE) of multi-mesh gill-nets (g per 100 m<sup>2</sup>). Although Matern et al. (2019) did not find significant differences in fish biomass between managed and unmanaged gravel pit lakes, we used BPUE to control for potential fish-induced effects (e.g. predation) on



**Fig. 2.** Schematic visualization of the biodiversity sampling. Adapted from Nikolaus et al. (2022)

other taxonomic groups (Trovillion et al., 2023). Lake's submerged macrophyte coverage was calculated by extrapolating the transectbased macrophyte sampling based on depth strata. The share of the shoreline that was covered with reeds (emerged macrophytes, e.g. *Phragmites* sp., *Thypha* sp. and *Schoenoplectus lacustris*) was also determined. Both measures were also used as predictor variables to explain the biodiversity of other taxonomic groups.

#### 2.5 Statistical analyses

We performed one-way ANOVA to identify differences in species richness, Simpson diversity index and the number of endangered species between the five lake categories (Control, O, A, AO, AOB). In case of significant ANOVA results, a TukeyHSD (Tukey's Honestly - Significant Difference) post-hoc test was performed, to identify specific pairwise differences among lake categories. If the assumptions required for ANOVA (normal distribution of residuals and homogeneity of variance) were not met, we used Kruskal-Wallis tests and paired Wilcoxon tests with p-value adjustment (Benjamini & Hochberg, 1995).

Multivariate regression analysis was used to reveal relationships between biodiversity metrics and recreational use intensities (expressed as use densities) while controlling for environmental covariates. In these models the lake categories were not considered and we used recreational use intensities instead along the full lake gradient. All predictor variables were z-standardized prior to the regression analysis to obtain standardized beta coefficients, that are equivalent to effect sizes. As species richness and the number of endangered species were integer data we used generalized linear models (GLM) with Poisson or binomial distributions to analyze these metrics. The procedure to obtain recreational use densities based on the standardized visitor counts as well as dimension reduction (leading to three use intensity variables) and the selection of environmental variables is described in the Appendix.

We identified all relevant variables explaining the selected biodiversity measures within each taxonomic group using model selection based on the Akaike information criterion (AIC). Model selection was performed using the stepAIC function (Venables & Ripley, 2002) with forward and backward selection. To allow testing our study hypotheses, the three variables describing recreation intensity (human use, angling use and dog use) were excluded from the variable selection procedure and always kept in the final models. All statistical analyses were performed with the software R (R v. 4.2.0, R Core Team, 2022).



**Fig. 3.** Use densities of humans (A), swimmers (B), boats (C), anglers (D), and dogs (E) based on standardized counts per lake use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating). Densities are shown per ha lake area for boats and per km shoreline for the rest. Different letters above boxplots indicate significant differences (p < 0.05) amongst lake use categories. Note the different scales of y-axes.

#### 3. Results

## 3.1 Standardized user counts

The standardized user counts confirmed the predefined lake use categories (Fig. 3, Appendix Table A5). Human use in general, angling, swimming, dog walking and boating densities all showed significant differences in the expected directions among the pre-defined lake use

categories (all p < 0.05). For example, swimming and general human use densities were significantly greater in recreation lakes (AOB lakes) compared to all other lake categories. As expected, angling did not occur in control lakes and lakes without angling but other usage (O lakes). Boat use occurred almost exclusively in AOB lakes. The density of dogs was very low in control lakes and in almost all lakes that were exclusively used by anglers only (A lakes), but was much greater in other lake types.



**Fig. 4.** Boxplots of species richness, Simpson diversity index and number of endangered species per lake use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating) for waterfowl (A, B, C), songbirds (D, E, F), damselflies (G, H, I) and dragonflies (J, K, L). Differences among all use categories within all taxonomic groups were non-significant (post - hoc Tukey's test or pairwise Wilcox test, p > 0.05). Note the different scales of y-axes.

Despite aiming for environmental comparability among lakes with different use categories, we detected significant differences (p < 0.05) in the lake morphology (Appendix Table A5): Control lakes were significantly smaller than lakes with multiple uses (O, AO and AOB lakes), while angling only lakes (A) and lakes with angling in combination with other uses (AO lakes) were also significantly smaller than highly frequented recreation lakes (AOB lakes). Significant differences were also detected in maximum depth and mean depth of the lakes. Control lakes were significantly shallower than O and AOB lakes, and A and AO lakes were significantly shallower than AOB lakes. The shoreline length and the percentage of urbanization in a 100 m buffer around the lake (Appendix Table A5) tended to be smaller in control lakes compared to AOB lakes and AOB lakes tended to have a lower percentage of forest around the lakes; however, these differences were not significant after post-hoc testing (Appendix Table A5).

# 3.2 Waterfowl

Species richness, Simpson diversity index and number of endangered waterfowl species did not significantly differ between lake use categories as indicated by univariate comparisons (Fig. 4, Appendix Table A6). Also, the multivariate regressions with selected environmental variables as controlling covariates did not show significant effects of recreational use intensities of humans, anglers or dogs on waterfowl diversity (Table 3). Richness of waterfowl species was significantly positively associated with lake area and SDF (p < 0.01), and the Simpson diversity index with lake area (p = 0.01), while all other environmental predictors were less important or dropped during the variable selection process. Macrophyte coverage was the only significant predictor for the number of endangered waterfowl species (p = 0.01).

Use intensities were no significant predictors in the regression models with separate use intensities for the breeding season and the summer season of water fowl (Appendix Tables A9–A11).

#### 3.3 Songbirds

Univariate comparisons did not reveal significant differences in

# Table 2

Overview of predictors used in full multiple linear regression models to explain species richness (sr), Simpson diversity index (si), and number of endangered species (es) and results of the final models after model selection with forward and backward selection by AIC. Use densities (angling, dog and humans/km) were always kept in the final model (if these are not grey, no significant model could be fitted).

	2		~	X		*		*		<b>4</b> •<		ý.		齐		*			A priori expected relations									
	waterfowl songbirds		damselflies			dra	dragonflies		am	amphibians			fish		macrophytes		riparian herbs			riparian trees		rees	with biodiversity					
	sr	si	es	sr	si	es	sr	si	es	sr	si	es	sr	si	es	sr	si	es	sr	si	es	sr	si	es	sr	si	es	6.1.1 1.11.2
Mean depth (m)													x	х	х	X	Х	х	x	х	х							+ fish <sup>1</sup> ; - amphibians <sup>2</sup>
Lake area (na)	+	+	x																			(.)		(.)				+-
Bolotivo donth rotio				+	+	X	×	X	x	-	×	x	~									(+)	x	(+)	×	x	x	+-
Shoroling development factor		v	(1)			~	~		~		~	~	×.	×	×		~	~	X (1)	x	л 	~						+-
Total phosphor (mg/l)		X	(+)		X	X	×	×	X	T	×	×	X	X	- T			~	(+)	×	×	X	X	X				T ish5, all aveant fish2.6.14
Total prosphor (mg/l)							×,	×	×	×	×	×				×	+	×	(-)	x	X							<ul> <li>- all except fisherer</li> <li>- adopata<sup>14</sup></li> </ul>
Nitrate (NO- mg/l)							^	^	^	-	^	^								v								_6
nH-value																			v	Ŷ	×							- 7
Secchi denth																			^ +	Ŷ	Ŷ							+6
Macrophyte coverage (%)	(-)	v					v	+	l v	v	v	v	v	v	v	v	v	v		^	^							+2, 10,13
Reed (%)	~	Ŷ	~		v	v	Û		Ŷ	Ŷ	Ŷ	Ŷ	^	^	~	Û	Ŷ	Ŷ										12. 10.16
Age (vears)	<u>^</u>	^	^	Ŷ	Ŷ	Ŷ	^		· ^	^	^	^				+	Ŷ	Ŷ	×	×	×	×	×	×	×	+	x	+5,6,8
Urbanisation (%)				^	~	~											~	^	^	~	~	^	~	~	v	v	v	+12
Agriculture (%)	v	×	Y	v	v	v	v	v	v	v									(+)	v	(+)	+	v	v	Ŷ	Ŷ	Ŷ	+ birds: - odonata plants <sup>7,12,14</sup>
Forest (%)	L ^	~	~	Ŷ	Ŷ	Ŷ	^	~	~	^			×	×	(-)				(.)	~	(.)		^	~	Ŷ	Ŷ	Ŷ	+ all <sup>2,8</sup>
Wetland (%)				^	~	~	x	×	×	+			Ŷ	Ŷ	×										^	~	~	+2,14
Distance to lentic water (m)	v	v	v				~	~	~				Ŷ	v	(+)	v	v	v	v	v	v							_2
Distance to street (m)	L ^	~	^	×	x	x							Â	^	(.)	l î	~	^	L ^	~	~							+8
Distance to settlement (m)					~	~																-	x	х	x	x	x	_12
Open sites/m																			x	x	x	-	x	x	x	×	x	+ herbs_macroph 6: -trees
Trail length/shoreline length																						x	x	x				·····, ···· , ····
Angling use/km	x	х	х	x	х	x	x	х	х	х	х	х	x	х	х	x	(+)	х	х	х	х	x	x	x	x	х	х	- all except fish <sup>2,10</sup> , + fish <sup>5</sup>
Dog use/km	x	x	x	(-)	-	x	x	x	x	x	x	x	x	x	x	(-)	x	x	(+)	x	x	-	x	(+)	x	x	x	_11
Human use/km	x	х	х	x	(+)	x	х	-	x	х	х	х	х	х	х	+	x	х	x	х	х	+	х	x	x	х	х	<ul> <li>all except herbs<sup>2,9,10</sup>; plants<sup>9</sup></li> </ul>
Fish biomass (g /100m <sup>2</sup> )	х	х	х				х	х	x	-	х	х	х	х	х													+ birds <sup>15</sup> ; - others <sup>2, 13</sup>
Number of lake visits	х	х	х																									+
+/- = significant, p < 0.05 (+/-) = trend, p < 0.1						х	x = in model, but p > 0.1 x = not in final model, but predictor in full model																					

songbirds (p  $\,=\,$  0.01). By contrast, human use intensity tended to be positively related to the Simpson diversity index of songbirds, although

songbird diversity indices between the five lake categories (Fig. 4, Ap-

pendix Table A6). However, the multivariate regression analysis indi-

cated significant negative relations between dog abundance and species

richness and Simpson diversity index of songbirds (Table 2, Table 3,

Appendix Table A7). Dog abundance was negatively and SDF positively

related to the species richness of songbirds (p = 0.05). Increasing dog

density was also negatively related to the Simpson diversity index of

effects were not statistically significant (p = 0.08). Shoreline length was a significant and positive environmental covariate of the Simpson diversity index of songbirds. The Poisson GLM to predict the number of endangered songbird species was not significant.

The seasonal GLMs predicting species richness, Simpson diversity index and the number of endangered songbird species, based on use intensities during the breeding season and during summer separately, revealed that recreational use intensities during both seasons did not significantly affect species richness of songbirds, although dog use during summer tended to correlate negatively with the species richness of songbirds (p = 0.07, Appendix Table A9). Density of dogs was also significantly negatively related to the Simpson diversity index of songbirds in both breeding and summer seasons (both p = 0.03, Appendix Table A10).

# 3.4 Damselflies

There were no significant differences between the five lake use categories in the univariate comparison of damselfly diversity (Fig. 4, Appendix Table A6). Also, the multivariate analysis of species richness of damselflies was not significant. Yet, human use intensity was a significantly negative predictor of the Simpson diversity index of damselflies (p = 0.01). Significant environmental predictors were macrophyte coverage as positive and amount of reed as negative predictor (Appendix Table A7). Because endangered species were found only at two AO lakes (one endangered species each), no model was fitted.

<sup>1</sup>Brucet et al. (2013); <sup>2</sup> Hecnar and M'Closkey (1997); <sup>3</sup> He and Legendre (1996); <sup>4</sup> Wetzel (2001); <sup>5</sup> Matern et al. (2022); <sup>6</sup>Hilt et al. (2022), <sup>7</sup>Coutris et al. (2011), <sup>7</sup>Vestergaard and Sand-Jensen (2000), <sup>8</sup> Rashidi, Chamani, and Moshtaghi (2019); <sup>9</sup>Nikolaus et al. (2022); <sup>10</sup>Müller et al. (2003); <sup>11</sup>Sime (1999), <sup>12</sup>Deutschewitz et al. (2003), <sup>13</sup>Knorp and Dorn (2016), <sup>14</sup>Holtmann et al. (2018); <sup>15</sup>Found et al. (2008); <sup>16</sup>Schindler et al. (2003).

#### Table 3

Multiple linear regressions to predict species richness based on recreational use intensities and selected environmental variables. Shown are only the results of the final model, after model selection. For full models with all variables included see Table 2. For the species richness of damselflies, amphibians and riparian trees models were overall insignificant. SDF = shoreline development factor, TP = total phosphor, SRP = soluble reactive phosphor (for macrophyte species richness). Significance of variables is indicated in bold (p < 0.05).

	Waterfowl	Songbirds	D <b>ragonflies</b>	Fish	Macrophytes	Riparian herbs
Intercept	2.29 (0.05), p < 0.01	2.34 (0.05), p < 0.01	1.12 (0.10), p < 0.01	1.97 (0.06), p < 0.01	1.07 (0.31), p < 0.01	3.94 (0.02), p < 0.01
Humans (per km)	0.01 (0.07), p = 0.90	0.09 (0.06), p = 0.16	-0.18 (0.17), p = 0.29	0.15 (0.07), p = 0.03	-0.12 (0.10), p = 0.21	0.23 (0.04), <b>p</b> < 0.01
Anglers (per km)	-0.07 (0.06), p = 0.20	-0.04 (0.05), p = 0.42	0.10 (0.10), p = 0.32	0.09 (0.06), p = 0.16	0.06 (0.08), p = 0.44	0.02 (0.03), p = 0.50
Dogs (per km)	0.01 (0.07), p = 0.92	-0.13 (0.07), p = 0.05	0.15 (0.15), p = 0.29	-0.13 (0.08), p = 0.09	0.17 (0.09), p = 0.05	-0.15 (0.04), <b>p</b> < 0.01
Area (ha)	0.18 (0.07), <b>p</b> = <b>0.01</b>					
SDF	0.14 (0.05), <b>p</b> = <b>0.01</b>		0.35 (0.14), <b>p</b> = <b>0.01</b>		0.12 (0.06), p = 0.05	
Shorleline length (m)		0.19 (0.05), <b>p &lt; 0.01</b>	-0.29 (0.14), <b>p</b> = <b>0.04</b>			0.04 (0.02), p = 0.08
Distance to settlement (m)						-0.19 (0.03), <b>p &lt; 0.01</b>
Agriculture (%)			-0.15 (0.10), p = 0.15		0.12 (0.07), p = 0.06	0.12 (0.02), <b>p &lt; 0.01</b>
Wetland (%)			0.25 (0.10), <b>p</b> = <b>0.01</b>			
TP/SRP (mg/l)					-0.24 (0.12), p = 0.05	
NO <sub>3</sub> (mg/l)					-0.17 (0.08), <b>p</b> = <b>0.04</b>	
TOC (mg/l)			-0.38 (0.12), <b>p</b> < 0.01			
Age				0.19 (0.06), <b>p</b> = <b>0.01</b>		
Secchi depth (m)					0.17 (0.07), <b>p</b> = <b>0.01</b>	
Macrophyte cover (%)	-0.10 (0.06), p = 0.09					
Fish BPUE (g/100 m <sup>2</sup> )			$-0.33 (0.14), \mathbf{p} = 0.02$			
Open sites/m						−0.19 (0.04), <b>p</b> < 0.01
Ν	39	39	38	38	39	39
AIC	204.38	197.63	164.89	180.26	218.75	363.26
BIC	216.02	205.94	181.27	188.44	233.72	376.57
Pseudo R <sup>2</sup> (Cragg - Uhler)	0.60	0.32	0.57	0.47	0.69	0.96

#### 3.5 Dragonflies

Univariate analysis did not reveal significant differences in species richness and Simpson diversity index of dragonflies. The number of endangered species differed between the lake use categories as indicated by the Kruskal-Wallis test (Fig. 4, Appendix Table A6), however, the Wilcoxon post-hoc analysis did not detect significant pairwise differences between specific use categories. Only two control lakes contained one endangered species each.

Recreational use intensities were no significant predictors for the richness of dragonfly species, while SDF and share of wetland around the lake (in 100 m buffer) were positive and shoreline length, TOC, and fish biomass were negative and significant predictors (Table 3). The regression model to explain the Simpson diversity index of dragonflies was not significant.

# 3.6 Amphibians

The species richness of amphibians was rather low with a maximum of five species per lake. Univariate analysis (Kruskal-Wallis test) showed that the lake use categories A, AO and AOB had significantly lower species richness than O lakes (Fig. 5, Appendix Table A6). There were no significant differences in Simpson diversity index and number of endangered amphibian species between lake use categories, and the regression models for species richness and the Simpson diversity index were also insignificant. The occurrence of endangered species was positively related to SDF and the distance to the next water body, while recreational intensities were not significantly related to the amphibian biodiversity indicators (Appendix Table A8).

#### 3.7 Fishes

Control lakes had a significantly lower fish species richness than A, AO and AOB lakes, and O lakes had significantly lower fish species richness than A and AO lakes (Fig. 5, Appendix Table A6). There were no significant differences in the Simpson diversity index of fishes between the lake use categories. The number of endangered fish species tended to be lower in O lakes compared to A, AO and AOB lakes. Fish biomass did not significantly differ among lake use categories (Appendix Table A5). The multivariate regression analysis showed fish species richness was significantly and positively related to human use intensity (p = 0.03) and to lake age (p = 0.01). For the Simpson diversity index of fishes angling intensity (p = 0.05) and total phosphorous concentration (p = 0.05) were significant positive predictors. For endangered species the model did not converge.

### 3.8 Macrophytes

No significant differences were found between the lake use categories and macrophyte diversity (Fig. 5, Appendix Table A6). Macrophyte species richness was explained positively by the Secchi depth and negatively by nitrate (NO<sub>3</sub>). In addition, macrophyte species richness tended to be positively associated with the SDF (p = 0.05) and the share of agricultural land around the lake (albeit not significantly, p = 0.09), and negatively associated with the soluble reactive phosphorus concentration (p = 0.05), but did not relate to recreational use intensities (Table 3). The Simpson diversity index was neither explained by recreational use intensities, nor by selected environmental variables. Similar to species richness, the number of endangered species was negatively associated with nitrate (p = 0.03) and in tendency positively related to agriculture (p = 0.09), while recreation intensity did not relate to the number of endangered macrophyte species (Appendix Table A8).

#### 3.9 Riparian herbs

AOB and A lakes had significantly greater species richness than AO lakes. We did not observe significant differences between the lake use categories for the Simpson diversity index and the number of endangered species of riparian herbs (Fig. 5, Appendix Table A6).

The multivariate analysis showed that recreational use might have shaped species richness of riparian herbs (Table 3). Human use intensity was significantly positively related to species richness (p < 0.01), whereas dog density was negatively associated with the species richness of riparian herbs (p < 0.01). Significant environmental predictors were the distance to settlements, openness (both negatively related to species



**Fig. 5.** Boxplots of species richness, Simpson diversity index and number of endangered species per use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating) for amphibians (A, B, C), fishes (D, E, F), submerged macrophytes (G, H, I) riparian herbs (J, K, L) and riparian trees (M, N, O). Significant differences between use categories are indicated by different lowercase letters above the respective boxplots (post - hoc Tukey's test or pairwise Wilcoxon test, p < 0.05). Note the different scales of y-axes.

richness) and agriculture (positive). The regression model for the Simpson diversity index was not significant. For endangered species dog use intensity tended to be positively related to the number of endangered species, but the effect was not significant (p = 0.06, Appendix Table A8).

#### 3.10 Riparian trees

There were no significant differences of the riparian tree diversity between the lake use categories (Fig. 5, Appendix Table A6). The Poisson regression model for species richness was not significant. The Simpson diversity index of riparian trees was significantly positively predicted by lake age. Recreational use intensities did not significantly relate to the Simpson diversity index (Appendix Table A7). For endangered tree species we used a binomial regression model, which was not significant.

# 4. Discussion

Our first hypothesis (H1) that primarily environmental variables determine the biodiversity of gravel pit lakes was mostly supported. In line with H1, for most taxa environmental factors, especially lake morphology and trophic state, were stronger and more consistent predictors of biodiversity than recreational activities. We found mixed support for the second hypothesis (H2) that non-mobile taxa, especially plants, show greater recreation-induced impacts than mobile taxa, especially outside the breeding season. In contrast to our expectations we did not find weaker impacts of dogs on songbirds off the breeding season, which implies that dog impacts remain important all year around. Our third hypothesis (H3) that recreational impacts on biodiversity scale with human-use intensity independent of the kind of recreational activity was supported. For the density of dogs negative impacts dominated and therefore our results imply that dog walking has greater impacts on biodiversity at lakes than the total number of human use density, which confirms our fourth hypothesis (H4). Note that in our regression models dog abundance (without humans) was quantified while controlling for total human use density, which allows the impact of dogs to be isolated from the human disturbance effect. The positive impacts of angling and general human use on the diversity of fishes was in support of our fifth hypothesis (H5), i.e., some recreational activities can also have positive impacts on biodiversity indicators.

# 4.1 Recreational uses versus environmental factors as predictors of lake biodiversity

Lake morphology, lake age, land use and trophic state were stronger predictors of lake biodiversity than variables that quantified the intensity of recreational use. The most plausible explanation is that environmental variables are more important for habitat selection and species persistence at a given lake than recreational disturbances. Usually, environmental conditions are reported to shape species compositions (Birk et al., 2020; Kail et al., 2023; Sun et al., 2022; Timm & Möls, 2012; Xiong et al., 2023) and these effects of the environment might be more pronounced than effects of recreational impacts. Previous studies in recreation ecology of aquatic systems usually took place at only one or two waterbodies, suffered from low sample sizes, missed controls and did not consider environmental confounders (summarized in Schafft et al., 2021). These methodological limitations and the pervasive publication bias overreporting negative findings (Schafft et al. 2021) might have contributed to the common assumption (Reichholf, 1988; Tuite et al., 1983) that recreational uses are main drivers of biodiversity loss at lakes or rivers. By considering a large gradient of recreational use intensity, including control lakes without any recreational use, we revealed that influences on aquatic and riparian biodiversity are more complex and often solely or mainly driven by environmental factors. Especially larger lakes with long shorelines and high shoreline development can apparently mitigate disturbance impacts by humans by

providing sufficient shelter habitats. Islands, bulges and bays might also serve as visual and acoustic barriers and reduce impacts on waterfowl and other wildlife (Bregnballe & Aaen, 2009; Tablado & Jenni, 2017). If flight reactions still occur, birds do not necessarily disperse to another lake, but rather distribute within lakes (Stalmaster & Kaiser, 1998). Further, the impact of human disturbance on wildlife is often non-linear and also depends on characteristics of species and the context in which interactions occur, making general assumptions, particularly if based on single case studies, difficult or impossible (Bregnballe & Aaen, 2009; Pirotta et al., 2022; Schafft et al., 2021; Tablado & Jenni, 2017). Recreational activities can indeed negatively impact a wide variety of taxa, but depending on the characteristics of the waterbody environmental factors can usually be considered stronger predictors of lake biodiversity.

# 4.2 The role of specific recreational activities for biodiversity

We found support for our general assumption that the intensity of recreational activities impacts biodiversity, but similar to Schafft et al. (2021) these effects were independent of the type of recreational activity. Biologically, it is more important how many humans in general interfere with a given system than the particular form of recreational activity that is present. We further assumed that high recreational use intensities during the breeding season have more pronounced impacts, particularly on waterfowl (Lafferty, 2001). However, our results did not reveal such seasonal impacts. An important factor might be that several species (e.g. coot (Fulica atra), moorhen (Gallinula cholorpus) or water rail (Rallus aquaticus)) are multibreeders with additional broods in summer (Murray, 2000) enabling them to compensate for possible disturbance-induced fitness drawbacks early in the year. Especially angling occurs early in spring, i.e. during the breeding season, and is often discussed as particularly strong disturbance to breeding waterfowl (Cryer et al., 1987; Park et al., 2006; Reichholf, 1988). Reichholf (1988) reported that already two anglers per km shoreline can have negative impacts on the biodiversity of waterfowl in a Bavarian river. We observed up to 17 anglers per km during the standardized user counts without measurable effects on lake waterfowl. Lakes and rivers can harbor different species with different noise and disturbance tolerances (Mayer et al., 2019), which can be one reason explaining the different findings. Another reason might be that Reichholf (1988) lacked proper controls and replication, which could have led to bias. Furthermore, lakes with plenty of fish that are associated with the presence of fishing activities and fisheries management may attract piscivorous bird species (Found et al., 2008), which can buffer the loss of more disturbance sensitive species when examining richness metrics. As a further factor, local angling clubs regularly establish protected no access zones offering improved habitat complexity that benefits vegetation and wildlife, including birds (Nikolaus et al., 2022). Susceptibility towards disturbances varies with habitat quality, and complex habitat provides more shelter (Tablado & Jenni, 2017), thereby protected zones established by anglers might mitigate negative effects of angling on waterfowl and songbirds diversity.

# 4.3 Dog walking is more impactful to local biodiversity than the human use density per se

In contrast to waterfowl, songbirds were more strongly affected by recreational disturbances. Especially dog walking was negatively associated with songbird richness and their Simpson index. Note that in our models we estimated an independent effect of dog abundance, by separately including human use density in the same models. Although statistically we can observe an isolated effect of dog abundance independent from human abundance, in reality in the study region these dogs were pet dogs, which means that each dog was accompanied by a human. As dogs are highly oriented on their caretaker (Topál et al., 2005), the behavior even of unleashed pet dogs is highly dependent on

their accompanying human. The human usually decides where to go, if the dog is unleashed or not, what the dog is allowed to do and thereby highly influences the magnitude of the impact that a pet dog can have on wildlife (Miller et al., 2001). Therefore, our results can be interpreted as ecological impacts of dog walking and not only the impact of dogs. Our results confirm our hypothesis that dog walking has greater ecological impacts than humans without dogs (Banks & Bryant, 2007). We think that at lakes with high human use intensities animals have habituated to 'harmless' humans, but that wildlife does not show the same response to dogs (Banks & Bryant, 2007). In contrast to humans, who often do not even notice hidden animals, dogs actively recognize and respond to wildlife, because of their much better hearing, olfactory and visual senses (Grimm-Seyfarth et al., 2021; Nussear et al., 2008). Habituation to dogs is further hindered because most dogs preserved their hunting instincts, even if not especially trained for and therefore cannot resist to chase wildlife (Sime, 1999). Already the scent of domestic dogs has been shown to repel a wide variety of wildlife (Kats & Dill, 1998). This suggests that dogs continue to be perceived as risk, and behavioral responses such as increased vigilance and flight responses negatively affect biodiversity, at least of songbirds.

We did not find stronger impacts of dogs on songbirds during the breeding season, which implies that dog impacts remain important all year around. The legal obligation to put dogs on leash during the breeding season, which could potentially mitigate their negative effects, was indeed insufficiently followed in our study lakes as we found no differences in the share of unleashed dogs between breeding (37.5% of all dogs counted) and summer season (35.6% of all dogs counted). However, the total number of dogs counted during the standardized visitor counting was higher in the breeding season. Therefore, it cannot be excluded that sensitive songbirds avoid dog walker-preferred lakes early in the year during territory establishment and continue avoidance all year round, as it is known for disturbances by humans in terrestrial environments (Bötsch et al., 2017). Overall, we found walked dogs, whether leashed or not, to have a greater impact on the biodiversity of lakes than the sole presence of humans, although in practical terms dogs and humans co-occur in most situations.

# 4.4 Positive effects of recreational activities on biodiversity indicators

As predicted angling use intensity, as both an independent predictor and part of the human use metric in general, was significantly positively related to fish species richness, confirming previous findings (Matern et al. 2019, 2022) from the study area. Fish stocking is a common fisheries management practice, which increases fish richness in gravel pit lakes (Matern et al. 2019, 2022), and high fish abundance is attractive to anglers (Birdsong et al., 2021; Meyerhoff et al., 2022). Yet, in disagreement with expectations, angling use intensity and related fisheries management measures including fish stocking were not the main recreational predictor of fish species richness. Instead, it was human use in general (including anglers). We assume that a confounder variable such as general accessibility of lakes by the public might have caused this result. Previous work has revealed that urbanization increases fish species richness and homogenizes freshwater fish communities (Rahel, 2000). It is possible that other anthropogenic vectors such as the illegal release of garden pond fish by private people further increased the number of fish species in the water bodies, which could explain the increase of the species richness over time or that the presence of more fish species attracts more people.

The positive relation of human use and riparian vegetation can be explained by the intermediate disturbance hypothesis (Wilson, 1990), with moderate disturbance frequencies allowing coexistence of tolerant and intolerant species, promoting highest species richness. At high disturbances, intolerant species will disappear. This phenomenon is observed not only for natural disturbances, such as wild fires, but also for anthropogenic disturbances, such as mowing (Uchida & Ushimaru, 2014). Meadows without mowing have a lower plant species richness

than meadows that are mowed once or twice per year (Uchida & Ushimaru, 2014). If meadows are mowed more often then the disturbance is too high and the plant species richness lowers again. At lakes used by anglers and other recreationists we observed mowing the shoreline as common practice, not only to facilitate anglers' access, but also water access for bathing or swimmers and on camp grounds. At recreation lakes it is also very common to implement artificial beaches, which includes sand addition (Kalybekov et al., 2019) and beach grooming for maintenance and litter avoidance (Uzarski et al., 2009). On the one hand, this beach management completely reduces plant cover (Uzarski et al., 2009), but on the other hand it allows for existence of sandspecialized species that would naturally not occur and increases plant species richness at recreation lakes. The intermediate disturbance hypothesis (Wilson, 1990) can also be applied to trampling effects (Liddle, 1975). High trampling intensities primarily destroy the vegetation and compact soils, which result in reduced vegetation cover and species richness (Ballantyne & Pickering, 2015; O'Toole et al., 2009). When trampling occurs at low intensities trampling-resistant plant species will even enrich the species composition, because they tolerate compacted soils or are more resistant to physical damage, while less tramplingresistant species still co-occur (Ballantyne & Pickering, 2015; Bonanno et al., 1998). We did not directly compare highly trampled with undisturbed vegetation plots, but instead focused on whole lakes represented by multiple vegetation plots as sampling units. This might explain the positive effect of human use on plant species richness, because even lakes with high use intensities had low disturbed shoreline plots (Bonanno et al., 1998; Liddle & Scorgie, 1980; Meyer et al., 2023). Usually trampling impacts occur concentrated at water access points (Liddle & Scorgie, 1980; Meyer et al., 2023; O'Toole et al., 2009), which can lead to microhabitat mosaics. Additionally, habitat management can mitigate trampling effects, e.g. in angler managed water bodies with protected no access zones, which promote natural succession processes, where trampling-sensitive plants increase in abundance (Nikolaus et al., 2022). Different trampling intensity along the shoreline can therefore result in co-existence of trampling tolerant and intolerant plant species even at lakes with high human use (Meyer et al., 2023; Nikolaus et al., 2022), maintaining richness at whole lake scales (which was the unit of observation in our work).

## 4.5 Impact of recreational activities on individual taxa

Waterfowl: Previous studies found waterfowl to be very sensitive to recreational activities (Bell et al., 1997; Franson et al., 2003; Park et al., 2006; Reichholf, 1988; Yalden, 1992). This study found neither species richness, nor Simpson diversity index or number of endangered water fowl species being related to recreational use intensity. Control lakes did not host more waterfowl species than recreational lakes with very high use intensities, which was best explained by habituation effects to humans, especially at lakes with high recreational uses (Keller, 1989). Our findings suggest that often-described behavioral responses to disturbances by waterfowl such as flight initiation or alert behavior (Stock et al., 1994; Frid & Dill, 2002) do not necessarily scale up to lake-level biodiversity metrics (Buckley, 2013; Stock et al., 1994). However, we cannot exclude that certain species generally avoided recreational sites and moved to unsampled sites instead and that specific species were lost from the species pool as we focused on richness related measures and not on species identity.

Songbirds: As shown in our study the main predictor for songbird diversity was the shoreline length, which is again in line with the species area relationship concept (He & Legendre, 1996). The relationship of recreational use intensities with songbird biodiversity were of minor importance. Possible reasons explaining our findings could be that lakes with high recreation intensities had also large protected no access zones and that songbirds used the recreation infrastructure too. High human use intensity is often associated with particular infrastructure, such as trails, waterski facilities, floating islands and jetties, which might

provide artificial habitat and resources. For example, shrubs along trails serve as suitable feeding and nesting habitats for some songbirds (Williams et al., 2011), jetties or floating islands as resting grounds. In some recreation lakes the installed waterski cables were used as resting structure, similar to power lines cables. This supports the hypothesis that environmental conditions and especially habitat availability are the main drivers of biodiversity and impacts of recreation on songbirds at lakes are minor.

Dragonflies and Damselflies (Odonata): We found a negative relationship of human use intensities with the Simpson index of damselflies, which probably was associated with reduced structures required by Odonata for egg laying and emergence out of the water during metamorphosis. Lakes with high human use densities offered long stretches of sandy beaches for recreation, which provide little habitat complexity resulting in low benthic invertebrate richness (Brauns et al., 2007). Our results are in line with reported biodiversity decrease of damselflies and dragonflies with increasing anthropogenic pressure, especially with fragmentation of riparian vegetation (Müller et al., 2003). In contrast to Müller et al. (2003), we found no negative impacts of angling on Odonata. Angling intensity was not negatively associated with the diversity of Odonata. Previous reports probably resulted from impacts on vegetation, which were controlled for and disappeared in our study. However, as expected, we identified a negative effect of lake's fish biomass on dragonfly species richness indicating an often described, indirect impact of fish predation (Knorp & Dorn, 2016).

Amphibians: Impacts of recreational disturbance on amphibian biodiversity was difficult to assess, given their low species richness with a maximum of five species per lake. Generally, the studied gravel pit lakes were considered rather unsuitable for amphibians, as they prefer fishless water bodies (Shulse et al., 2010), while all studied lakes contained fish (Matern et al., 2022). Although no significant associations between recreational uses and amphibian biodiversity were found, angling lakes had lower species richness compared to lakes without angling but other recreational uses. We found Rana sp. very common in lakes without angling and missing in almost all lakes used for angling. Despite comparable fish biomasses, lakes with angling hosted more predatory fish species (Matern et al., 2019) and therefore, predation pressure on amphibians might have been higher (Hartel et al., 2007; Sequeiros et al., 2018). Only coexistence of common toad (Bufo bufo) and Pelophylax sp. with predatory fish is reportedly very common (Hartel et al., 2007). Correspondingly, common toad was present in all studied lakes.

Fishes: We expected that lake morphology and especially the total phosphorus concentration in the water would be the most important predictors for fish diversity as described in the literature (Jeppesen et al., 2000; Matern et al., 2022). A high lake productivity with abundant phytoplankton lead to higher carrying capacity for fish (Jeppesen et al., 2000). In our study, fish biomass was highly correlated with total phosphorus, and the Simpson index was also mainly predicted by total phosphorus concentration. However, fish species richness was only explained by lake age and human use intensities. Gravel pit lakes as artificial water bodies often lack direct connection to other water bodies and are thus, not easily naturally colonized by fish. Colonization happens primarily by intentional stocking or illegal release (Gimenez et al., 2023; Matern et al., 2019) and unintentional introductions via gears (e. g. for fishing or boating) that are moved between different waterbodies (Smith et al., 2020).

Vegetation: While riparian herbs diversity was highly influenced by recreational impacts as in detail already discussed, the diversity of riparian trees and of aquatic macrophytes was not associated with recreation intensities. The assumption that clear-cutting of riparian trees and already discussed mowing practices for recreational purposes should have negative impacts on the diversity of riparian trees, might be of less importance than natural succession processes and simply the presence of forests around the lakes (Marburg, Turner, & Kratz, 2006). Although recreational impacts on aquatic macrophytes have been shown

(e.g. Bertrin et al., 2018; Clayton & Tanner, 1988; Sagerman et al., 2020; Wegner et al., 2023) our results did not reveal any relationship of macrophyte diversity with recreation intensity. We did not find effects of angling intensity on submerged macrophytes, despite high densities of benthivorous fish, especially common carp (Cyprinus carpio), reportedly affect macrophyte cover (Bajer et al., 2016). Densities of benthivorous fish might not have exceeded critical thresholds (approx. 100 kg  $ha^{-1}$ ; Vilizzi et al., 2015). In addition, aquatic macrophytes are often locally removed by anglers to avoid hook entanglement and tackle loss (Löki et al., 2021; Williams & Moss, 2001), even if most anglers highly value dense aquatic vegetation (Williams & Moss, 2001). However, moderate disturbance by anglers and clearcutting of dominant reeds can enhance macrophyte biodiversity (Goulder, 2001). Nikolaus et al. (2021) found increased macrophyte cover in angler-managed lakes and assumed that the mosaic of open riparian sites along the bank provide more light in the littoral zone and thereby enhance macrophyte growth. Macrophytes depend on light for growth (Hilt et al., 2022) and also many recreationists prefer clear water, e.g. for swimming (Vesterinen et al., 2010). However, most people frown upon macrophytes in swimming areas, and clearcutting macrophytes became common practice to increase attractiveness of waters for recreation (Clayton & Tanner, 1988). Still, not recreation intensity but nitrate concentration, water transparency (Secchi depth) and SDF were the main predictors for macrophyte diversity in our study. This finding is not surprising as light, nutrient availability and lake morphology are the main constraints for macrophyte growth (Hilt et al., 2022). We conclude that negative impacts of recreational activities on submerged macrophytes maybe less common than often believed.

### 5. Limitations

While our study's strength lies in its comprehensive assessment of multiple taxa at whole lake scale for a substantial sample of 39 lakes, there are important limitations. Primarily, the study is based on observational data and correlations and accordingly, the observed outcomes might not represent causal relations (Larsen et al., 2019). The standardized visitor counting was performed at all lakes at the exact same time, but we did only cover the spring and summer season (April-August). These two seasons are the ones that were expected to have the highest recreation intensities in that region (Venohr et al., 2018) and we covered the same seasons in which we performed the biodiversity sampling. However, we note that for several lakes the visitor counts did not take place in the same year as the biodiversity sampling, with partly one or two years in between. Although species richness, composition and abundances could be altered in between due to changes in recreation intensities or due to year-specific environmental conditions, this short time periods should not affect the longterm effects of recreational use intensities, expected to influence biodiversity. Furthermore, the species sampling, except the sampling of Odonata, was not always carried out by the same person. We aimed to mitigate differences in expertise by intensive in person trainings, but we cannot exclude sampler effects. The multiple taxa approach brought the shortcoming that we were not able to study each taxonomic group in detail. This has led to a reduced sampling effort for some taxa. Nevertheless, we consider our regression models to be robust, because the same potential methodological error applies to all lakes. Another shortcoming is the focus on species richness as a measure of biodiversity, because a high number of species does not always reflect a natural species community and the metric shadows species turnover and species identity effects (Hillebrand et al., 2018). To address this shortcoming, we incorporated the number of endangered species into our analysis as additional conservation-related metric. However, with the chosen indices we were not able to pay attention to species identities or species turnover (Hillebrand et al., 2018). Therefore, we cannot rule out that recreational use might impact sensitive taxa or might cause shifts in species communities.

# 6 Conclusions and implications

Our study did not support the frequently expressed assumption that recreational activities such as angling are a strong threat to waterfowl and other taxa. In fact, we found an overwhelming relevance of environmental factors in shaping biodiversity in and at lakes, with only secondary effects of recreation. We also found that dog walking had more systematic effects than human use intensity per se and that general human use intensity had greater impacts than single activities like angling. Therefore, similar to Schafft et al. (2021) we conclude that conservation will foremost benefit from restoring appropriate environmental conditions and that selectively banning or constraining one particular form of recreation may have high social costs at low conservation benefits. For selected taxa that are predation sensitive (e.g. amphibians), specific activities such as angling may still be harmful by elevating predation pressure indirectly through fostering the fish populations. Human use in general did not negatively affect birds, which contradicts common assumptions. By contrast, no habituation effects of songbirds were observed towards dogs so that dog walking should be considered more critical in the context of biodiversity disturbance than human recreational activities per se, although in reality dog use and human presence go hand-in-hand. Further, it is already mandatory in the study region to keep dogs on the leash during the breeding season (§ 33 NWaldLG, Lower Saxony's law on forest and landscape management), but our data suggest that this law is widely ignored, likely increasing disturbance stimuli related to dog walking. To conclude, our study revealed that for the biodiversity of most taxa environmental variables are more important than recreation impacts. Lake morphology and for some taxa trophic state and land use were the most important drivers of biodiversity, not recreation. Lake morphology, and long structured shorelines specifically, can provide more suitable habitat and at the same time mitigate disturbance impacts at gravel pit lakes. Hence, high shoreline development factors and maybe even islands could be already planned during commissioning and dredging of gravel pit lakes. Moreover, large-scale restoration of natural habitats seems a more suitable management tool (Radinger et al., 2023) than selectively constraining or banning access of lakes to humans. We urge caution against selectively constraining selected forms of recreation (e.g., angling), while maintaining access to other recreationists (e.g., dog walking), as such effects are unlikely to benefit conservation, while carrying substantial conflict potential for human welfare.

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### Credit authorship contribution statement

Malwina Schafft: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. Robert Nikolaus: Data curation, Methodology, Writing – review & editing. Sven Matern: Data curation, Methodology, Writing – review & editing. Johannes Radinger: Formal analysis, Writing – review & editing. Andreas Maday: Data curation, Writing – review & editing. Thomas Klefoth: Conceptualization, Funding acquisition, Project administration, Resources, Writing – review & editing. Christian Wolter: Conceptualization, Supervision, Writing – review & editing. **Robert Arlinghaus:** Data curation, Methodology, Writing – review & editing.

# **Declaration of Competing Interest**

This work received funding from three angler associations and one co-author is an employee at one of these organizations. The funding organizations had no influence on the data collection or interpretation of the data.

# Data availability

Data is available via www.fred.igb-berlin.de (https://fred.igb-berlin. de/data/package/807) and the respective metadata are published in the Freshwater Metadata Journal. (https://doi.org/10.15504/fmj.2023.53)

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# Appendix. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2023.126545.

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