Recreation ecology: impacts of recreational angling and other water-based activities on freshwater biodiversity

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M.Sc., Malwina Schafft
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Dekan der Lebenswissenschaftlichen Fakultät: Prof. Dr. Dr. Christian Ulrichs

Gutachter/innen: 1.

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List of papers

This thesis is based on five papers, which are referred to in the text by their roman numbers (I – V).

Paper I

Schafft, M., Wegner, B., Meyer, N., Wolter, C., & Arlinghaus, R. (2021). Ecological impacts of water-based recreational activities on freshwater ecosystems: A global meta-analysis. *Proceedings of the Royal Society B*, *288*(1959), 20211623.

Paper II

Meyer, N., **Schafft, M.**, Wegner, B., Wolter, C., Arlinghaus, R., Venohr, M., & von Oheimb, G. (2021). A day on the shore: Ecological impacts of non-motorised recreational activities in and around inland water bodies. *Journal for Nature Conservation*, *64*, 126073.

Paper III

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Paper IV

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Paper V

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Authors contributions

Author of this thesis: Malwina Schafft (MS)

List of co-authors: Robert Arlinghaus (RA)

Thomas Klefoth (TK)

Andreas Maday (AM)

Sven Matern (SM)

Robert Nikolaus (RN)

Goddert von Oheimb (GVO)

Johannes Radinger (JR)

Markus Venohr (MV)

Benjamin Wegner (BW)

Christian Wolter (CW)

Paper I: **MS (large)**, with RA and CW (minor) conceptualized and designed the meta-analysis and the systematic review. **MS (large)** with B.W. and N.M. performed the acquisition of data, literature screening and extraction of relevant information for effect size estimation. **MS (entire)** performed the analysis and drafted the manuscript. Interpretation of results, critical revision of the manuscript for important intellectual content and final approval was performed by all authors **(MS large)**.

Paper II: NM, RA, **MS (partial),** CW and GVO designed the work. Literature screening and coding was performed by **MS (large)**, BW and NM. NM performed the data analysis and interpretation and wrote the first draft of the manuscript. All authors contributed to the critical revision of the manuscript **(MS, partial)**.

Paper III: **MS (large)**, RA, CW, and TK conceptualized and designed the study. **MS (partial)**, RN, SM, and AM performed data sampling. **MS (entire)** with support of JR and RA performed the statistical analysis. **MS (entire)** drafted the manuscript. Interpretation of results, critical revision of the manuscript for important intellectual content and final approval was performed by all authors **(MS large)**.

Paper IV:	RN, TK CW, RA conceptualized and designed the study. RN AM and **MS (partial)** performed data sampling. RN performed the statistical analysis. RN, RA and **MS (partial)** drafted the manuscript. All authors contributed to the interpretation of results, critical revision of the manuscript for important intellectual content and final approval **(MS partial).**
Paper V:	RN, CW, TK, & RA conceptualized and designed the study. RN, AM, SM and **MS (partial)** performed data sampling. RN performed the statistical analysis. RN drafted the manuscript. All authors contributed to the interpretation of results, critical revision of the manuscript for important intellectual content and final approval **(MS partial).**

Content

Abstract

Recreational activities at freshwater ecosystems have been increasing during the recent years. While water-based recreation is beneficial for human well-being, it can also have adverse effects on freshwater ecosystems. Recreational angling is considered to be a particular threat to freshwater ecosystems, due to long stays of anglers directly at the shoreline, even at night. As the biodiversity crisis is particularly pronounced in freshwater ecosystems, impacts should be mitigated by adequate nature conservation measures. At the same time, it is crucial to also minimize social costs of these measures. Therefore, a solid scientific evidence is needed to identify and quantify the impacts of all water-based recreational activities in a comparative way. First, I conducted a comprehensive literature synthesis to recapture the existing evidence about recreational impacts on freshwater ecosystems. I performed a global meta-analysis to compare the magnitude of impacts of shore-bound activities, shoreline angling, swimming and boating on different levels of biological organization. The recreational activities did not differ significantly in the magnitude of effects, although boating impacts were the strongest and most consistent. Effects were mainly reported on individual level, especially for individual birds, while impacts on higher levels such as population and especially community level should be more relevant for nature conservation. Although water fowl are known to be very sensitive towards human disturbance, impacts on water fowl were moderate and strongest impacts were found on invertebrates and plants caused by shore-bound activities and boating.

The narrative review on the impacts of non-motorized, non-consumptive activities in and around freshwater ecosystems further approved that the responses of sessile and mobile organisms to human disturbance differ, because plants were more strongly impacted than animals. The review highlighted the need of more studies on community level and underrepresented taxonomical groups and I considered these findings in my empirical analyses.

In the first empirical study I compared the biodiversity of several taxonomic groups (water fowl, songbirds, dragon flies, damselflies, amphibians, fishes, aquatic macrophytes, riparian herbs and trees) of gravel pit lakes with different intensities and combinations of recreational activities. The results were in line with the results of the meta-analysis that human presence and general intensity of use were more relevant than the specific recreational activity, such as angling. Although the presence of angling had positive impacts on the diversity of fishes it also showed negative impacts on amphibian diversity. This aspect was also verified by the second empirical study with the focus on impacts of angling management, in which I compared the biodiversity of angler-managed and unmanaged gravel pit lakes.

With the last study I present a potential solution to mitigate impacts of angling and other recreational uses on freshwater ecosystems. Protected riparian areas installed by angling clubs in small gravel pit lakes can positively influence habitat quality and benefit biodiversity. Aside from the intended positive impact on the fish abundance, I also detected positive contributions of small-scale riparian protected areas on habitat structure, riparian vegetation, local fish abundance and abundance of sensitive songbirds at the lake-scale. Again, I did not find impacts on disturbance sensitive water fowl. The often-reported impacts on individual level of water fowl (e.g. flight reactions) do not necessarily transmit to higher levels of biological organization. All empirical studies have shown that recreational impacts are minor compared to other threats such as pollution, habitat loss and degradation as main threats of freshwater biodiversity represented by environmental variables related to eutrophication, lake morphology and land use.

In conclusion, human use in general is the main driver of recreational impacts, while the specific activity itself is of less importance in regard to ecological impacts. Consequently, selectively banning or constraining one particular form of recreation may have high social costs at low benefits for conservation. Conservation measures are more promising if stakeholders are involved in decision making. Spatial zoning might be an effective tool in nature conservation to improve habitat quality and thus protect biodiversity. Other recreation management options are also discussed in this thesis.

Deutsche Zusammenfassung

Freizeitaktivitäten an Süßwasserökosystemen nehmen in den letzten Jahren zu. Während wasserbasierte Freizeitaktivitäten von Vorteil für das menschliche Wohlbefinden sind, können aus ihnen auch negative Auswirkungen auf Süßwasserökosysteme entstehen. Angeln gilt dabei als Freizeitaktivität von der eine besondere Gefährdung für Gewässerökosysteme ausgehen könnte, aufgrund des langen Verweilens direkt am Ufer, teils sogar nachts. Da die Biodiversitätskrise in Süßwasserökosystemen besonders ausgeprägt ist, sollten negative Einflüsse durch adäquate Naturschutzmaßnahmen verringert werden. Dabei ist es essentiell die sozialen Kosten solcher Maßnahmen so gering wie möglich zu halten. Daher ist eine solide wissenschaftliche Evidenzgrundlage nötig um die negativen Einflüsse, die von wasserbasierten Freizeitnutzungen ausgehen zu identifizieren, zu quantifizieren und zu vergleichen. Als erstes führte ich eine umfangreiche Literatursynthese durch, um die bereits existierende Evidenzlage zu erfassen. Dafür nutze ich eine globale Metaanalyse, um das Ausmaß der Effekte von ufergebundenen Aktivitäten, Uferangeln, Schwimmen und Bootfahren miteinander zu vergleichen. Der Vergleich ergab, dass es keine signifikanten Unterschiede zwischen den Freizeitaktivitäten bezüglich der Stärke der Effekte gab, obwohl die stärksten und konsistentesten Effekte vom Bootfahren ausgingen. Am häufigsten wurden Effekte auf Individuen berichtet, insbesondere Individuen von Vögeln, obwohl Effekte auf höheren Ebenen der biologischen Organisation, wie Populations- oder Artgemeinschaftsebene ökologisch relevanter sind. Wasservögel gelten als besonders störungssensitiv, dennoch waren die Effekte auf Vögel vergleichsweise gering und die stärksten Effekte waren bei Invertebraten und Pflanzen zu sehen, versursacht durch Uferaktivitäten und Bootfahren.

Die narrative Übersichtsarbeit über die Einflüsse von nicht motorisierten und nicht konsumtiven Aktivitäten in und um Süßwasserökosysteme bestätigte, dass sich die Reaktionen von mobilen und sessilen Organismen auf Störungen durch Menschen unterscheiden, denn Pflanzen waren auch hier stärker beeinträchtigt als Tiere. Die Arbeit betonte außerdem die Notwendigkeit von mehr Studien auf Ebene von Artgemeinschaften und von unterrepräsentierten taxonomischen Gruppen. Die Ergebnisse berücksichtigte ich in meinen empirischen Studien.

In der ersten empirischen Studie, verglich ich die Biodiversität von verschiedenen taxonomischen Gruppen (Wasservögel, Singvögel, Libellen, Amphibien, Fische, Wasserpflanzen und Ufervegetation) von Baggerseen mit unterschiedlicher Intensität und Kombination von Freizeitaktivitäten. Die Ergebnisse stimmten mit den Ergebnissen der Metaanalyse überein. Die Anwesenheit von Menschen und die generelle Nutzungsintensität waren insgesamt relevanter als spezifische Freizeitaktivitäten, wie beispielsweise das Angeln. Obwohl das Angeln sogar positive Auswirkungen auf die Fischdiversität hatte, zeigten sich ebenso auch negative Effekte auf die Amphibiendiversität. Diese Ergebnisse wurden durch eine zweite empirische Studie bestätigt, bei der die Biodiversität in von Anglern bewirtschafteten Baggerseen mit unbewirtschafteten Baggerseen verglichen wurden.

Mit der letzten Studie präsentiere ich eine mögliche Managementoption, um negative Einflüsse des Angelns und anderer Freizeitaktivitäten an Gewässern zu reduzieren. Geschützte Uferzonen, die von Angelvereinen in Baggerseen festgesetzt wurden, können sich positiv auf die Habitatqualität und Biodiversität auswirken. Neben dem beabsichtigten positiven Effekt auf die lokale Abundanz von Fischen, konnte ich außerdem positive Einflüsse der geschützten Uferzonen auf die Habitatstruktur, Ufervegetation, und das Vorkommen von störungssensitiven Singvogelarten feststellen. Wieder fand ich keine Effekte auf das Vorkommen von störungssensitiven Wasservögeln. Die oft berichteten Auswirkungen auf Individuenebene von Wasservögeln (z.B. Fluchtreaktionen) durch Freizeitaktivitäten, wirken sich scheinbar nicht unbedingt auf höhere Ebenen der Biodiversität aus. Alle meine empirischen Studien haben gezeigt, dass Auswirkungen von Freizeitnutzungen gering sind, im Vergleich zu anderen Gefährdungen der Biodiversität, wie bspw. Umweltverschmutzung, Habitatverlust und -verschlechterung als Hauptursachen der (Süßwasser-)Biodiversitätskrise, was sich repräsentativ in dem starken Einfluss der untersuchten Umweltvariablen der Gewässertrophie, -morphologie und der umgebenden Landnutzung wiederspiegelt.

Zusammenfassend ist die allgemeine Anwesenheit und Abundanz von Menschen hauptsächliche Auslöser von ökologischen Auswirkungen der Freizeitnutzung, während die Ausübung spezifischer Aktivitäten eine untergeordnete Rolle spielt. Demnach geht das Einschränken bestimmter einzelner Aktivitäten womöglich mit hohen sozialen Kosten einher, ohne hohen Nutzen für den Naturschutz zu bewirken. Naturschutzmaßnahmen sind erfolgversprechender, wenn Stakeholder in Entscheidungsprozesse eingebunden werden.

Räumliche Zonierung durch Stakeholder kann eine mögliche Naturschutzmaßnahme sein, die Habitatqualität zu verbessern und die Biodiversität zu schützen. Es werden auch weitere mögliche Maßnahmen des Besuchermanagements im Rahmen dieser Dissertation diskutiert.

1. Background

Freshwater ecosystems are attracting humans for recreation (Venohr et al., 2018). Recreational activities in and at freshwater ecosystems are increasing in popularity in the recent years (Brooker et al., 2023; Venohr et al., 2018). This trend has even been accelerated by the corona pandemic which has led to more people spending more time outside, enjoying nature and therefore also spending more time in and at water bodies (Britton et al., 2023; Pröbstl-Haider et al., 2023). For example, the interest and the number of sold fishing licenses increased during the pandemic in many countries (Britton et al., 2023). The pandemic has also highlighted the importance of outdoor recreation for human well-being, especially mental health (Pröbstl-Haider et al., 2023).

Recreational activities that take place at freshwater ecosystems include shore bound activities, such as walking, biking, riding a horse or camping along the shoreline. Trails close to the shoreline are usually preferred and therefore more frequented than trails farther away from the shoreline (Liddle and Scorgie, 1980; Spernbauer et al., 2023). For other activities the dependence on water is more obvious, for example for recreational angling. The activity itself takes place at the shoreline directly at the water's edge or in boats. The intention of the activity is, apart from recreation and other motivations, the catch of fish (Birdsong et al., 2021). Swimming, snorkeling and diving are activities that take place in the water. Especially on hot and sunny days water bodies attract a very high amount of people at the same time, which can lead to crowding effect, because the cooling in the water is a very popular strategy to cope with the heat (Venohr et al., 2018). This form of recreation might increase with the increasing temperatures worldwide due to the global warming (Miller et al., 2022). Boating is also an activity that increases in popularity with warm weather conditions although it is an activity that can be performed all year round (Miller et al., 2022). There are muscle powered boats like canoes or paddle boats, wind-powered boats and motor boats. While boating can be seen as a sports activity, especially with muscle-powered boats, boats are not only used for pleasure but also as vehicles to access the open water or other parts of the water body to conduct another recreational activity such as swimming or angling.

Outdoor recreation is an ecosystem service provided by freshwater ecosystems that benefits human well-being (Lynch et al., 2023; McDougall et al., 2020; Meyerhoff et al., 2022, 2019).

However, freshwater biodiversity is also highly threatened (Albert et al., 2021; Lynch et al., 2023; Reid et al., 2019), creating a trade-off between benefits for human well-being and potential detrimental ecological impacts caused by water-based recreation (Venohr et al., 2018). Habitat loss and simplification, pollution, invasive species and climate change are the main threats for aquatic biodiversity (Reid et al., 2019). Impacts by recreationists on freshwater biodiversity may include disturbance of wildlife (Frid and 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). Conservation measures to mitigate detrimental ecological impacts of water-based recreation should be based on robust evidence to maximize the benefit for wildlife and minimize costs on human well-being.

1.1. Ecological framework

Ecological impacts in general can either be natural or anthropogenic impacts (Figure 1). An impact is a stimulus that causes a reaction of an individual plant or animal. For plants these reactions are any physiological response, for animals, reactions also include increased vigilance, e.g. increased heart beat in the presence of a predator or a change in behavior, e.g. a flight reaction. Impacts on individual reactions can be compensated by habituation effects (Bötsch et al., 2018; Keller, 1989; Stock et al., 1994). Besides reactions of individuals impacts can also have further consequences and these can affect different levels of biological organizations. While the consequences injury, e.g. caused by a boat propeller strike or a change in body condition are effects on individual level, the fitness (ergo the reproduction and mortality or harvest of multiple individuals) can scale up to effects on population level, although additional broods (Keller, 1989) and density dependent growth can also compensate fitness effects (Lorenzen and Enberg, 2002). If the impact cannot be compensated at population level and even lead to such dramatic effects that the population would go extinct, then the community level will be affected. Any shift in the species composition, is an effect on community level, which also includes the (unintentional) introduction of neobiota and (fish) stocking. If key species are affected, then we can also expect changes in the ecosystem. Any change of the environment and any direct or indirect habitat modifications, e.g. trampling effects and clear cutting of vegetation (O'Toole et al., 2009) are changes on ecosystem level. Changes on ecosystem level again can alter the reactions of individuals towards a stimulus, because high and dense vegetation provide cover to hide. Less cover can increase the actual and the perceived risk of an individual animal and cause more vigilance and flight reactions (Tablado and Jenni, 2017).

Stock et al. (1994) describes that an increased heartbeat of a birds can be similarly caused either by human presence or by the arrival of a mating partner. Therefore, he warns to be careful with the term 'disturbance' in a scientific context because it already includes a negative evaluation of an effect. In the scientific context we should study effects while the evaluation of these effects should then be evaluated in a normative framework to determine if these observed effects are relevant or negligible (Figure 1). Relevant negative effects could then be called 'disturbance' and protection measures should be established to mitigate the anthropogenic impacts.

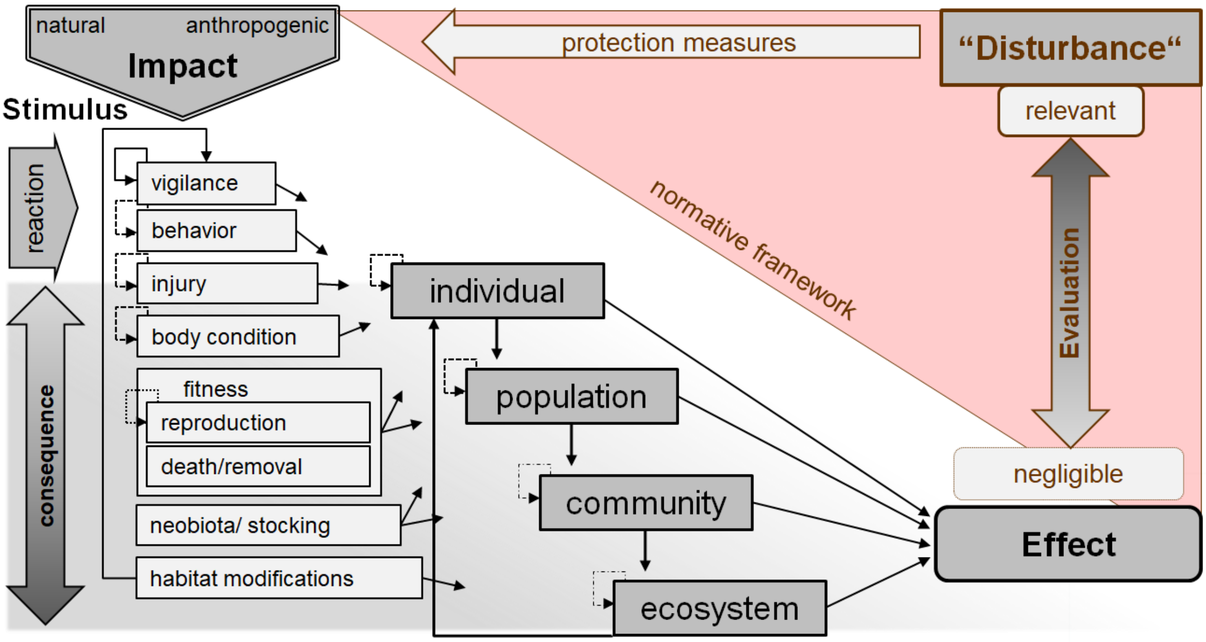


Figure 1: Natural and anthropogenic impacts can cause reactions of individuals and consequences on different levels of biological organization. Each effect can either be compensated or exceed to higher levels of biological organization from individual to population to community and up to ecosystem level effects. The evaluation of the observed effects should be part of a normative framework to assess if the effects are negligible or relevant and adequate protection measures have to be implemented to mitigate the anthropogenic impacts than cause negative relevant ecological effects (adapted after Stock et al., 1994).

Recreational users in water bodies or along the shoreline can have ecological impacts on freshwater ecosystems already simply by getting access to the water body and by being present at the water body (Figure 2). The access to a water body usually includes the physical damage of vegetation due to trampling (Andrés-Abellán et al., 2005; O'Toole et al., 2009; Spernbauer et al., 2023). Often the access for recreationists is even facilitated by clearcutting of vegetation, mowing and building infrastructure, e.g. boat ramps, landing stages, angling docks, water-ski facilities or beaches (Furgała-Selezniow et al., 2022; Kalybekov et al., 2019; Neely et al., 2022; Oliver, 1985; Radomski et al., 2010; Smith et al., 2019). Changes in the habitat structure can affect many wildlife species of different taxa, e.g. on dragonfly species which rely on vegetation for egg laying and emergence of the larvae (Müller et al., 2003). Once a recreational user has access to the water body the human presence can be perceived as predation risk by wildlife (Frid and Dill, 2002) and can cause avoidance reactions, which are often called disturbance effects (Stock et al., 1994). A special form of recreation is hunting and fishing, because these activities involve the removal and harvest of organisms. The impacts on the target organism can be seen as intended impacts, which in turn can also cause unintended consequences on other organisms and their habitat.

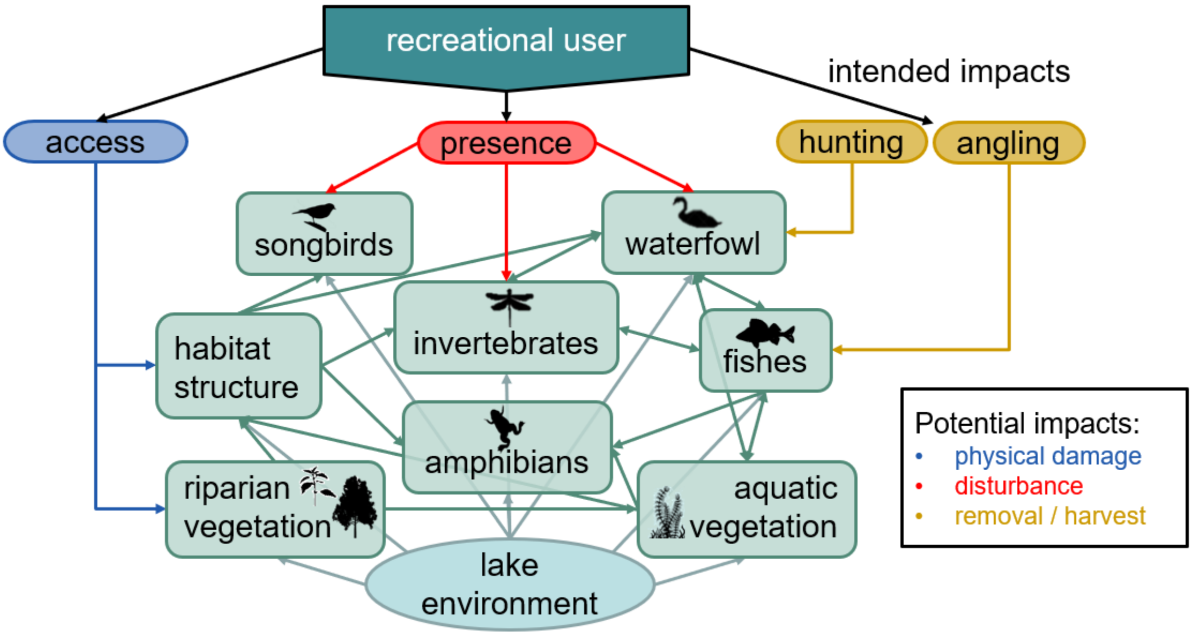


Figure 2: Recreational users can affect wildlife through multiple pathways: 1. Physical damage to riparian vegetation and changes in habitat structure by getting access to the water body (blue), 2. Disturbance of wildlife due to the (human) presence and 3. Removal and harvest as intended impacts of hunting and angling activities which can have indirect effects on non-target organisms.

The focus of the literature about potential ecological impacts of angling is usually on impacts on target organisms (Figure 3). Fishes are usually the main target organism of angling and there is abundant literature about the impacts of angling on fish (Arlinghaus et al., 2007; Buoro et al., 2016; Lewin et al., 2006). The catch and following removal of fishes has impacts on the fish population like altered demographic and size structure or timidity reviewed by Lewin et al. (2006). Although in most cases the intention associated with angling is the harvest of fish, it happens that the caught fish will not be removed from the ecosystem and instead released back into the water (Arlinghaus et al., 2007). This is especially the case if the fish is so small that it was not able to reproduce, yet and it is also suggested to spare very big individuals because these have been shown to be very experienced spawners, which are important for the recruitment of the fish population (Arlinghaus et al., 2007; Gwinn et al., 2015).

Released fish still face the consequences of hooking and handling outside of the water, which was reviewed by Arlinghaus et al. (2007). Release consequences can be either lethal or sublethal. Lethal consequences can again directly impact the fish population. Also, sublethal consequences can affect the population if the fitness of the fish is impaired, while sublethal consequences that only induce stress temporarily do usually not affect the fish population. The fish population can also be affected by management of anglers to maintain a sustainable fish stock. Fish stocking is a common practice to manage the fish stock which can have impacts on the fish population and the species composition of water bodies (e.g. Matern et al., 2022, 2019; Zhao et al., 2016).

Nevertheless, angling can also have impacts on non-target organisms. Angling spots along the shoreline are usually characterized by trampling effects on the soil and the vegetation on land and in the water (O'Toole et al., 2009) and are often associated with habitat modifications (Radomski et al., 2010). The presence of anglers can have disturbance effects on wildlife (Knight et al., 1991; Reichholf, 1988). The altered fish populations and species compositions caused by anglers can also affect other animals through increased or reduced predation pressures (e.g. Hecnar and M'Closkey, 1997) or as prey (Found et al., 2008). Altered fish communities may affect submerged macrophytes, e.g. by the introduction of benthivorous fish that uproot macrophytes (Bajer et al., 2016).

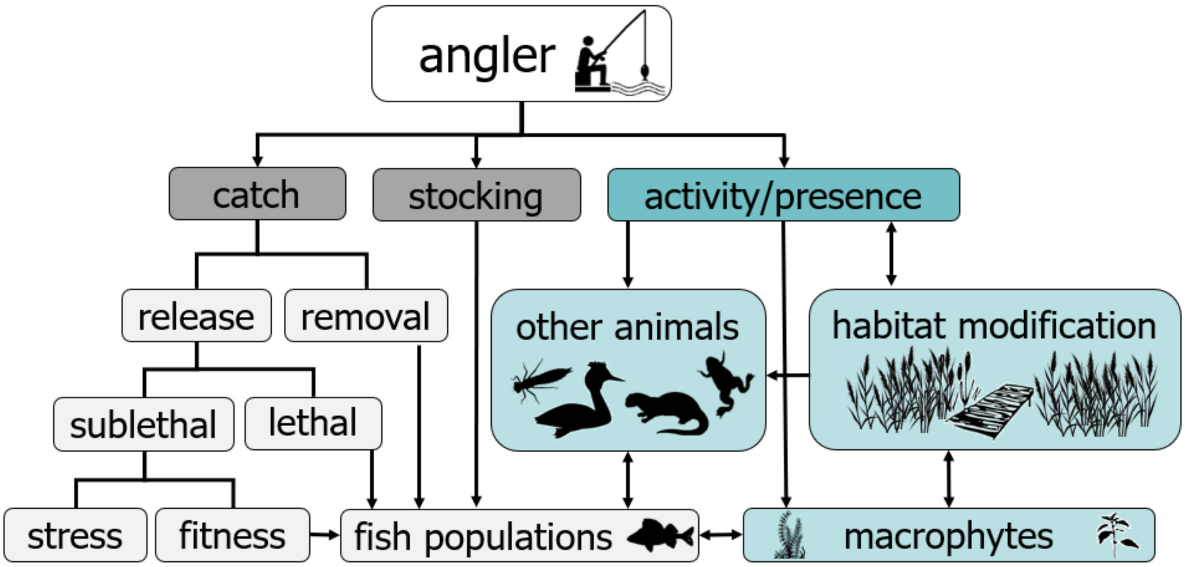


Figure 3: Possible angling impacts: the catch and stocking of fish as target organism are the main impacts of angling. The activity and presence of anglers can also have impacts on non-target organisms. In addition, angling can have indirect impacts through the changes in fish populations, which can cause impacts on other animals and plants.

Ecological impacts caused by recreation on freshwater ecosystems may lead to restrictions of angling and other recreational activities in order to mitigate those impacts (see Chapter 1.2). Nonetheless, it is often not clear what the actual impacts are, because of contradicting scientific findings. While we can find a lot of studies reporting effects on individual level e.g. on vigilance and other behavioral changes there is a knowledge gap on impacts on higher levels of biological organization, especially on community level **(Paper I)**. Therefore, it is not certain, that recreational impacts do necessarily exceed to higher levels of biological organization. In addition, the scientific literature so far has focused on birds, while there is little evidence on other taxonomic groups (**Paper I** and **II**). Although already the possibility of detrimental impacts can justify restrictions according to the precautionary principle (see Chapter 1.2: Legal framework), thorough evidence is needed to find the best solutions, that actually benefit nature conservation at low costs for human well-being.

1.2. Legal framework

There is the necessity to mitigate anthropogenic impacts, as it is already stated in the convention on biological diversity (CBD) by the united Nations in 1992 in Rio de Janeiro. The CBD acknowledges the need of measures to mitigate the impacts of human activities on biodiversity loss even when there is a lack of full scientific certainty about the impacts:

"Reaffirming also that States are responsible for conserving their biological diversity and for using their biological resources in a sustainable manner,
Concerned that biological diversity is being significantly reduced by certain human activities.
Aware of the general lack of information and knowledge regarding biological diversity and of the urgent need to develop scientific, technical and institutional capacities to provide the basic understanding upon which to plan and implement appropriate measures,
Noting that it is vital to anticipate, prevent and attack the causes of significant reduction or loss of biological diversity at source,
Noting also that where there is a threat of significant reduction or loss of biological diversity, lack of full scientific certainty should not be used as a reason for postponing measures to avoid or minimize such a threat."

Therefore, there exist laws to mitigate anthropogenic impacts on biodiversity, as for example the European council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora by the European Union (EU) or the Federal Act for the Protection of Nature (BNatSchG) by Germany to implement measures to protect the nature from anthropogenic impacts. In this thesis I will focus on German law, especially in Lower Saxony and European law, because my empirical studies took place in Lower Saxony, Germany

First of all, public access to the open landscape for recreational purposes is guaranteed for pathways, roads and unoccupied areas by the §59 BNatSchG. The access to forests is clarified in laws of the federal states of Germany and in Lower Saxony §23 NWaldLG permits the access for recreation to all unoccupied landscapes, including forest. In addition, the §25 WHG discusses the common utilization ('*Gemeingebrauch*' in German), which permits the use of water bodies to the public. Still, there exist also restrictions of public access and recreational uses in order to mitigate detrimental impacts on nature, because §59 BNatSchG also says that public access can be restricted for strong reasons, e.g. nature conservation.

In German law we can find general restrictions, e.g. that it is forbidden to harm, disturb or catch wild living animals, and to take or damage wild living plants without reasonable cause (§39, Abs 1 BNatschG, Germany). Although these laws are general prohibitions, there also exist exceptions, like for hunt and fisheries, for which licenses have to be obtained that include proper training and for which also specified laws exist (BJagdG and for Fisheries each German federal state has its own Fisheries Law e.g. §57 Nds FischG, Lower Saxony). While in general wild animals are ownerless by german law (§960 BGB), the fishing rights are bound to the ownership of a water body (§1, (2) Nds FischG, Germany). The fishing rights are coupled with the obligation to nurture and manage the water body in order to maintain a sustainable fish stock (e.g. §1, §40 Nds FischG, Germany). The management is bound to the codes of good practice (Lewin et al., 2010) and there exist general and local angling and harvest restrictions about the legal size, closed seasons and protected spawning areas by the federal state fisheries laws or installed by angling clubs. In many industrialized countries, fishing in inland waters is mainly performed by recreational fisheries, especially anglers, whereas commercial fisheries are of minor importance (Arlinghaus et al., 2002; Cooke et al., 2015). Fishing rights are usually sold to angling clubs and angling associations (Arlinghaus et al., 2002; Daedlow et al., 2011). Anglers need a public angling license from the state authorities that is pending an examination and additionally a private angling permit from the fishing rights holder (Daedlow et al., 2011). Due to these responsibilities, training and engagement to "their" water bodies anglers can be environmental stewardships of aquatic ecosystems (Shephard et al., 2023).

Possible measures to mitigate anthropogenic impacts can be spatial and/or temporal restrictions of these threatening activities. Spatial restrictions can be effective to protect very sensitive areas - areas that inhabit threatened species or biodiversity hot spots. Biotopes that are protected by German law are for example natural or nearly natural areas of lentic and lotic inland waterbodies including their shorelines and all actions that could severely affect these biotopes are prohibited (§30 (2) BNatSchG, Germany). The designation of nature reserves is also a measure with spatial restrictions (§23 BNatSchG, Germany). All actions that that lead to damage or change and severe disturbance are prohibited in the nature reserve and its conservation aims (§23 (2) BNatSchG, Germany). These conservation aims are individually determined depending on the worthiness of the respective area, ergo the present species and biotopes and the naturalness of the area. Therefore, in each case we can find different restrictions. Usually the public should have access to nature reserves, if this is not in contradiction with the conservation objectives of the nature reserve (§23 (2) BNatSchG, Germany), but the access can be restricted to pathways (§ 16 (2) NNatSchG). Certain recreational activities, e.g. camping and campfires can be forbidden completely (e.g. §4, VO NSG Elligastwiesen Germany). Usually exemptions of all or certain prohibitions are made for fisheries and hunting together with forestry, agriculture and maintenance work (e.g. §4, VO NSG Domäne Stolzenau/Leese and §4, VO NSG Untere Allerniederung im Landkreis Verden, Germany). Within the nature reserve there can also be spatial and/or temporal restrictions, e.g. angling and hunting in the flooding area of the river Aller from 1. November till 31. March (§4 VO NSG Untere Allerniederung im Landkreis Verden, Germany). There exist multiple other types of protected areas in the German law (§20 - §30 BNatSchG, Germany), but another example of spatial zoning are National parks. These usually protect a large area, with different protection status (Von Ruschkowski and Mayer, 2011). The core zone is usually the area with the highest protection status with the objective of process conservation and public access is very limited (Chen et al., 2024; Stoll-Kleemann, 2001; Von Ruschkowski and Mayer, 2011). Another example of spatial restrictions regarding fisheries is the § 43 and §53 Nds. FischG that states that the authorities can designate protected areas in fish spawning ground or overwintering habitats and in many cases angling clubs themselves install protected (spawning) areas in their water bodies (Nikolaus et al., 2022).

Temporal restrictions are a measure to mitigate impacts during sensitive seasons. Usually the reproductive, rearing, overwintering, moulting and migratory periods of animals are seen as such sensitive periods and it is in general not allowed to disturb protected species and bird species during these sensitive periods (§44 (1) Nr.2 BNatSchG, Germany). Also hunting is prohibited during the breeding season of wildlife §22 (4) BJagdG (Germany) and there also exist closed seasons for fisheries for many species (§53 (1) Nr.1, Nds. FischG). It is also not allowed to cut reed from 1. March until 30. September §39 (5), Nr.3 BNatSchG). The obligation to put dogs on leash during the breeding season from 1. April until 15. July (§33 (1) NWaldLG) in Lower Saxony (and in some other German federal states) is another example of temporal restrictions.

According to the German law (BNatSchG §23 (2)) already the possibility of destruction, damage, change of the nature reserve or its elements or sustained disturbance that could be caused by an activity is sufficient to prohibit these activities. This is in line with the precautionary principle in environmental law (e.g. CBD 1992). On the other hand, there is also debate about the relevance (in German '*Erheblichkeit'*) of disturbance effects (Stock et al., 1994), which can be seen in the already mentioned §44 (1) BNagSchG, that particularly protected species should not be disturbed 'relevantly'. In the next sentence the §44 explains that a relevant disturbance is given, when the conservation status of the local population of a particularly protected species is impaired. This means that the focus regarding the relevance of a disturbance is on the population level. The conservation status of the local population is not impaired if displaced individuals can find alternative habitats and if possible breeding failures can be compensated by increased breeding success in the following seasons (OVG Lüneburg, 2016). Impact on the individual level should therefore be negligible, as long as impacts on individual fitness (reproduction and mortality) do not exceed to significant and long lasting impacts on the whole population (LANA, 2010). Disturbances or even the death of single Individuals, caused for example by discarded fishing line in which a bird of a particularly protected species gets entangled, may in such a case not be considered as relevant. This applies especially for common and widely spread species (LANA, 2010). Nevertheless, the LANA (2010) further explains that in case of generally very rare species with low population sizes a relevant adverse effect can already occur if the fertility, breeding success or probability of survival of single individuals is impaired or at risk. Still, it is clear that individual fitness effects are meant, which exceed effects on vigilance and flight reactions.

However, it is debatable if this approach is practicable and a proportional mean. If we again consider the example from above, there will always be the chance, that fishing line, which gets entangled in vegetation will litter the environment and poses the risk, that a particularly protected species could get entangled in it and die. Pühringer (2011) has found a dead Eurasian Eagle-Owl (*Bubo bubo*) entangled in fishing line and an Eurasian Bittern *(Botauris stellaris)* with a fishing lure and hook in its beak. The Eurasian Bittern died after it was tried to remove the hook by surgery. These are tragic examples of how (angling) litter can cause deaths of rare and protected species, because especially *B. stellaris* is a rare species, with a small population in Germany (950-1100 Individuals 2005-2009) and a decreasing population trend (Grüneberg et al., 2015).

The logic consequence would be to prohibit angling as a whole to mitigate the impacts, because the Eurasian Bittern is a migrating species, which means this could happen anywhere along its migration route. In practice this would not be a proportional mean for anglers on the one hand, on the other hand the entanglement in fishing line of wildlife in general and especially of highly threatened and rare species does probably not occur very often (Ryan, 2018) and is therefore not one of the main threats of these species.

Habitat loss and simplification, pollution, invasive species and climate change are the main threats for aquatic biodiversity (Reid et al., 2019). As habitat loss is in general in all realms the main threat for biodiversity (Caro et al., 2022). Consequently, nature conservation has developed from the protection of single species to the protection of habitats. For example the Council Directive 92/43/EEC also known as 'habitats directive' does not only include lists of species, but also a list of habitats to be protected in the annexes: Annex I covers natural habitat types whose conservation requires the designation of special areas of conservation, Annex II covers species whose conservation requires the designation of special areas of conservation, Annex III species in need of strict protection, Annex IV species whose taking in the wild and exploitation may be subject to management measures. This List of annexes showes that the focus of conservation shifts to habitat conservation by e.g. installing protected areas for certain habitat types and species. The Habitat directive clarifies that all species and habitats of these mentioned annexes should be in a favourable conservation status, which is defined in Article 1 for habitat as:

"*its natural range and areas it covers within that range are stable or increasing, and the specific structure and functions which are necessary for its long-term maintenance exist and are likely to continue to exist for the foreseeable future, and the conservation status of its typical species is favourable as defined"*

and for species as:

"*population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis."*.

This definition also shows that although species conservation is still important, even there the focus is in the conservation and provision of suitable habitat for these species. The definition also clarifies that in the habitat directive the population level is of importance regarding the species, while impacts on individual level are ignored in the definition of the conservation status.

In the end it is always a case by case decision, if an impact is seen as relevant and should be mitigated with adequate measures, which depends on which species is affected (§44 (1) BNagSchG) and its local conservation status. It is also of importance if a protected area might be affected and which kind of protected area, because according to §23 BNatSchG conservation areas can be accessible to the public if the conservation aim of the respective conservation area permits it and actions that cause long-lasting disturbances should be prohibited. While clear definitions for the habitats directive exist, we do not find clear definitions for each conservation area, which disturbances are seen as relevant. Therefore, case by case decisions have to be made by the authorities. In some cases, disturbances are defined as relevant only if the population level is affected (e.g. BVerwG 9 A 14.07, judgement 09.07.2008; OVG Lüneburg 4 LC 156/14, judgement 1.12.2015) in other cases already the possibility of disturbances is seen as relevant, because of the precautionary principle (e.g. VGH Kassel 4 C 328/16.N, judgement 9.3.2017; OVG Niedersachsen 4 KN 343/15, judgement 19.04.2018).

The impacts of recreational activities as additional threat to biodiversity by disturbance effects or habitat modifications need to be identified and quantified. Proper measures and solutions are necessary to conserve nature and protect biodiversity, while avoiding high costs for human well-being. Therefore, scientific evidence is needed to compare recreational impacts to other threats and environmental impacts on biodiversity and facilitate decision making depending on the conservation objectives case by case.

2. Objectives, Dissertation Structure, and Research Questions

The aim of this dissertation was to deepen the knowledge about ecological impacts of water-based recreational activities on freshwater ecosystems. A key aspect was to identify angling impacts on multiple freshwater taxa and across organizational levels and to compare the magnitude of the effects to the impacts of other recreational activities. The overall aim of this thesis was then to discuss possible management applications to mitigate recreational impacts on freshwater biodiversity. To do this I followed a framework outlined in Figure 4:

First, I conducted a literature synthesis with a comprehensive global meta-analysis in **Paper I** with the objective to examine the existing evidence, in which we compared the magnitude of angling impacts to the magnitude of ecological impacts of other recreational activities. In **Paper II** we reviewed the impacts of shore-bound and swimming activities. Both papers focused on the question on which level of biological organization the effects were observed and if the effects exceed from individual level to higher levels of biological organization. I conducted three empirical studies in gravel pit lakes in lower Saxony in Germany. I examined local effects of angling and other recreational impacts in **Paper III** and the impacts of angler management in **Paper IV** in which we compared the biodiversity of multiple taxa in angler managed and unmanaged gravel pit lakes. In **Paper V** we assessed spatial zoning as possible solution to harmonize angling and biodiversity. We examined the effect of protected zones installed by angling clubs in order to foster the fish population. We tested if these protected zones might also benefit other taxa.

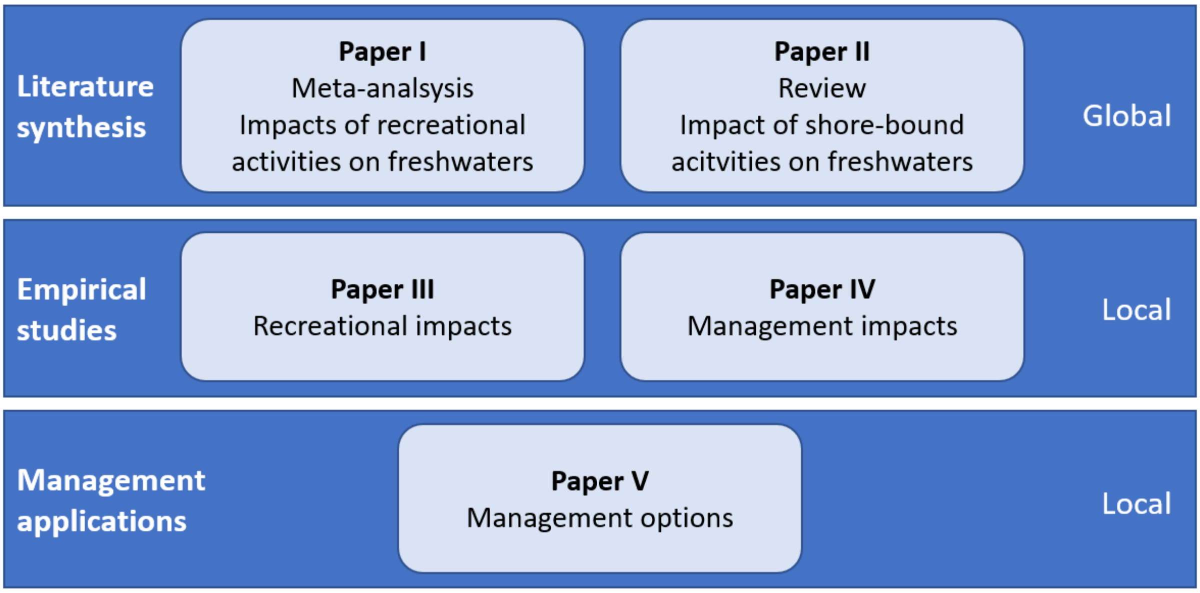


Figure 4: Conceptual outline of the dissertation structure with the Papers to identify and compare the ecological impacts on different components of freshwater biodiversity of angling and other recreational activities on a global and a local scale and possible management implications.

With these five Papers I want to answer the following research questions:

- What are the ecological impacts of angling and other recreational activities (**Paper I, II, III, IV**)?
- Are there angling specific impacts or is the presence of humans in general of more importance regarding disturbance impacts (**Paper I, III, IV**)?
- Do recreational impacts exceed effects on individual level to higher levels of biological organization - population, community and ecosystem level (**Paper I-V**)?
- Which taxonomic groups are most affected by recreational impacts (**Paper I-V**)?
- How severe are recreational impacts on biodiversity compared to other aspects/environmental conditions (**Paper III, IV**)?
- Is spatial zoning a management option to mitigate recreational impacts? Do protected riparian areas benefit fish and other taxa? (**Paper V**)

3. Methodological Overview

3.1. Systematic literature research

We conducted a systematic literature search **for Paper I and II** from November 2018 until February 2019, following the guidelines for systematic research by Siddaway et al. (2019). We searched both peer-reviewed and grey literature in different languages to compile the best available evidence base. We constructed a search term containing synonyms for recreation AND aquatic AND impacts AND environment. The full search term is shown in the supplemental material of **Paper I**. We adapted the search terms for seven different literature databases and yielded 13,115 articles. After removing duplicates, 11,919 articles were left for in-depth screening. An additional 1,884 references were obtained from reference lists of acquired full-text articles.

3.1.1. Screening and exclusion criteria

By screening titles, abstracts and full texts we excluded articles that did not study (1) impacts of recreational activities, (2) impacts on other systems than aquatic ecosystems, (3) impacts that were not ecological. In addition, we excluded articles of other languages than English, German, French or Spanish as these were not accessible to the authors. The following studies were retained: (1) studies that compared organism/ecosystem responses to the presence of recreational activities (impact) vs. lack of the recreational activity (control), (2) studies that compared organism/ecosystem responses to different intensities of a recreational activity (observational study), (3) organism/ecosystem responses to a specific compound/substance/aspect that is associated with a specific recreational activity compared to a control within an experiment in situ or in mesocosms. After in-depth text retrieval, further studies were excluded providing only aggregated information for multiple recreational activities. Another 141 articles had to be excluded because effect size estimation was not possible due to lacking control/comparator or missing data that could not be retrieved by contacting authors. The final meta-analysis was done on 94 articles from which effect sizes were derived.

The activities analyzed in **Paper II** include biking, relaxing at the shore, nature observation, swimming, snorkelling, scuba diving and walking on land or in the water. Literature about consumptive activities (e.g. angling and hunting) and boating activities were excluded. This selection yielded 445 publications. After full-text screening we excluded papers for the following reasons: from marine environments, no reference to specific activities or laboratory studies, reporting cumulative effects from several activities, no reference to impacts and reviews. The main analysis of **Paper II** consists of 26 publications. The information provided by the retrieved papers was manually extracted and saved in a standardized form similar to **Paper I** (details **in Paper II**).

3.1.2. Data extraction

Data from the 94 articles that met inclusion criteria for **Paper I** were extracted by three trained Researchers from tables, results and figures to calculate effect sizes. Every article was reassessed by the first author of **Paper I** to ensure a uniform coding procedure and comparability between effect sizes of extracted values and coded categories. We conducted a meta-analysis with four categories of water-based recreational activities characterized by increasing interaction with water, following a gradient from shore to open water: (1) shore activities with (almost) no direct interaction with water (walking, dog walking, biking, horse riding, picnicking, camping, hunting, wildlife viewing), (2) shoreline recreational angling with direct interaction with water, but the activity itself situated at the shoreline, (3) swimming which has direct interaction with water but predominantly occurs in the nearshore zone, often combined with shoreline stays (including swimming, snorkelling and diving), (4) boating as an (almost) exclusively open water activity (including motor boating, jet skiing, water skiing, sailing, rowing, paddling, kite surfing, wind surfing, stand up paddling and boat angling).

3.1.3. Statistical analysis

To quantify ecological response to impacts of recreational activities in **Paper I**, we used a measure for standardized mean differences Hedge's g (Borenstein et al., 2011). An effect size of zero would indicate no effect. The further away from zero, the larger the effect. Effect sizes were coded so that negative values indicate negative ecological impacts and positive values show positive impacts (details in **Paper I**).

To compare the magnitude of effect for different categories, e.g. recreational activities, levels of biological organization and taxonomic groups, we calculated summary effect sizes for subgroups of the dataset by using multilevel modelling in R (R4.0.5, R Core Team, 2017). We took dependencies among effect sizes within one study into account by using multilevel models with not only study, but also species and response measure (nested within each other: random = ~ 1 | Study_ID/taxa/Response.measured) to calculate mean effect sizes over multiple studies. We performed multi-level meta-analysis using the function ma.rmv (metafor package (Viechtbauer, 2010)). We analysed the possible influences of moderators as confounding factors such as publication type, peer review, year of publication, study design, habitat type, taxa and type of water body (lentic or lotic) with multilevel metaregression models with analysis of variance (Q-test), which is an approach to explain heterogeneity in effect sizes (Borenstein et al., 2011).

We originally aimed to identify studies that compared the ecological impacts of recreational activities relative to controls lacking recreational activities. Yet, many studies lacked controls. Therefore, we included studies comparing low and high impacts sites, thereby testing for the impact of recreational uses intensity. We compared the summary effect sizes of these two different approaches to examine the effect of an increase in the intensity of each recreational activity.

To calculate summary effect sizes in meta-analysis each effect size from the original studies is usually weighted by inverse variance or by a measure of study quality (Borenstein et al., 2011). As sample size was often obscured by pseudo replication in original studies, inverse variance was not an appropriate measure of weighting in our case. Instead, we weighted the effect sizes by a quantitative measure of study validity. Following suggestions by Norris et al. (2012) and Christie et al. (2019), we assessed study validity by eight criteria to obtain weights for each single effect size. Details of the weighting procedure are given in **Paper I**. To assess sensitivity regarding the weights by study quality, we compared summary effect sizes per recreational activity weighted by the inverse variance to the summary effects weighed by our quantitative study validity weight. In addition, we used a qualitative study validity measure to examine differences between low, medium and high validity studies. We assigned every validity measure to a predefined criterion for low, medium (if possible) and high validity (details in **Paper I**). A study was given a low overall validity if it scored ‘low’ in one or more criteria. If a study scored ‘high’ in each of the criteria it was given a high validity. All other left-over studies, that did not score ‘low’ in any of the criteria, were given a medium validity.

3.1.4. Publication bias

Studies with significant results and therefore large effects are more likely to be published (Kvarven et al., 2020), and this publication bias can influence the summary effect size of meta-analyses (Kvarven et al., 2020). To test if publication bias might affect results, we performed Egger's regression test (Egger et al., 1997) to assess if a relationship between effect size and the variance of effect size was present in the four subgroups of recreational activities. In addition, we used fail-safe *n* (fsn function in metafor package) as a second measure to detect publication bias. It indicates the number of studies/effect sizes needed to reduce the significance level of the summary effect size. The fail-safe number is considered robust when it is greater than 5k+10, were k is the number of effect sizes (Rosenthal, 1979).

3.2. Empirical studies

Paper III, IV and **V** were empirical studies all conducted in Lower Saxony at gravel pit lakes.

3.2.1. Study site and lake selection

The studies of **Paper III, IV** and **V** were conducted in the Central Plain ecoregion of Lower Saxony in north-western Germany (Figure 5), where natural lentic waters are scarce. Of 35,048 ha of total standing waters in Lower Saxony, 73 % by area and more than 99 % by number are potentially artificial lakes. These artificial water bodies consist mainly of ponds and small gravel pit lakes with a surface area of less than 10 ha (Cyrus et al., 2020).

Artificially created aquatic habitats, such as gravel pit lakes or ponds, could maintain and increase native freshwater biodiversity by providing refuge and secondary habitats for rare or endangered species (Damnjanović et al., 2019; Oertli, 2018). The origins of artificial lake ecosystems are often relatively recent (less than 100 years of age; Zhao et al., 2016), where artificial lakes are often created by mining for mineral resources (Saulnier-Talbot and Lavoie, 2018). The resulting numerous artificial lakes (for simplicity henceforth referred to as 'gravel pit lakes') have become common elements in many cultural landscapes across the industrialized world (Oertli, 2018).

Most gravel pit lakes in Lower Saxony, and in Germany as a whole, are managed for recreational fisheries by angler associations and clubs. These lakes are thus exposed to regular stocking with species of fisheries interest, and are subject to access and harvest rules, regular controls by fisheries inspectors, and fishing club activities, such as collecting litter and the cleaning and development of the littoral zone (Arlinghaus et al., 2017). In **Paper IV** a set of gravel pit lakes managed by recreational fisheries (defined as managed lakes) was selected and compared with another set of gravel pit lakes not experiencing any form of legal angling and recreational fishing-related management (defined as unmanaged lakes; Table 1). Managed lakes were identified through a survey of all organized angling clubs in the Angler Association of Lower Saxony. Lakes were selected according to the following criteria: the lake was of small size (1–20 ha), and had not been dredged in the last 10 years ('old age'). Gravel pits not managed by anglers were identified in close vicinity to the managed lakes, where possible.

For the study in **Paper III** we used the sample of lakes with and without recreational fisheries of **Paper IV** and strategically added lakes with specific, potentially outstanding recreational human 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 (Table 1). 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.

For the study in **Paper V** we took a subsample of the lakes of **Paper III**, which included only the lakes that had a no-fishing zone assigned by the angling club with signs indicating the fishing ban and, in some cases, also a trespassing ban. The fishing clubs had to have voluntarily assigned parts of riparian zones at their lakes that are not allowed to be accessed from the bank or by boat to fish in or from outside the area. The protected areas were typically placed at known or suspected fish breeding grounds or were otherwise largely inaccessible to the public. The access restrictions typically also applied to other recreational users, which was indicated by signposts at the lake shoreline.

Table 1: Overview and description of lake categories with sample size for each of the empirical Papers III, IV and V.

Study	Lake categories	uses	N
Paper III	control	control lakes with no use	6
	O	no angling but other usage	6
	A	angling use only	6
	AO	angling and other uses combined (no boating)	16
	AOB	recreation lakes with high use intensities including angling, other activities as well as camping, boating, waterskiing or windsurfing	5
Paper IV	managed	lakes managed by recreational fisheries	16
	unmanaged	lakes not experiencing any form of legal angling and recreational fishing-related management	10
Paper V		Lakes managed for recreational fisheries, with a no-fishing zone assigned by the angling club with signs indicating the fishing ban and, in some cases, also a trespassing ban.	15

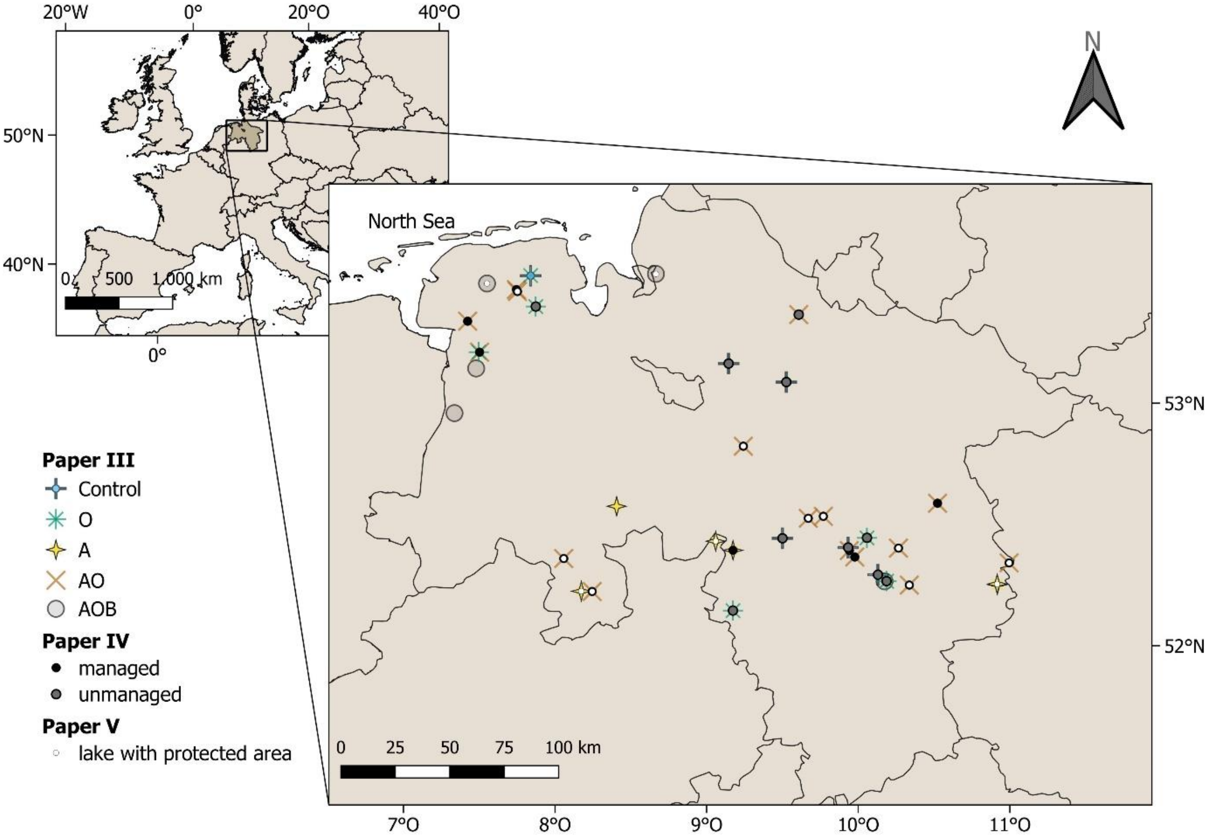


Figure 5: Map of all sampled gravel pit lakes in Lower Saxony

3.2.2. Biodiversity sampling

In **Paper III and IV** we investigated species richness, Simpson Index, the number of endangered species, and the conservation value (the latter only in Paper IV) across multiple taxa ranging from non-mobile (plants), predation-sensitive (amphibians and odonata) to mobile taxa (fish and birds). Particularly, we also included waterfowl and songbirds as these groups are prominent in conservation conflicts associated with recreation. Fish were included as angling and associated stocking might directly and indirectly affect their species richness and density (Cyrus et al., 2020; Matern et al., 2019). Lake biodiversity data were collected using the same methods in **Paper III, IV and V** and comprised birds (waterfowl and songbirds, Odonata (dragonflies and damselflies), amphibians, fishes (only **Paper III and V**), aquatic macrophytes, riparian vegetation (herbs and trees). The methods are schematically visualized in Figure 6 and in detail described in **Paper IV** (except fishes, see Matern et al., 2019). Waterfowl species were identified (Dierschke, 2016; Svensson et al., 2017) 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. 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 x 23 cm x 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 larger than 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^2 plots. Trees taller than 2 m were identified and counted along these transects, and herbs were assessed within the 1 m^2-plots.

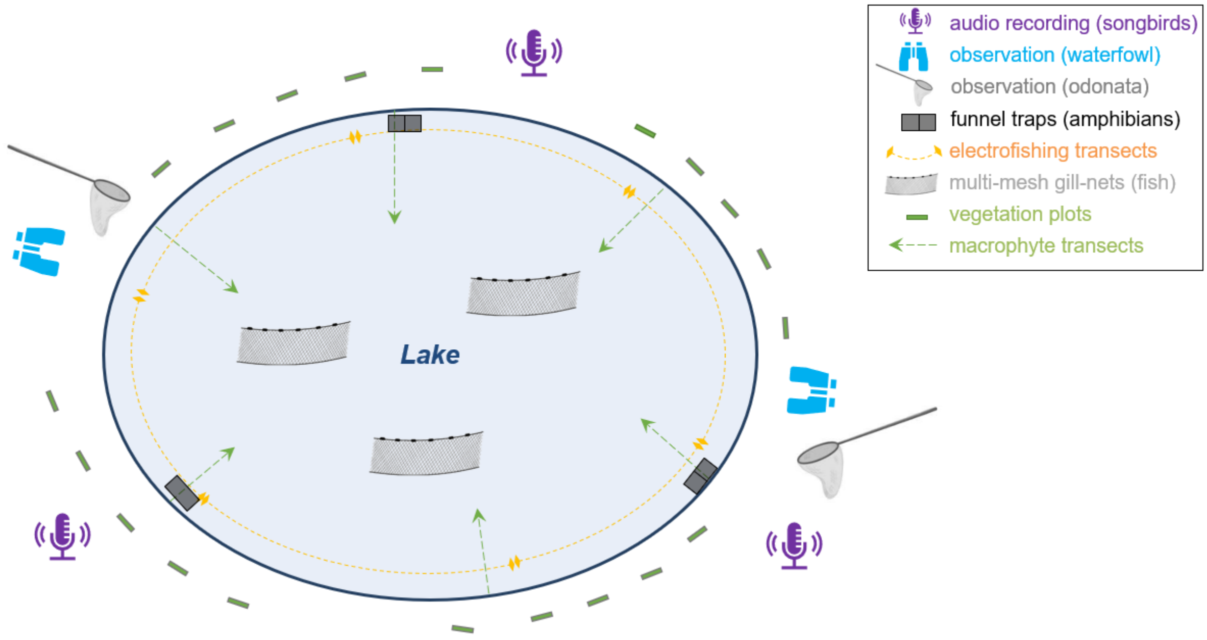


Figure 6: Schematic visualization of the biodiversity sampling. Adapted from Paper III and V.

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 Simpson Index (Pielou, 1969), also called "dominance index", which summarizes species richness and dominance. The inverse Simpson Index (D), i.e. the reciprocal of the Simpson Index, ranges from one in lakes with only one species to infinite in lakes with all individuals belonging to different species. The Simpson 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 (www.rote-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, CPUE of gill-nets (as number of individuals per 100 m^2 net area) was considered, too. We additionally estimated the biomass of fish per lake using the total biomass per unit effort (BPUE) of gill-nets (g per 100 m^2). 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 other taxonomic groups (Trovillion et al., 2023). Lake's submerged macrophyte coverage was calculated by extrapolating the transect-based macrophyte sampling based on single depth strata. The share of the shoreline that was covered with reed (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.

To weight rare and threatened species more heavily in **Paper IV** an index of taxonspecific conservation value for the study region was estimated following Oertli et al. (2002). To that end, each species was ranked according to its threat status on the Red Lists of Lower Saxony (Altmüller and Clausnitzer, 2010; Garve, 2004; Korsch et al., 2013; Krüger and Nipkow, 2015; Podloucky and Fischer, 2013). Species of Least Concern were ranked lowest: c(0) = 20 = 1. All species classified with an increasing threat status category r according to the regional Red List were weighted exponentially more strongly following Oertli et al. (2002). The conservation index value increases with more species of a given taxon being threatened or rare.

To test for differences in species composition across all lakes in **Paper IV**, the pooled species inventory by lake type (managed and unmanaged) was used, and the Sørensen index (Sørensen, 1948) as a measure of community similarity was calculated. As an indicator for whether species compositions are substantially (i.e. biologically meaningfully) different or not, so called ‘faunal breaks’ as well as ‘floral breaks’ were searched for. Following Matthews (1986), faunal or floral breaks among lake types were assumed to occur when the Sørensen index was < 0.5.

In **Paper V** we additionally determined an abundance-weighted (i.e. coverage-weighted) sensitivity value (Sveg) of the community for each vegetation plot, based on species-specific trampling tolerance (Briemle et al., 2002; Ellenberg, 1952) ranging from 1 (intolerant to trampling) to 9 (very tolerant to trampling). Using the species-specific flight initiation distances (FIDs, extracted from Garniel and Mierwald, 2010; and from Krüger, 2016), an abundance-weighted FID value was calculated in **Paper V** for each lake for the community of songbirds and waterfowl, respectively.

3.2.3. Environmental variables

We assessed multiple environmental variables to control for confounding factors such as lake morphology, water quality and land use in the analyses of **Paper III, IV and IV**. Data were collected using the methods described in detail in **Paper IV**. 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®land use classes (© GeoBasis-DE/BKG 2013, AdV – Working Committee of the Surveying Authorities of the States of the Federal, 2006): agricultural land, forest, urban, mining, wetland, water bodies and other, in QGIS 3.4.1 with GRASS 7.4.2 on a 10 × 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).

In **Paper V** we also assessed habitat quality using the plot design and protocol of Kaufmann and Whittier (1997) and calculated the indices following Kaufmann et al. (2014a) for each plot. The Lakeshore Physical Habitat Quality Index was calculated, which is composed of several individual indices (Kaufmann et al., 2014b): The Lakeshore Anthropogenic Disturbance Index, the Riparian Vegetation Cover Complexity Index and the Littoral Cover Complexity Index. In addition, the extent of different shoreline structures was visually determined for each electrofishing transect for **Paper V**. We differentiated the extent (in percentage of transect length) of woody (e.g. branches, trees, roots, deadwood) and plant (reeds, submerged or floating aquatic macrophytes, shoreline herbal vegetation) structures in the littoral and the riparian part of the shoreline (see also Matern et al., 2022).

3.2.4. Recreational use

Recreational use was assessed for **Paper III, IV and V** as described in detail in **Paper IV** during each site visit. Recreational uses were counted and classified into classes: 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 access points and in seemingly undisturbed reference points. 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 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 the same year (2019) for **Paper III**, using a roving creel approach and a stratified random sample design described in detail by Malvestuto (1983), Pollock (1994) and in **Paper III**. The roving creel approach comprised a stratified design with twelve fixed dates as primary sampling units evenly allocated to weekdays and weekend days and two time shifts, morning (10 am - 2 pm) and afternoon (2 - 6 pm) as secondary sampling unit. Each sampling day consisted of four instantaneous counts (Hoenig et al., 1993), with each count being approximately one hour apart from the next (e.g. at 10 am, 11 am, 12 am and 13 am).

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 non-standardized counts during our on-site visits with GLMMs, 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). Thereby, we were able to infer recreational intensity from the non-standardized observations also for the seven lakes which lacked a standardized visitor counts.

3.2.5. Modelling Biodiversity measures

In **Paper III** and **Paper IV** the impact of recreational activities and the presence of recreational fisheries management on aquatic and riparian biodiversity was tested in two steps: First univariate comparisons of biodiversity metrics among lake types and second multivariate analyses with environmental variables as confounders. To prevent covariance among environmental variables in the multivariate models in **Paper III, IV and V**, before each analysis we performed dimension reduction with PCA and the variance inflation factors (VIF, Neter et al., 1996) for all variables was calculated.

For the univariate comparisons in **Paper III** 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 and Hochberg, 1995).

For the univariate comparisons in **Paper IV** the impact of the presence of recreational fisheries management on taxon-specific species richness, Simpson diversity index, richness of threatened species, conservation value between lake types (managed and unmanaged gravel pits) were assessed using the Student's *t*-test (in cases of variance homogeneity) or Welch's *F*-test (in cases of variance heterogeneity) whenever the error term was normally distributed (Shapiro–Wilk-test). Otherwise, a Mann– Whitney *U*-test of median differences was used.

Multivariate regression analysis in **Paper III** 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 are described in detail in **Paper III**. 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 and 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).

In the multivariate analysis of **Paper IV** a multivariate redundancy analysis (RDA) was conducted to examine whether recreational fisheries management explained variation in environmental variables or in species richness across multiple taxa in the multivariate space. In addition to lake type, all relevant environmental variables (e.g. trophic state, surface area/steepness, land use, riparian/littoral habitat structure, water chemistry), intensity of recreational use (non-standardized counts), gravel pit age, and catchment were included in the multivariate analysis of species richness. With the RDA, a forward selection process (Blanchet et al., 2008) was used to identify the environmental predictors that explained the most variance in species richness across different taxa and lakes, including management as a key variable of interest in this study. Using the variance inflation factor (VIF, Neter et al., 1996), correlated environmental variables were removed before model building. All data were scaled and centered (transformed to z-values) before analysis. The degree of explanation was expressed using the adjusted coefficient of multiple determinations (R^2 adj). Variables significantly explaining variation in richness across lakes were also assessed using analysis of variance (ANOVA) at a significance level of $P < 0.05$. All calculations and analyses were carried out in R 3.5.1 using the VEGAN package (Oksanen et al., 2018; R Core Team, 2013).

In **Paper V** the Lakeshore Anthropogenic Disturbance Index, the Riparian Vegetation Cover Complexity Index and the Littoral Cover Complexity Index, the sensitivity value per riparian vegetation plot, cover of submerged macrophytes, cover of the reed zone (i.e. emergent macrophytes), all fish, small fish (length < 10 cm), large fish (length > 20 cm for most species, see **Paper V** for exceptions) were analyzed in linear mixed-effects models by using the package “glmmTMB” in R with lake identity as random effect (Brooks et al., 2017; R Core Team, 2021). We tested whether the indices were different between plots within protected areas and outside them, while controlling for the other lake environment using the PC-scores. For the count data of fish abundance, we modeled a negative binomial distribution of the response variables and the length of each transect was considered as offset in the models to account for different fishing effort (i.e., relative abundance). We analyzed the effect of the protected zone extension (as proportion of total shoreline) on FID values of birds. For waterfowl we included a random effect of season and lake in the model.

4. Key findings and discussion

In this section I will present what my thesis adds to the existing evidence. First, I will discuss the existing evidence regarding the topic, before I present and discuss the respective key findings of the five Papers of my thesis.

4.1. Impacts of presence and intensity of recreational activities on freshwater ecosystems

The presence of recreational activities at freshwater ecosystems can have negative ecological impacts due to the creation of access to the shore and trails, introduction of new (invasive) species and the human presence with disturbance of wildlife and shoreline habitats (Venohr et al., 2018). Recreational uses such as walking, angling and boating impair riparian habitats , e .g by the establishment of fishing and spots and beaches for swimming (Brauns et al., 2007; O'Toole et al., 2009) or general access to the water (Meyer et al., 2023) and thereby impact littoral plants (Bonanno et al., 1998; Meyer et al., 2023; O'Toole et al., 2009) or invertebrates (Brauns et al., 2007; Meyer et al., 2021; Spyra and Strzelec, 2019; Wolter and Arlinghaus, 2003). Nutrient inputs due to feeding of waterfowl or fish, also to attract fish for angling purposes, feces of bathers or resuspension of sediments by boating can accelerate the eutrophication of water bodies and thereby influence macrophytes and the occurrence of algal blooms (Amaral et al., 2013; Hadwen et al., 2005; Venohr et al., 2018; Yousef et al., 1980). In general human presence can cause disturbance of wildlife especially birds (Dear et al., 2015; Fernández-Juricic et al., 2007; Knight and Knight, 1984; Reichholf, 1988; Wichmann, 2010). Activities that are associated with increased noise and/or speed, as motor boating and kite surfing provoke more disturbance responses than quiet and slow activities, e.g. walking (Krüger, 2016). In the meta-analysis of **Paper I** we also found that boating had the strongest negative effects compared to swimming, shoreline angling and other shore uses, although there were no significant differences between the activities (Figure 7, Figure 8). Also dog walking, which could also be seen as a form of recreation that can cause increased noise (barking) and speed (if dog unleashed and agile), has stronger disturbance effects than humans without dogs (Banks and Bryant, 2007). The study of **Paper III** confirmed that humans with dogs have stronger impacts on biodiversity measures of some taxa than humans per se (Table 2).

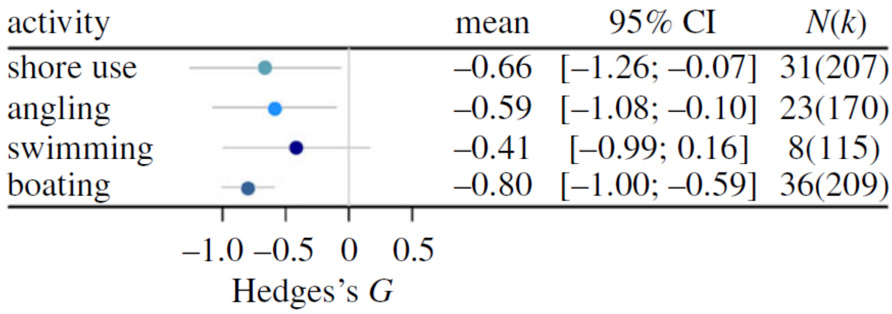


*Figure 7: Forest plot of the meta-analysis in **Paper I** with mean effect sizes of recreational activities. Shown are mean summary effect sizes (mean), 95% confidence intervals (95 % CI), number of studies (N) and number of effect sizes (k). Effects are significant if 95 % CI (horizontal lines) do not overlap the vertical zero line.*

The recreation ecology literature also focusses on another activity: angling is reported to have severe impacts on wildlife, although it is usually an activity which is not associated with increased levels of noise and speed. Long stays of anglers sometimes even at night in sensitive habitats can disturb breeding birds and other wildlife (Knight et al., 1991; Reichholf, 1988). Lost and discarded angling tackle, including baits with hooks, lead shots and fishing line also can have lethal consequences for piscivorous species and other taxa (Franson et al., 2003; Nemoz et al., 2004; Ryan, 2018; Scheuhammer and Norris, 1996; Sears, 1988) more than other forms of litter by non-angler recreationists (Ryan, 2018). Nevertheless, in comparison to other forms of recreation angling did not have stronger impacts than other recreational activities in the meta-analysis of **Paper I** (Figure 7). In fact, impacts of recreational activities seems to depend less on the form of recreation, but on human presence and human use intensity as shown in **Paper I** and **III** (Figure 8, Table 2).

Many studies lack real controls with no uses and instead compare low intensities of recreational use to higher intensities of recreational use (e.g. Bonanno et al., 1998; Keller, 1989; Knight and Knight, 1984; O'Toole et al., 2009; Smith et al., 2019). The ecological impacts of recreational use in general increase with the use intensity (Monz et al., 2013; Venohr et al., 2018). Increases in density and frequency of recreational uses result in higher ecological impacts, e.g. of wildlife disturbance (Lozano and Malo, 2013) and trampling (Bonanno et al., 1998; O'Toole et al., 2009; Seer et al., 2015). Recreational impacts in freshwater quality are more density dependent than in terrestrial environments (Monz et al., 2013). While under some circumstances depending on the recreational activity the presence of the activity can be more important than the intensity, e.g. as found for impacts of paddle boats on macrophytes in the Spreewaldregion (Wegner et al., 2023), the meta-analysis in **Paper I** has shown that the effects of low vs high intensity comparisons were stronger than the effects of comparison of no-use control sites. As we can imagine, one person walking on vegetation, might cause some injuries maybe even the death of few plant individuals. If this single impact is repeated over and over again, not only more plant individuals will be affected by the damage, but also more trampling resistant species might be favored. Intense trampling does in addition cause soil compaction which further limits the growth and species composition of the vegetation or might completely hinder vegetational growth and leave barren soil at highly trampled sites. This example shows, that the intensity of recreational use in general might be more relevant than the presence of certain activities or the presence of humans at all (Figure 8).

In the empirical study of **Paper III** impacts on biodiversity scale with human-use intensity and dog density, but not with angling intensity (Table 2). Nevertheless, the presence of angler management can also lead to an increase of other recreational uses (**Paper IV**), probably due to increased accessibility of the water bodies. As there is usually a combined effect of multiple stressors (Pirotta et al., 2022), in this case of multiple recreational activities at the same water body it is logical that recreational impacts increase with general human use intensities. Although in **Paper IV** angler managed lakes had higher recreational use densities than unmanaged lakes, there were no differences in any of the studied biodiversity metrics.

Recreational fishing often engenders feelings of care and responsibility in anglers, because the sustainable and responsible use of fish populations is essential to maintain their own personal well-being (Löki et al., 2023; Shephard et al., 2023). Fish stocking is a very popular and common practice to achieve that aim to maintain a sustainable fish stock (Klefoth et al., 2023), although fish stocking is often not effective (Buoro et al., 2016; Radinger et al., 2023; Terui et al., 2023) and can have negative impacts on other organisms (Bajer et al., 2016; Buoro et al., 2016; Hecnar and M'Closkey, 1997; Vilizzi et al., 2015). Other management options implemented by anglers to maintain a sustainable fish stock are size limits, bag limits, closed seasons, protected spawning areas and habitat enhancement and some of these measures might also benefit other taxa than fish as target organisms (Arlinghaus et al., 2015). Scale-restricted riparian protected areas voluntarily assigned by recreational fishing clubs can have positive outcomes for habitat quality and biodiversity, particularly by reducing trampling and access to anglers and other recreationists (**Paper V**, Figure 13). It is possible that the management of recreational fisheries and the involvement of angling clubs in environmental stewardship and environmental education mitigates or even outperforms the negative ecological impacts which are caused by the practice of this recreational activity.

Many observational studies try to investigate which single recreational activity or aspect causes ecological impacts. With my thesis I examined what is already known about the ecological impacts and identified knowledge gaps (Table 3). With the empirical studies I was able to broaden the scientific evidence with studies on a whole lake scale with multiple lakes, while many other studies compare sites within the same water body (e.g. Andrés-Abellán et al., 2005; Asplund and Cook, 1997; Bessa et al., 2017; Bonanno et al., 1998; O'Toole et al., 2009; Smith et al., 2019) or compared only very few water bodies (e.g. Keller, 1989; Knight and Knight, 1984; Poiger et al., 2004; Sears, 1988). Nevertheless, also the empirical studies presented in this thesis are observational. Although we included environmental covariates as confounding factors and assessed the intensities and combinations of different recreational activities, the only way to substantiate the correlative evidence presented here is with an experimental BACI study design.

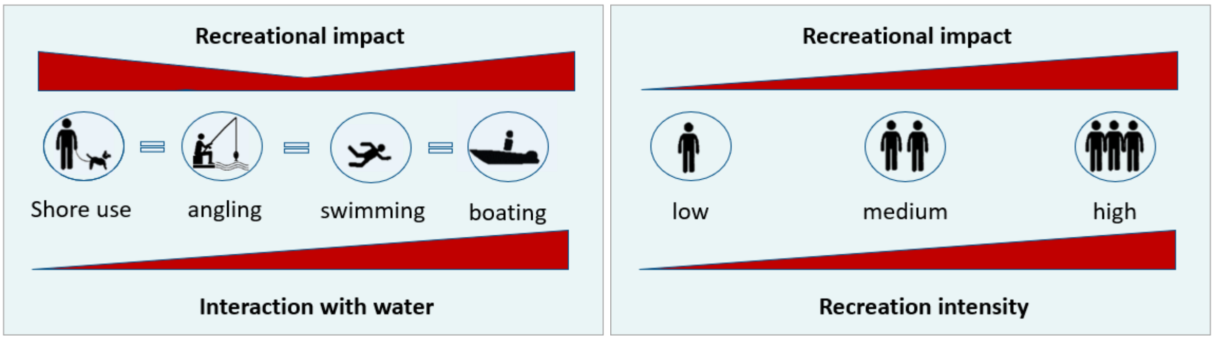


Figure 8: Although boating showed the strongest ecological effects, there were no significant differences between the recreational activities in regard to the magnitude of effects. We observed no increase of effect with increased interaction with water of the respective activity. Human use in general and the use intensity are the main drivers of recreational impacts, while the specific activity itself is of less importance in regard to ecological impacts.

4.2. Impacts of freshwater recreation across levels of biological organization

Ecological impacts affect different levels of biological organization as described in chapter 1.1 and Figure 1. Recreational impacts on individual level include the disturbance of birds and following changes in behavior due to experimental canoeing and shore walking (Fernández-Juricic et al., 2007) and flight responses because of boating (Knight and Knight, 1984), poisoning with UV-screens that cause increased mortality and weight changes in mollusks in the laboratory (Schmitt et al., 2008) or with lead that causes increased lead concentrations in the blood of mute swans (*Cygnus olor*) at gravel pit lakes with recreational angling (Sears, 1988), injuries of turtles with boat propeller strikes (Bulte et al., 2010) or fishhooks (Nemoz et al., 2004) and injuries of individual plants due to boat propellers (Asplund and Cook, 1997). If the impacts on individual level cannot be compensated by other individuals of the population, or by additional broods (Keller, 1989) the impact exceeds to population level which includes changes in abundances and reproductive success, e.g. the number of bird breeding pairs at lakes with and without angling (Völkl, 2010) and the increase of bird nests after the prohibition of angling (Erlinger, 1981). Recreational activities can also affect the community level such as decreased species richness in presence of angling (Reichholf, 1988), or in plants due to trampling (Bonanno et al., 1998), changes in community composition in angler managed ponds (Wood et al., 2001) or at beaches (Brauns et al., 2007) or the introduction of invasive species with boating, diving or fishing gear (Bacela-Spychalska et al., 2013; Jacobs and MacIsaac, 2007). Impacts of recreation on ecosystem level can cause changes of habitats, habitat quality and environmental compartments, such as changes in water quality due to camping (King and Mace, 1974) increased turbidity of the water due to boating (Ailstock et al., 2002) and the contamination of lakes with UV-screens because of swimming (Poiger et al., 2004), the pollution of sediments around boat mooring locations (Ostendorp et al., 2009), littering in the water and at the shore (O'Toole et al., 2009) and soil compaction, decrease of vegetation height and increase of barren area because of trampling (Andrés-Abellán et al., 2005; O'Toole et al., 2009).

While in general, impacts on individual level can be important warnings and understanding of mechanisms, impacts on higher levels of biological organization are ecologically more relevant (Figure 10; Clements, 2000). Although recreational impacts on ecosystem, community and population level are more important than effects at individual level (Buckley, 2013), the scientific literature focusses on recreation effects at individual level (Baas et al., 2020; Buckley, 2013; Buoro et al., 2016). A terrestrial meta-analysis by Bateman and Fleming (2017) about the ecological impacts of tourism concludes that the impacts are overreported, because mainly physiological responses were covered.

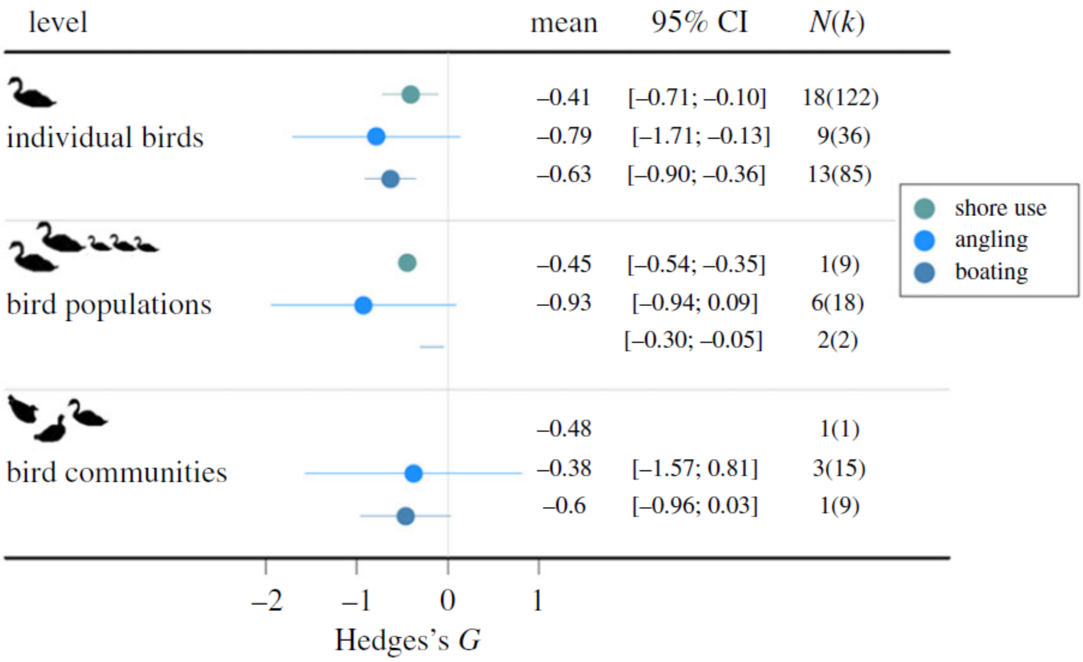


Figure 9: Forest plot of the meta-analysis in ***Paper I*** *with mean effect sizes per level of biological organization of birds (individual birds, bird populations and bird communities) and per recreational activities. Shown are the mean summary effect sizes (mean), 95% confidence intervals (95% CI), number of studies (N) and number of effect sizes (k). Effects are significant if 95% CI (horizontal lines) do not overlap the vertical zero line. If k = 2 the two effect sizes are given instead of 95% CI.*

The meta-analysis of **Paper I** revealed that also the literature about ecological impacts of water-based recreation focusses on effects on individual level (Figure 9). No general pattern could be identified if impacts increase or decrease from individual level to higher levels of biological organizations, but recreational impacts on birds were most pronounced at the individual level and not significant at the community level (Figure 9, Figure 10). Also **Paper III** showed no impact of recreation on waterfowl diversity (Table 2). **Paper IV** did not identify any impacts of angler management on any of the biodiversity indicators of several taxa. However, trampling effects of recreational activities were apparent at community and ecosystem level in **Paper I, II, III** and **V** (Figure 11, Figure 13 Table 2). Any form of recreation can have ecological impacts across levels of biological organization as shown in **Paper I**. The ecological relevance of the often-reported behavioral responses of individuals is questionable. Frequent disturbances can exceed the effects to higher levels of biological organizations, e.g. because of fitness consequences. Also cascading effects because of shifts in feeding grounds are theoretically possible (Frid and Dill, 2002; McDuie et al., 2021), but more studies on higher levels of biological organization of good study validity (on the scale of whole water bodies with consideration of cofounding factors, preferably BACI design) are needed to verify these potential impacts (Table 3).

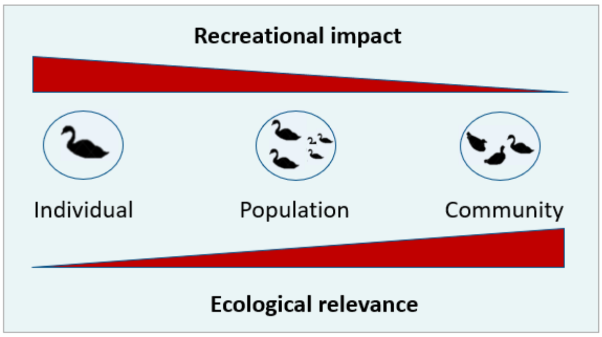


Figure 10: Impacts of water-based recreation can have effects on different levels of biological organization. In the case of water fowl recreational impacts are most pronounced at the individual level and not significant at the community level, while impacts on higher levels (such as population and community level) are ecologically more relevant than impacts on individual level.

4.3. Ecological impacts of freshwater recreation across taxonomic groups

Birds and mammals are seen as disturbance sensitive taxonomic groups (Dertien et al., 2021). Especially breeding birds and in general animals in breeding or other sensitive periods (reproductive, rearing, overwintering, moulting and migratory periods) are affected by human disturbance (Lafferty, 2001), because human presence can be perceived as predation risk by wildlife (Frid and Dill, 2002). In these sensitive periods the animals are temporarily less mobile, e.g. because they have to warm and protect the nest or their offspring; during migratory periods and in winter they have less resources and flight reactions might cost too much energy and birds during moulting might temporarily even lose the ability to fly. Flight reactions during the breeding season can result in less reproductive success in great crested grebes (*Podiceps cristatus*) (Keller, 1989). Disturbance by boating and pedestrians of wintering bald eagles (*Haliaeetus leucocephalus*) can lead to reduced feeding activity (Stalmaster and Kaiser, 1998). Flight reactions of animals because of recreational disturbance have been studied for birds (e.g. Keller, 1989; Stalmaster and Kaiser, 1998), mammals (Barocas et al., 2022), reptiles (Moore and Seigel, 2006; Selman et al., 2013), amphibians (Rodríguez-Prieto and Fernández-Juricic, 2005) and fish (Jacobsen et al., 2014). However, these behavioral responses are highly context dependent, because of habituation (Barocas et al., 2022; Bateman and Fleming, 2017;

Bessa et al., 2017; Keller, 1989); e.g. the same bird species (*Podiceps cristatus*) can have a higher flight initiation distance towards researchers in a boat at a lake with no usual boat use compared to lakes with frequent boat use (Keller, 1989). Some birds even attacked the researchers when they tried to remove the bird from its nest in order to count the eggs to measure the reproductive success. With the aid of flight initiation distances (FIDs) it is often tried to determine the disturbance sensitivity of birds, and other taxa (Bötsch et al., 2018; Mayer et al., 2019; Tablado and Jenni, 2017), although this behavioral measure might not have implications on higher levels of biological organization (Bateman and Fleming, 2017; Buckley, 2013; Stock et al., 1994). While birds as highly mobile organisms show flight responses to avoid detrimental impacts caused by water-based recreation, less mobile or sessile organisms are not able to evade the area of impact and might therefore suffer severer impacts (Figure 12; Eckrich and Holmquist, 2000).

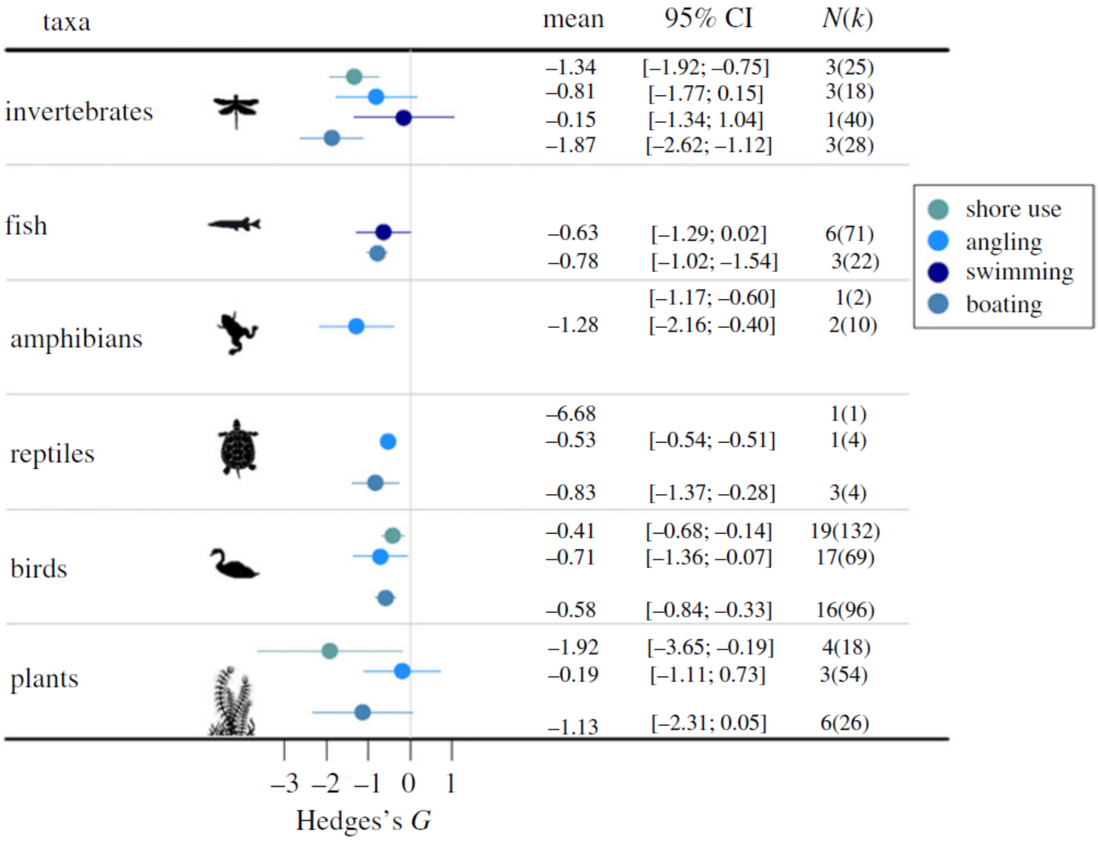


*Figure 11: Forest plot of the meta-analysis in **Paper I** with mean effect sizes per taxon and per recreational activity. Shown are the mean summary effect sizes (mean), 95% confidence intervals (95 % CI), number of studies (N) and number of effect sizes (k). Effects are significant if 95 % CI (horizontal lines) do not overlap the vertical zero line. If k = 2 the two effect sizes are given instead of 95% CI. If k = 1 the one effect size is given instead of mean summary effect size.*

In **Paper II** the responses of sessile and mobile organisms to human disturbance differed substantially. Plants were more strongly impacted than animals (**Paper II**). Also, in the meta-analysis in **Paper I** the strongest negative effects were observed in invertebrates and plants, while the effects on birds were comparatively low (Figure 11). In the empirical studies we did not find any recreational effects on waterfowl (Table 2, **Paper III, IV** and **IV**), but on songbirds (**Paper III** and **V**). The diversity of songbirds was affected by the density of domestic dogs (accompanied by humans), but not by humans alone (Table 2). The extent of protected riparian zones was associated with the FIDs of the songbird community at lakes with more disturbance sensitive species communities at lakes with larger share of protected riparian areas (**Paper V**). Despite the potentially high mobility of songbirds because of their ability to fly the actual mobility might be restricted due to high territoriality (Searcy and Beecher, 2009). This high territoriality can even lead to complete avoidance of an area due to moderate disturbance during territory establishment in early spring (Bötsch et al., 2017). Yet, songbirds can still decide to avoid areas of impact, while less mobile or even sessile organisms cannot evade an area (Eckrich and Holmquist, 2000). Therefore, impacts e.g. of trampling and wave action on macroinvertebrates and plants might be stronger than on mobile organisms (**Paper I, II, III, V**, Figure 12).

Although the behavioral avoidance reactions attract attention, are easily detectable and therefore also easy to study, these might not be the effects that we should focus on from a conservation perspective. In fact, there is already a lot of evidence about flight reactions and other changes in behavior especially of birds, while other effects and other taxonomic groups are studied poorly (**Paper I and II**). While trampling impacts on the vegetation are also well studied, we need more studies on underrepresented groups such as freshwater mammals, reptiles and amphibians (Table 3).

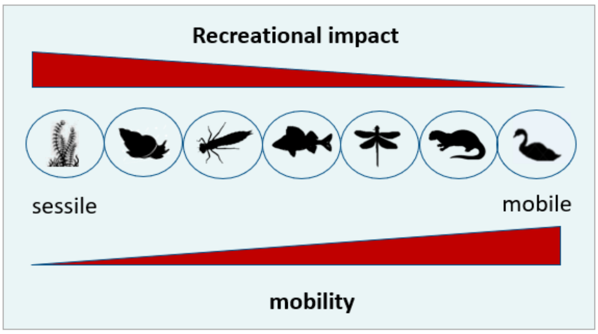


Figure 12: Mobile organisms can avoid detrimental impacts caused by water-based recreation by evading the area. Less mobile or sessile organisms are not able to evade the area of impact and might therefore suffer severer impacts.

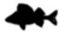
4.4. Recreational impact compared to environmental factors

To study the impact of anthropogenic pressures on the environment it is essential to consider that in ecological systems there is high natural variability and confounding influences are present (Norris et al., 2012). Many ecological studies have found that land use, habitat quality or availability and other environmental conditions shape wildlife communities (Birk et al., 2020; Kail et al., 2023; Sun et al., 2022; Timm and Möls, 2012; Xiong et al., 2023). Also the often studied flight responses of wildlife depend on multiple environmental factors (Mayer et al., 2019; Tablado and Jenni, 2017). In addition, there is usually a combined effect of multiple stressors (Eastwood et al., 2023; Pirotta et al., 2022). This means on the one hand that recreational impacts do on top of other existing pressures impair wildlife and environment and thereby exacerbate the biodiversity crisis. On the other hand the habitat degradation, that is caused by other impacts than recreation can worsen recreational impacts, that could be harmless in ecosystems with high habitat quality, e.g. due to more shelter and therefore less perceived risk (Frid and Dill, 2002; Mayer et al., 2019; Møller, 2008; Tablado and Jenni, 2017). Therefore, simple study designs in ecology produce inaccurate estimates of biodiversity responses (Christie et al., 2019). The focus on one single aspects at a low number of water bodies without the consideration of confounding factors in observational studies (e.g. Erlinger, 1981; Reichholf, 1988) might lead to false or exaggerated results and interpretations about the ecological impacts of water-based recreation.

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 (**Paper I**). Therefore, most of the studies included in the meta-analysis of **Paper I** were of low validity and no study of high validity could be identified. Studies of lower validity tended to report stronger negative effects than studies with medium validity, which is an indicator of publication bias contributing to overreporting of recreational impacts (Bateman and Fleming, 2017). In the empirical study of **Paper III** recreational uses of water bodies tended to have lower impacts on biodiversity compared to other environmental factors (Table 2). Especially lake morphology and trophic state were found to be stronger associated with biodiversity change of freshwaters than recreational activities. Also, in **Paper IV** non-fishing-related environmental variables had stronger effects on local species presence than recreational fisheries management or the presence of recreational anglers. Water bodies managed or even created for recreational purposes can also provide suitable habitat for wildlife and thereby enhance biodiversity (Chovanec, 2023). Habitat degradation, fragmentation and destruction are the main threats of freshwater biodiversity (Dudgeon, 2019; Reid et al., 2019), while human disturbance is of minor relevance (Caro et al., 2022). This means that by reducing other anthropogenic impacts it might be possible to benefit freshwater ecosystems and ecosystem services, including recreation, at the same time (Dudgeon, 2019; Oberdorff, 2022; O'Higgins et al., 2020).

However, the evidence base about ecological impacts of water-based recreation and its implications on nature conservation still need further approval with robust study designs. The best way to study impacts remains the before-after-control-impact (BACI) design with multiple sampling units at the scale of whole water bodies designed as an experiment with random allocation of the impact and considering confounding factors in the analysis (Christie et al., 2019; Norris et al., 2012). These studies do not exist yet in recreational ecology regarding freshwaters (**Paper I,** Table 3), probably because it is not easy to experimentally and randomly allocate and control the number of groups of recreationists to certain water bodies and exclude all other recreational uses, especially at the scale of whole water bodies.

*Table 2: Overview of predictors used in full multiple linear regression models in **Paper III** 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).*

	 waterfowl			 songbirds			 damselflies			 dragonflies			 amphibians			 fish			 macrophytes			 riparian herbs			 riparian trees			A priori expected relations 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	
Mean depth (m)													x	x	x	x	x	x	x	x	x							+ fish[1]; - amphibians[2]
Lake area (ha)	+	+	x																									+[3]
Shoreline length (m)				+	+	x	x	x	x	-	x	x										(+)	x	(+)	x	x	x	+[3]
Relative depth ratio													x	x	x				x	x	x							+[6]
Shoreline development factor	+	x	(+)	x	x	x	x	x	x	+	x	x	x	x	+	x	x	x	(+)	x	x	x	x	x				+[4]
Total phosphor (mg/l)							x	x	x	x	x	x				x	+	x	(-)	x	x							+ fish[5]; - all except fish[2,6, 14]
Total organic carbon (mg/l)							x	x	x	-	x	x																- odonata[14]
Nitrate (NO$_3$ mg/l)																			-	x	-							-[6]
pH-value																			x	x	x							-[7]
Secchi depth																			+	x	x							+[6]
Macrophyte coverage (%)	(-)	x	-				x	+	x	x	x	x	x	x	x	x	x	x										+[2, 10,13]
Reed (%)	x	x	x	x	x	x	x	-	x	x	x	x				x	x	x										+[2, 10,16]
Age (years)				x	x	x										+	x	x	x	x	x	x	x	x	x	+	x	+[5,6,8]
Urbanisation (%)																									x	x	x	+[12]
Agriculture (%)	x	x	x	x	x	x	x	x	x	x									(+)	x	(+)	+	x	x	x	x	x	+ birds; - odonata, plants[7,12,14]
Forest (%)				x	x	x							x	x	(-)										x	x	x	+ all [2, 8]
Wetland (%)							x	x	x	+			x	x	x													+[2,14]
Distance to lentic water (m)	x	x	x										x	x	(+)	x	x	x	x	x	x							-[2]
Distance to street (m)				x	x	x																						+[8]
Distance to settlement (m)																						-	x	x	x	x	x	-[12]
Open sites/m																			x	x	x	-	x	x	x	x	x	+ herbs, macroph.[6]; -trees
Trail length/shoreline length																						x	x	x				
Angling use/km	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	(+)	x	x	x	x	x	x	x	x	x	x	- all except fish[2,10], + fish[5]
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	x	x	x	(+)	x	x	-	x	x	x	x	x	x	x	+	x	x	x	x	x	+	x	x	x	x	x	- all except herbs[2,9,10]; plants[9]
Fish biomass (g /100m^2)	x	x	x				x	x	x	-	x	x	x	x	x													+ birds[15]; - others[2, 13]
Number of lake visits	x	x	x																									+

+/- = significant, p < 0.05
(+/-) = trend, p < 0.1
x = in model, but p > 0.1
x = not in final model, but predictor in full model

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

Table 3: Collection of studies about recreational impacts on freshwater ecosystems with either interesting findings or study designs with promising study validity (BACI design, whole lake scale with multiple lakes, experimental approaches, or consideration of confounding factors).

Study	Taxa / compound	Recreational activity	Impact	Level	Specifics
Found et al. (2008)	birds	angling	management	community	piscivorous birds prefer lakes with angling
Franson et al. (2003)	birds	angling	lead fishing weights and other tackle	individual	large sample size; lead poisoning and ingested weights and tackle found in 1.2 - 9.1 % of individuals
Sears (1988)	birds	angling	toxicity	individual	lead poisoning increased in gravel pit lakes with fishing
Matern et al. (2019)	fish	angling	angler management	community	higher species richness in angler managed gravel pit lakes
Wood et al. (2001)	invertebrates	angling	management	community	unmanaged sites had higher macroinvertebrate diversity compared to managed/stocked ponds, but are at greater risk of drainage
O'Tool et al. (2009)	plants and other	angling	trampling, littering	multiple	Riparian and littoral vegetation affected
Jacobs and MacIsaac (2007)	zooplankton	angling	dispersal	community	experimentally fouling of fishing line with zooplankton, dispersal possible
Bright et al. (2003)	birds	boating	presence	individual	behavior before and after boating disturbance in low boating and high boating area (BACI)
Asplund and Cook (1997)	plants	boating	damage, motor	multiple	increased macrophyte biomass, coverage, and shoot height in experimental plot without boating
Vermaat and Debruyne (1993)	plants	boating	wave action	individual	wave action negatively affected plant growth in an in-situ experiment with a breakwater (BACI)
Ailstock et al. (2002)	water	boating	resuspension of sediments	ecosystem	shallow water zones very sensitive
Yousef et al. (1980)	water	boating	sediment resuspension	ecosystem	experimental mixing increased phosphorous content and chlorophyll a concentration (BACI)
Stasko et al. (2012)	zooplankton	boating	dispersal	community	dispersal of zooplankton attached to canoes verified, but environmental variables explained the greatest amount of variation in community composition among lakes
Bacela-Spychalska (2013)	shrimps	boating, diving	introduction of invasive species	community	transport of invasive shrimp with boating and diving gear
Jacobsen et al. (2014)	fish	boating, angling	presence, noise	individual	experimental disturbance; no difference in fish response was detected between boating with and without angling
Barocas et al. (2022)	mammals	boating, fishing, tourism	presence	individual	behavioral responses of otters towards humans in multiple lakes with and without fishing and tourism

Randler (2006)	birds	dog walking	noise	individual	experimental dog barking via sound recorder increased the vigilance of coots
Ryan (2018)	birds	fishing and other	plastic littering	individual	Monofilament fishing line one of main reasons of entanglement of birds in plastics.
Lozano and Malo (2013)	birds	human density, fishing, boating		population, community	confounding factors included human activity reduces bird richness and abundance of some species
Keller (1989)	birds	multiple	researchers by boat	individual, population	compensation by multiple broods per year
Spyra and Strzelec (2019)	invertebrates and plants	multiple	multiple	multiple	whole lake scale, plant cover and invertebrate occurrence were significantly reduced in recreational ponds
Wegner et al. (2023)	macrophytes	paddle boating	damage, paddling	individual, community	critical impacts were already reached at moderate paddling frequency
Acuña et al. (2023)	bacteria	swimming	water quality, sun screen	community	changes in biodiversity were especially fast when increasing recreation from none to low
Brauns et al. (2007)	macro-invertebrates	swimming	artificial beach	population, community	altered species composition reduced species richness, because of reduced structural complexity of habitats
Poiger et al. (2004)	water	swimming	pollution/toxicity	ecosystem	occurrence of UV-filter compounds in multiple lakes before during and after swimming season (whole lake scale)
Meyer et al. (2023)	plants	swimming, shore use	trampling	community	composition and the vegetation cover differed between bathing and control sites, but did not correlate with visitor counts
Rodríguez-Prieto and Fernández-Juricic (2005)	amphibians	walking	presence	individual, population	decreased abundance with proximity to recreational areas; experimental disturbance decreased stream bank use
Guillemain et al. (2008)	birds	walking	presence	individual	waterbodies with more tourists did not host fewer birds; most heavily disturbed water body hosted the highest wildfowl density
Hardiman and Burgin (2011)	macro-invertebrates	walking	trampling	community	experimental canyoning (in-stream walking) altered species composition with rapid recovery, but abundance decreased without full recovery
Bowles and Maun (1982)	plants	walking	trampling	multiple	experimental trampling caused long term effects of vegetation (BACI)
Andrés-Abellán et al. (2005)	plants and soil	walking	trampling	community, ecosystem	observational and experimental trampling effects
Fernández-Juricic et al (2007)	birds	walking and canoe	presence	individual	experimental pedestrian and canoe disturbance during breeding causes behavioral changes

5. Management implications

In this section I want to discuss management options to mitigate the impacts caused by water-based recreation. Although the above reported results about the ecological impacts of water-based recreation show that other anthropogenic pressures might be more relevant, recreation as additional pressure should be harmonized with conservation perspectives to further reduce potential impacts.

An important measure for biodiversity management in landscapes to mitigate recreational impacts is visitor guidance (Leung et al., 2018; Manning et al., 2017). Visitor guidance and any other form of recreation management can be achieved either directly or indirectly as shown in Figure 14 (Leung et al., 2018; Manning et al., 2017). Direct measures regulate the behavior while indirect measures influence or modify the behavior of visitors (Manning et al., 2017; Reddy et al., 2017).

Direct measures are prohibitions and restrictions of recreational use, e.g. in conservation areas or general laws (see Chapter 1.2. Legal framework). The degree of control of direct measures is high and can even be enhanced with surveillance of the area to check compliance of the regulations. Whereas the individual choice is restricted, which can lead to resistance (Mason, 2005; Stoll-Kleemann, 2001; Von Ruschkowski and Mayer, 2011). Therefore, direct measures should be defined by or together with stakeholders (Hoppenreijs et al., 2023) rather than top down regulations to reduce resistance and stakeholder conflicts (Figure 14), especially if local communities depend or interact with natural systems, as it is usually the case for freshwater ecosystems (Hoppenreijs et al., 2023). This increases the acceptance and thereby the compliance of the regulations (Von Ruschkowski and Mayer, 2011). In addition, conservation measures can be more effective when local and traditional knowledge of stakeholders is considered (Hoppenreijs et al., 2023; Löki et al., 2023; Mason, 2005; Shephard et al., 2023).

To avoid resistance towards measures of nature conservation indirect measures should be prioritized over direct measures (Mason, 2005). Indirect measures are for example the increase or decrease of accessibility and environmental education (Manning et al., 2017) or nudging of the desired behavior without formal constraints (Reddy et al., 2017). Education of recreationists to basic concepts of (recreation) ecology, could lead to more visitors to stay on path, put dogs on leash and to avoid disturbance of wildlife (Kleiner and Hunziker, 2023; Manning et al., 2017; Mason, 2005). Campaigns to educate recreationists especially if equipment has to be rent or bought to conduct the activity, as it is the case for example for Stand up paddling, can be very promising to change the behavior of recreationist and reduce disturbances, because the information can be provided on-site and at the beginning of the recreational experience (Kleiner and Hunziker, 2023). Some activities such as angling automatically involve environmental education (Löki et al., 2023), mainly because of the obligation to obtain a fishing license in many countries (Arlinghaus et al., 2021), which requires a proof of ecological knowledge and recreational activity skill (Manning et al., 2017). The increase of accessibility through roads, trails, parking lots and the availability of infrastructure for certain recreational activities, e.g. water ski facility, docks for boating and angling, food, drinks, and toilet facilities, can attract and thereby concentrate the recreational activities to desired locations and reduce the recreational pressure in other locations (Holman and Bennett, 1973; Manning et al., 2017). The accessibility to other locations can be decreased by not providing infrastructure on the one hand and by creating barriers, such as thorny bushy vegetation belts, hedges of vegetation or constructed with dead wood piles (Benjes hedges), scree walls or other barriers of natural or artificial material (Cole, 1993). Barriers and fences of natural material should be prioritized over artificial material, because these can additionally increase the habitat complexity and provide habitat (Bolding et al., 2004; Cole, 1993; Harvey et al., 2005).

Both measures direct and indirect can be either established at the landscape scale or at the scale of water bodies (Figure 14). Visitors can be attracted to recreation lakes with very high recreational use intensities by providing the respective already mentioned infrastructure and recreational facilities, to concentrate recreational use (Benkhard et al., 2023; Manning et al., 2017; Spernbauer et al., 2023). Some activities like water skiing might not only attract those that want to perform water skiing themselves, but also many other recreationists, that want to watch water skiers while performing other recreational activities, e.g. swimming or sunbathing (Jaakson, 1971). Thereby the recreational pressure on surrounding water bodies should be decreased. The same procedure can be established at a smaller scale within water bodies, also to reduce conflicts between different groups of recreationists. The segregation of recreational activities within water bodies is an appropriate measure to allow multiple recreational uses at a water body without risks of harm and other conflicts, e.g. the entanglement of swimmers in fishing line or the injury of swimmers by water-skiers (Benkhard et al., 2023; Jaakson, 1971). Regarding environmental impacts, it is suggested to concentrate use on trails with hard surfaces and/or trails with favorable trail slope alignment to avoid erosion and nutrient input due to trail use close to the shoreline of water bodies (Spernbauer et al., 2023). Protected (riparian) zones can be established (**Paper V**), to reduce the pressure on sensitive habitats (Benkhard et al., 2023), such as spawning, rearing and breeding habitats of wildlife or areas with trampling sensitive vegetation (Figure 13). Protected riparian areas voluntary established by recreational fishing clubs (**Paper V**) are a good example of direct and also indirect stakeholder-oriented visitor guidance. Fishing clubs often establish protected riparian no-access zones to conserve spawning habitats of fishes. This aim is achieved either with signs and fences or with bushy and/or thorny vegetation or both. These zones do on the one hand indeed enhance the fish abundance as target and on the other hand also benefit other taxa, e.g. disturbance sensitive songbirds and trampling sensitive vegetation and increase the habitat complexity (**Paper V**). It is important to manage recreational visitors at broad scales, because their impacts and the distribution of wildlife also covers large areas (Gutzwiller et al., 2017). Although large areas including whole water bodies with reduced or no access to recreationists seem to be necessary to accomplish broad scale recreational visitor management, small patches with reduced impacts are also important and can benefit biodiversity (**Paper V**) and are highly relevant for biodiversity conservation at the landscape scale (Riva and Fahrig, 2022).

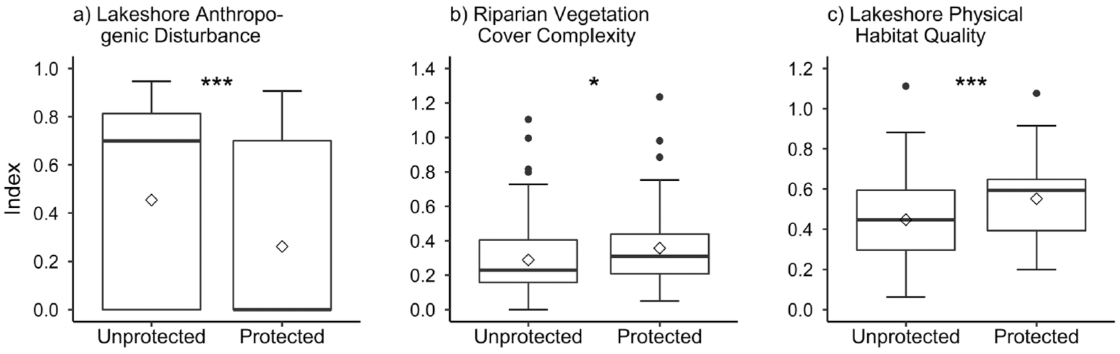


*Figure 13: Comparison of habitat quality indices in **Paper V** for plots inside ("Protected", N = 55) and outside ("Unprotected", N = 146) protected areas at small gravel pit lakes in Lower Saxony, Germany. ◇= Mean, —= Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers, *** = very high significance (p < 0.001) and * = significant (p < 0.05).*

In addition to the above-mentioned examples of spatial measures, temporal measures are also relevant to manage recreation and potential impact on biodiversity (also explained in Chapter 1.2.). While spatial measures aim to reduce impacts on sensitive habitats e.g. no boating in shallow water or close to reed belts (**Paper I**), the aim of temporal or spatio-temporal measures also is to mitigate the impacts on sensitive periods, such as reproductive, rearing, overwintering, moulting and migratory periods of animals and germination or flowering periods of plants. Examples of temporal measures are the closed seasons for hunting and fishing and the obligation to put dogs on leash during the breeding season (see Chapter 1.2 Legal framework). Temporal restrictions seem to be more common for mobile organisms, while spatial restrictions are common for both sessile and mobile organisms. In fact, both sessile and mobile organisms benefit from both temporal as well as spatial visitor guidance, because also sessile taxa, such as plants have more and less sensitive periods, e.g. the germination of seedlings as a very trampling-sensitive period (Kuss and Graefe, 1985). Often spatial and temporal measures are combined as spatio-temporal measures, e.g. that mowing inside of a protected area is allowed only twice per year (§4, (4), 5.a regulation of the NSG „Großes Meer, Loppersumer Meer“) or that angling is allowed in parts of a conservation area only from July to October (§5, regulation of the NSG “Gustavsee”, Bavaria, Germany). Still, the effect of protected areas is in debate (Santangeli et al., 2023) and also other measures of visitor guidance might not be effective especially if only certain activities are restricted while others are maintained (**Paper I**). Measures of visitor guidance should therefore be total recreational use oriented rather than centered on single activities.

The results presented in this thesis suggest, that not human presence or intensity is the main driver of biodiversity, but other environmental conditions. Although visitor guidance is an important tool to manage biodiversity, habitat enhancements are a tool that is far more promising for nature conservation (Figure 14) as habitat degradation is one of the main threats of freshwater biodiversity (Dudgeon, 2019; Geist and Hawkins, 2016; Reid et al., 2019), while human disturbance is of minor relevance compared to other threats (Caro et al., 2022). As intact habitats with cover and shelter can further mitigate impacts of human disturbance (Jimenez et al., 2022; Møller, 2008; Tablado and Jenni, 2017), it is crucial to put more emphasis in habitat enhancement or restoration as management tool, because natural recovery is limited in freshwater ecosystems (Geist and Hawkins, 2016). Measures to enhance or restore aquatic habitats are the addition or promotion of natural vegetation, dead wood or artificial structures as shelter, feeding or spawning habitat (Knaepkens et al., 2004). An increase of habitat complexity can further be achieved by reversing the straightening of watercourses of rivers and of the embankment of river and lake shorelines (Hering et al., 2015; Ostendorp et al., 2020). Barrier removal or installation of fish ladders in rivers is also an important measure to allow (fish) migration within the river (Katz et al., 2007). Water quality improvement can be achieved with erosion control structures to reduce sediments or by controlling nutrient and pollutant inputs by agriculture and other sources (Katz et al., 2007). The creation of shallow water zones is a very effective measure to enhance fish populations, especially in water bodies with steep slopes, that lack these very productive riparian zones (Radinger et al., 2023). Such ecosystem-based management outperforms species-focused approaches, e.g. fish stocking (O'Higgins et al., 2020; Radinger et al., 2023). Habitat enhancements are a good tool to prioritize protection of habitats and processes rather than protection of single species (Geist and Hawkins, 2016). In general, it is important also to reduce other anthropogenic impacts than recreation and thereby benefit freshwater ecosystems with their wildlife and ecosystem services at the same time (Dudgeon, 2019; Hoppenreijs et al., 2023; Oberdorff, 2022; O'Higgins et al., 2020).

Recreation management

Measures

Direct measures:

- Regulating recreational activities
- Regulating gear/means involved in recreation,
- Directing recreational visitor flows and access points,
- Constraining or banning certain or all recreational activities.

Indirect measures:

- Providing information and outreach,
- Nudging of desired behaviors without formal constraints,
- Indirectly guiding visitors flows through infrastructure management (boat ramps, access points, paths),
- Participatory bottum-up development of local management plans

Spatial and temporal measures:

- Spatio-temporal zoning
- Spatio-temporal segregation of recreational activities

Do nothing (if no impacts and no conflicts)

Key principles

- Optimizing human well-being and recreational quality
- Minimizing stakeholder conflicts
- Focusing on process-based rather than species-identify based conservation
- Landscape perspective rather than just local management
- Preference of indirect vs. direct recreational use control
- Designing of adaptive, flexible, inclusive and generally diverse conservation systems
- Take a holistic perspective on recreation rather than an activity-specific focus
- Evidence based conservation planning based on local evidence

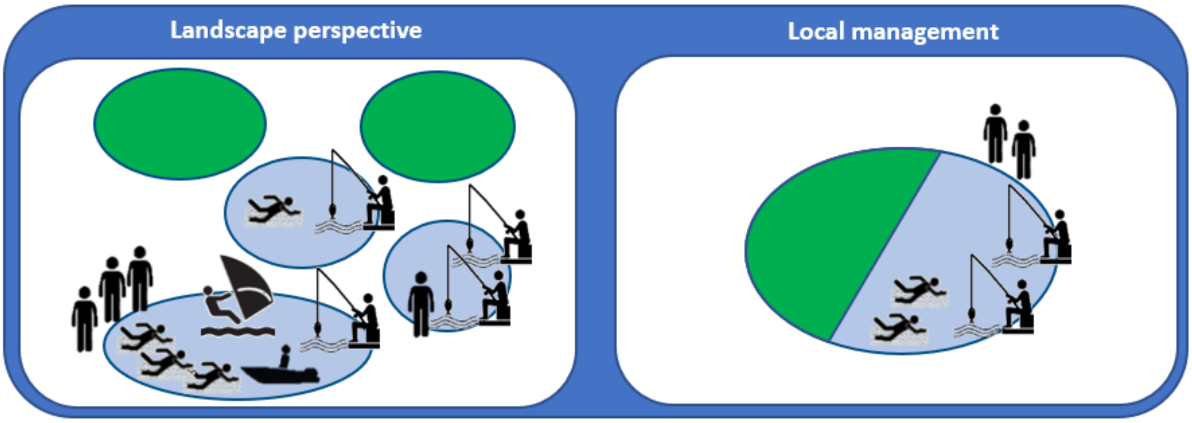


Figure 14: Recreation management in landscapes can be achieved by direct or indirect and spatial measures. Both include spatial and/or temporal measures. The measures should follow the key principles of recreation management.

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Appendices

Selbstständigkeitserklärung
Statement of authorship

Name surname Schafft

Vorname first name Malwina

Datum date 16.01.2023

Matrikelnummer student ID no. 602786

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Author for correspondence:
Malwina Schafft
e-mail: schafft@igb-berlin.de

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Ecological impacts of water-based recreational activities on freshwater ecosystems: a global meta-analysis

Malwina Schafft[1,2], Benjamin Wegner[1,2], Nora Meyer[3], Christian Wolter[1] and Robert Arlinghaus[1,2]

[1]Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
[2]Division of Integrative Fisheries Management, Department of Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany
[3]Institute for General Ecology and Environmental Protection, Technische Universität Dresden, Pienner Straße 7, 01737 Tharandt, Germany

MS, 0000-0003-0633-4063; BW, 0000-0002-6065-4386; NM, 0000-0001-5732-0791; CW, 0000-0002-2819-2900; RA, 0000-0003-2861-527X

Human presence at water bodies can have a range of ecological impacts, creating trade-offs between recreation as an ecosystem service and conservation. Conservation policies could be improved by relying on robust knowledge about the relative ecological impacts of water-based recreation. We present the first global synthesis on recreation ecology in aquatic ecosystems, differentiating the ecological impacts of shore use, (shoreline) angling, swimming and boating. Impacts were assessed at three levels of biological organization (individuals, populations and communities) for several taxa. We screened over 13 000 articles and identified 94 suitable studies that met the inclusion criteria, providing 701 effect sizes. Impacts of boating and shore use resulted in consistently negative, significant ecological impacts across all levels of biological organization. The results were less consistent for angling and swimming. The strongest negative effects were observed in invertebrates and plants. Recreational impacts on birds were most pronounced at the individual level, but not significant at the community level. Due to publication bias and knowledge gaps, generalizations of the ecological impacts of aquatic recreation are challenging. Impacts depend less on the form of recreation. Thus, selectively constraining specific types of recreation may have little conservation value, as long as other forms of water-based recreation continue.

1. Introduction

Freshwater ecosystems provide many services to humans [1] and generally have a high recreation value [2,3], which is reflected in higher property values for sites with freshwater access or views, for example [4]. Aquatic recreation, such as boating, swimming or fishing, satisfies many psychosocial benefits and generates relevant economic outcomes [2,5]. Recreation also provides important health benefits [6]. Therefore, limiting access to water bodies for conservation reasons can negatively affect human welfare [7,8].

However, recreational activities such as fishing, swimming or boating may negatively impact biodiversity or affect ecosystem functioning [2,9,10]. For example, recreational angling facilitates the spread of invasive species [11]. Disturbances by recreationists may also negatively affect wildlife or habitat quality [12,13], for example by causing flight reactions in birds [14]. In fact, escape behaviour could have strong fitness implications and affect population size [14]. Relatedly, shoreline access may cause trampling effects that reduce vegetation cover and compact soil [15], boating can reduce vegetation cover [16]. Human presence at the waterside particularly affects disturbance-sensitive

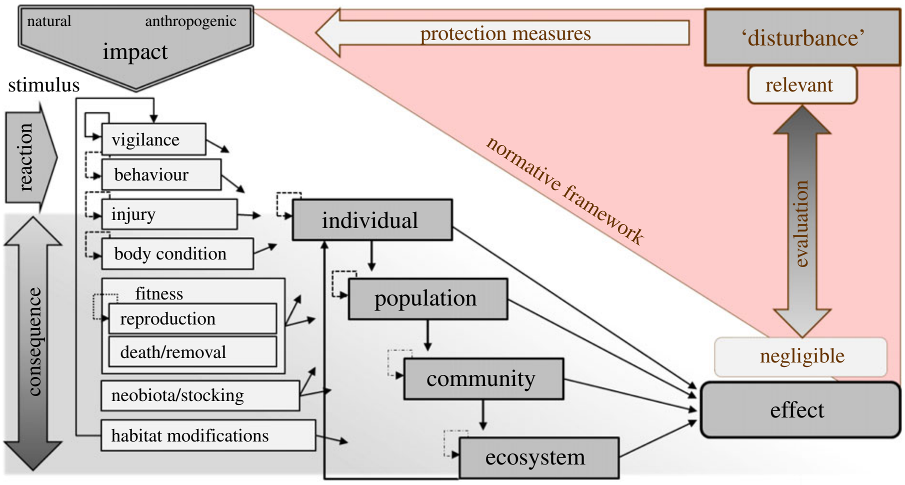

Figure 1. Conceptual framework: natural or anthropogenic impacts can cause stimuli for a reaction of individuals. Impacts can have direct consequences or reactions can cause indirect consequences, which can lead to effects on different levels of biological organization. Within the normative framework effects can be evaluated as negligible or relevant. If effects are evaluated as relevant they can be considered 'disturbances' and protection measures are needed to reduce impacts. Adapted after Stock *et al.* [22]. (Online version in colour.)

taxa [17] and may also affect ecosystem functioning [18] and ecosystem state, such as water quality [19]. Despite a long history of recreation ecology [20], a systematic synthesis of its effect sizes is currently lacking for aquatic ecosystems. This gap of synthetic knowledge complicates the design of conservation policies for aquatic recreation and may fuel stakeholder conflicts.

The impacts of recreation can be measured by magnitude, duration and frequency, all of which can have a series of ecological effects. We define ecological impacts as any visitor-related, biophysical changes to individuals, populations, communities or habitats [21]. Recreational impacts can scale across levels of biological organization (figure 1) [22]. The lowest level where consequences of recreation can emerge is the level of an individual organism, which includes behavioural, physiological, energetic and genetic impacts, such as increased vigilance [23], flight responses [24] and injuries [25]. Collective impacts resulting from elevated mortality or impaired recruitment can have population-level impacts, such as a reduced number of breeding pairs [26], reduced breeding success [27] or reduced abundance of macrophytes [28]. Community-level impacts are indicated by changing relative abundances of certain taxa, such as a reduced species richness [29], a change in the species composition [30] or the introduction of invasive species [11,31]. To provide a comprehensive picture, we analysed the recreational impacts of water-based recreation across all three levels of biological organization in a transparent and structured synthesis of ecological impacts of water-based recreation using comparable effect size metrics. In addition, we also examined impacts on environmental quality, such as water turbidity [19], littering and pollution of sediments [30], soil compaction [15] and reduced vegetation height or cover [16]. These aspects can indirectly affect species and are aesthetically relevant for humans and thus policy-making. Therefore, our work extends previous systematic reviews [20] that did not analyse the effect sizes of published works. Our synthesis aims to inform policy-making regarding the governance and management of water-based recreation.

Conflicts among conservation interests and outdoor recreational activities are well documented [32,33]. Disturbances to certain protected habitats or threatened species induced by recreation may justify conservation interventions that constrain, redirect or even ban certain or all forms of recreation [34]. In particular, the effects of aquatic recreation on disturbance-sensitive waterfowl species generate continuous conservation conflicts and have motivated far-reaching conservation actions, including access bans in many areas of the world [7,35]. In terrestrial ecosystems, a recent review of tourism-based effects on wildlife reported surprisingly few documented effects beyond individual reactions; hence, impacts associated with terrestrial recreation may be 'over-reported' [36]. Indeed, there could be knowledge gaps of human-induced impacts, particularly at higher levels of biological organization, such as populations or communities, because these are much more difficult to study than, for example, individual flight reactions [37]. However, these higher levels of biological organizations often determine whether conservation action to constrain recreation is warranted, which is both a legal and a normative question (figure 1).

Our objectives were to compare the relative magnitude of effects caused by different water-based recreational activities and examine for variation across different taxa. To that end, we conducted a meta-analysis, which is a structured and replicable method to compare the magnitude of effects derived from scientific literature using effect size metrics [38]. By synthesizing global knowledge in highly disparate literature, our meta-analysis provides the first comprehensive scientific synthesis of the ecological impacts of freshwater-based recreation. We examined the following hypotheses:

(1) Ecological impacts of water-based recreation vary by type of recreation, because activities vary in their degree of disturbance (e.g. boating versus shore-based activities [39]).
(2) Ecological impacts increase from shore to open water because open water activities involve intensified interaction with the whole system [21].
(3) Ecological impacts decay towards higher levels of biological organization (from individual towards population and community levels), because density dependence and other compensation processes buffer anthropogenic disturbances at the population or community levels [22,40].

2. Methods

We conducted a systematic literature search from November 2018 until February 2019, following the guidelines of Siddaway *et al.* [41]. Both peer-reviewed and grey literature were researched in different languages to compile a comprehensive evidence base using a transparent and replicable literature screening approach. We spent a considerable time developing and testing the search term, which included synonyms for recreation, aquatic, impacts and environment (see electronic supplementary material, S1). We used seven different literature databases and yielded 13 115 articles: Web of Science Core Collection $n = 6937$, Scopus $n = 4206$, BioOne $n = 1056$, Conservation Evidence $n = 39$, BASE $n = 596$ and ProQuest $n = 45$. The German literature database 'Natursport', which specifically compiles the ecological impacts of recreational activities, was used to identify grey literature. Here, we obtained 236 articles by selecting keywords with aquatic references, such as aquatic species, aquatic habitats and aquatic recreational activities (see electronic supplementary material, S1). We used Google and Google Scholar as additional sources with reduced search terms and obtained nine further articles in Google and 181 articles in Google Scholar. After removing duplicates, 11 919 articles were left for in-depth screening. An additional 1884 references were obtained from the reference lists of acquired full-text articles (electronic supplementary material, figure S1, S1).

(a) Screening and exclusion criteria

By screening titles, abstracts and full texts, we excluded articles that did not study (i) the impacts of recreational activities, (ii) the impacts on aquatic ecosystems or (iii) the ecological impacts (e.g. human health issues from *Escherichia coli*). In addition, we excluded articles of languages other than English, German, French or Spanish, as these were not accessible to the authors. For consumptive activities (angling and hunting) we excluded impacts on target species (e.g. the impacts on fish as target species for angling) to ensure comparability of effect sizes.

Screening and exclusion were performed by three trained raters. To assure reproducibility, we calculated Fleiss's κ [42] to assess inter-rater reliability with a subsample of 88 articles. $\kappa = 1$ indicates complete, and $\kappa \leq 0$ indicates no agreement among raters. We obtained free-marginal $\kappa = 0.48$ (95% CI [0.35, 0.62]) at 74% overall agreement, indicating moderate agreement. The first author tended to retain more articles that the other two excluded. Further inspection of these excluded articles proved the more exclusive approach to be more time-effective, and ultimately all raters reached a consensus on which articles to retain.

In total, we excluded 6283 and 3758 articles during the title and abstract screening, respectively. Because of concern that there might be a deficit of studies focusing on freshwater ecosystems, we did not exclude marine studies during the title and abstract screening, but we intended to focus on freshwater ecosystems in the first place. During full-text screening, however, we decided to focus solely on freshwater systems, as the sample size of suitable articles deemed sufficient. As result, we excluded 3526 marine articles. This decision is warranted because the species and environmental conditions in marine and freshwater ecosystems differ, hence, meta-analysis results from marine systems may not hold for freshwater systems and vice versa.

Studies were retained for in-depth analysis and effect size extraction that compared: (i) organism/ecosystem responses to the presence of recreational activities (impact) versus lack of recreational activity (control) using various designs, (ii) organism/ecosystem responses to different intensities of recreational activity (typically observational studies) and (iii) organism/ecosystem responses to a specific compound/substance/aspect associated with a specific recreational activity compared to a control within an experiment *in situ* or in mesocosms. After in-depth text retrieval, further studies were excluded, providing only aggregated information for multiple recreational activities, which did not allow breaking effect sizes down to specific activities. Another 141 articles had to be excluded because effect size estimation was not possible due to lacking control or comparator information or missing data that could not be retrieved, even after contacting the authors. The final meta-analysis was completed on 94 articles that met the inclusion criteria, from which effect sizes were derived.

(b) Data extraction

Data from the 94 articles were extracted by three trained researchers (M.S., B.W., N.M.) from tables, results and figures (using software webplot digitizer: https://automeris.io/WebPlotDigitizer/) to calculate effect sizes [38] (sample size, mean, standard deviation, standard error, test statistics or raw data). If important metrics were missing, the corresponding author was contacted to obtain the missing data. Every article was reassessed by the first author to ensure a uniform coding procedure and comparability between the effect sizes of extracted values and coded categories.

During coding, we differentiated four categories of water-based recreational activities characterized by increasing interaction strength with water from shore to open water to test hypotheses 1 and 2: (i) shore activities with (almost) no direct interaction with water (walking, dog walking, biking, horse riding, picnicking, camping, hunting, wildlife viewing), (ii) shoreline recreational angling with direct interaction with water, but the activity itself being situated at the shoreline, (iii) swimming, which has direct interaction with water but predominantly occurs in the near shore zone, often combined with shoreline stays (including swimming, snorkeling and diving) and (iv) boating as an (almost) exclusively open water activity (including motor boating, jet skiing, water skiing, sailing, rowing, paddling, kite surfing, wind surfing, stand up paddling and boat angling).

To examine which taxa were most affected by recreation and at which level of biological organization (hypotheses 1–3), we extracted information on taxonomic group (invertebrates, fish, amphibians, reptiles, birds, mammals, plants, phytoplankton and zooplankton) and species, type of recreational activity, the specific recreational impact studied (human presence, noise, trampling, pollution, toxicity, eutrophication, damage, injury, invasive species release) and the response variable measured. Response metrics included avoidance (e.g. flight initiation distances (FIDs), swimming speed), time budgets (e.g. time spent vigilant, time spent feeding), physiological responses (e.g. weight, heart rate, injuries), abundance (e.g. number of individuals, density or biomass), reproduction (e.g. number of nests, number of clutch losses, sum of offspring), biodiversity (e.g. species richness, α-diversity indices), community structure (changes in species composition, β-diversity indices), habitat structure (number of strata), water quality (e.g. pH, nutrient concentration, turbidity), pollution (number or weight of litter items) and soil compaction (bulk density, barren area). These response variables were assigned to levels of biological organization (individual, population or community) or to environmental quality. Impacts of recreation at the individual level included behavioural and physiological responses. Impacts were categorized at the population level whenever measures of abundance or total reproductive success were reported. Note that animal abundance as a response measure can be categorized as the impact on the individual level if it indicates avoidance behaviour of individuals, as in a study by Knight *et al.* [43], where the number of individual birds was counted when an angler was present or absent within the same season. By contrast, if the abundance of animals or plants was compared across systems (e.g. different lakes) relative to controls (control versus impact) or before and after a ban on recreational use (before versus after design), impacts were categorized at the population level. Impacts that altered the diversity of species or functional groups and species composition were categorized at the community level. Impacts on habitat structure (plant height or vegetation cover) or general environmental components, such as water, sediments or soil, were classified as impacts on the environment of animals, plants and humans. We further identified the location of the activity and the affected habitat type to examine whether certain habitat types were more affected than others.

To determine study validity, we systematically extracted information on study design, the number of water bodies examined as controls and treatments separately, whether a comparison was based on spatial or temporal separation of control and treatment and whether randomization was applied. We examined whether the study was controlled for possible confounding factors, how the control or comparator was specified and on which scale the study was conducted (comparison of water bodies or comparison of zones within a water body). These variables were used to assess the validity of each study and as weighting factors to control for study quality (see the section on sensitivity analysis and table 1). Additionally, we also noted author names, date of publication, dates of start and end of data collection, longitude and latitude of the study site or laboratory, language, name of journal and type of publication (scientific journal, book, conference proceedings, unpublished). We classified studies as peer-reviewed or not and as academic, governmental, non-profit or other to test with moderator analysis whether these factors influenced the results.

(c) Statistical analysis

To quantify the ecological response to the impacts of water-based recreational activities we used Hedges's *g* to measure standardized mean differences [38]. Hedges's *g* is a correction from Cohen's *d* for small or unequal sample sizes. Both estimates compare the means of the treatment group (e.g. recreation site) and the comparator group (e.g. control site), standardized by dividing the pooled standard deviation of the response variable:

$$d = \frac{\bar{x}_2 - \bar{x}_1}{S_{\text{pooled}}},$$

where $\bar{x}_1$ is the mean of the control/comparator group and $\bar{x}_2$ is the mean of the treatment group and S_{pooled} is the pooled standard deviation defined as S^2:

$$S_{\text{pooled}} = \sqrt{\frac{(n_2 - 1)S_2^2 + (n_1 - 1)S_1^2}{n_1 + n_2 - 2}},$$

where n_1 and n_2 are the sample sizes and S_1^2 and S_2^2 are the standard deviations of the comparator and treatment, respectively.

To convert *d* to *g*, a correction factor *J* was used to avoid small sample size bias:

$$J = 1 - \frac{3}{4(n_1 + n_2 - 2) - 1}$$

$$g = d \times J.$$

Zero effect size indicates no effect of recreation on the response variable. The more distant the effect size is from zero, the larger the effect. Effect sizes were coded so that negative values indicate negative ecological impacts and positive values show positive impacts of aquatic recreation. Whereas the direction of the effect size for mortality and survival might be quite intuitive, the interpretation of measures of FIDs is less clear. Larger impacts of anthropogenic and natural sources are associated with higher FIDs [36]. However, habituation effects in areas with high recreational activity can systematically lower FIDs [36]. In particular, study designs with spatial separation would, therefore, lead to positive effect sizes comparing treatment and controls when we assume lower FIDs to be a positive effect of recreation. Because comparing different measures and recreational activities would not be reasonable with this approach, we coded the habituation effects as an indicator for the degree of impact, even though habituation itself can be positively interpreted as it supports the coexistence of humans and wildlife [36].

(d) Subgroup analysis

To compare the magnitude of ecological effects reported for different forms of the aquatic recreation and across different taxa and levels of biological organization and to test hypotheses 1–3, we calculated summary effect sizes for subgroups of the dataset (e.g. for boaters and anglers or by taxon) and analysed the effect sizes using multilevel modelling [48] in R (R v. 4.0.5, R Core Team, 2017). Most studies yielded multiple effect sizes because responses were recorded separately for multiple recreational impact intensities, sites, species or at multiple time points. We considered sample dependencies among effect sizes through the multilevel models by nesting study, species and response measure (i.e. random = ~1 | Study_ID/taxa/Response.measured) to calculate mean effect sizes over multiple studies using the function ma.rmv (metafor package [48]).

(e) Weighting of effect sizes

To calculate summary effect sizes in the meta-analysis, each effect size from the original studies is usually weighted by its inverse variance or by a measure of study quality [38]. We weighted the effect sizes by a quantitative measure of study validity, because inverse variance was not appropriate as the sample size was often obscured by pseudoreplication in original studies. Following suggestions by Norris *et al.* [44] and Christie *et al.* [45], we assessed study validity by eight criteria to obtain weights for each single effect size. These criteria addressed the study design and number of sampling units (as whole water bodies), providing higher weights to a more robust study design (e.g. before–after–control–impact is considered of higher quality than before–after) or to studies that involve the randomization of study sites. Further details of the weighting procedure are provided in table 1.

To assess the robustness of our weighting approach, we compared the results with analyses in which weights were calculated by the inverse variance of effect size. In addition, we tested a qualitative validity measure to examine differences among low-, medium- and high-validity studies (table 1). A study was given a low overall validity if it scored 'low' on one or more criteria provided in table 1. If a study scored 'high' in each of the criteria, it was given high validity. All other studies were given medium validity.

(f) Moderator analysis

Finally, we analysed the possible influences of so-called moderators as confounding factors, such as publication type, peer review, year of publication, study design, habitat type, taxa and type of water body (lentic or lotic), with multilevel metaregression models with analysis of variance (*Q*-test), which is an approach to explain heterogeneity in effect sizes [38]. For categorical variables, we used only those as moderators if sufficient datasets (i.e. greater than 2 effect sizes from greater than or equal to 2 independent studies) for each moderator category were present.

(g) Publication bias

Studies with significant results and therefore large effects are more likely to be published [49], and this publication bias can influence the summary effect size of meta-analyses [49]. To test whether publication bias might have affected the results and as a further robustness check of our conclusions, we performed Egger's regression test [50] to assess whether a relationship between effect size and the variance of effect size was present in the four subgroups of recreational activities. In addition, we used fail-safe *n* (fsn function in metafor package) as a second measure to detect publication bias. This indicates the number of studies/effect sizes needed to reduce the significance level of the summary

Table 1. Study quality measures and according weights and categories. A main criterion to assess study validity was study design. 'Replication of sampling units' as whole water bodies and 'control of confounding factors' could lead to higher-quality weight (maximum 1). Weight was halved if low and high intensities were compared instead of a real control and also if effects within a water body were studied instead of a comparison between water bodies. A criterion for randomization was only included to identify high quality studies as a qualitative measure. Weights suggested by Norris *et al.* [44] and Christie *et al.* [45].

study design type	Norris *et al.* [46]	Christie *et al.* [47]	quality weights	Study quality
A—after impact only	1	0.0904	0.0904	low
CI—control versus impact	2	0.206	0.206	moderate
BA—before versus after	2	0.226	0.226	moderate
G—gradient-response	3		0.3	moderate
BACI—before–after–control–impact	4	$1+e^{1/-(0.661+0.0153\cdot\ln(n_{\text{impact sites}})+0.0647\cdot\ln(n_{\text{control sites}})+0.111\cdot\ln(n_{\text{control sites}})\cdot\ln(n_{\text{impact sites}}))}$	0.4	high
number of reference/control sampling units				
0	0		+0	low
1	2		+0.2	moderate
>1	3		+0.3	high
number of impact/treatment sampling units				
0	0		+0	low
1			+0.1	moderate
>1			+0.2	high
2	2			
>2	3			
replication of gradient–response models				
<4	0			low
4	2		+0.2	moderate
5	4		+0.4	moderate
>5	6		+0.6	high
controlled for confounding factors				
1—no			+0	low
2—yes			+0.1	high
randomized				
1—no				moderate
2—yes				high
real control				
1—yes			1/1	high
2—low versus high			1/2	low
scale				
1—water body			1/1	high
2—zone			1/2	low

effect size. The fail-safe number (FSN) is considered robust when it is above $5k + 10$, (with k = number of effect sizes) [51].

3. Results

We identified 178 studies (electronic supplementary material, table S2) investigating the ecological impacts of specific aquatic recreational activities (shore use 53, angling 52, swimming 11, boating 76). Effect sizes could be derived from 94 studies, with 31 (33%), 23 (24%), 8 (8%) and 36 (38%) emphasizing the effects of shore activities, (shoreline) angling, swimming and boating, respectively. These studies generated 701 effect sizes. Studies from Western Europe and North America dominated (with 31 (33%), 21 (22%), 12 (13%) and 8 (9%) studies conducted in the USA, Germany, United Kingdom and Canada, respectively; electronic supplementary material, S2).

Ecological impacts were reported for a range of taxa (invertebrates, fish, amphibians, reptiles, birds, mammals and plants) and different ecosystem compartments (soil, sediments and water). Of the 94 studies (electronic supplementary material,

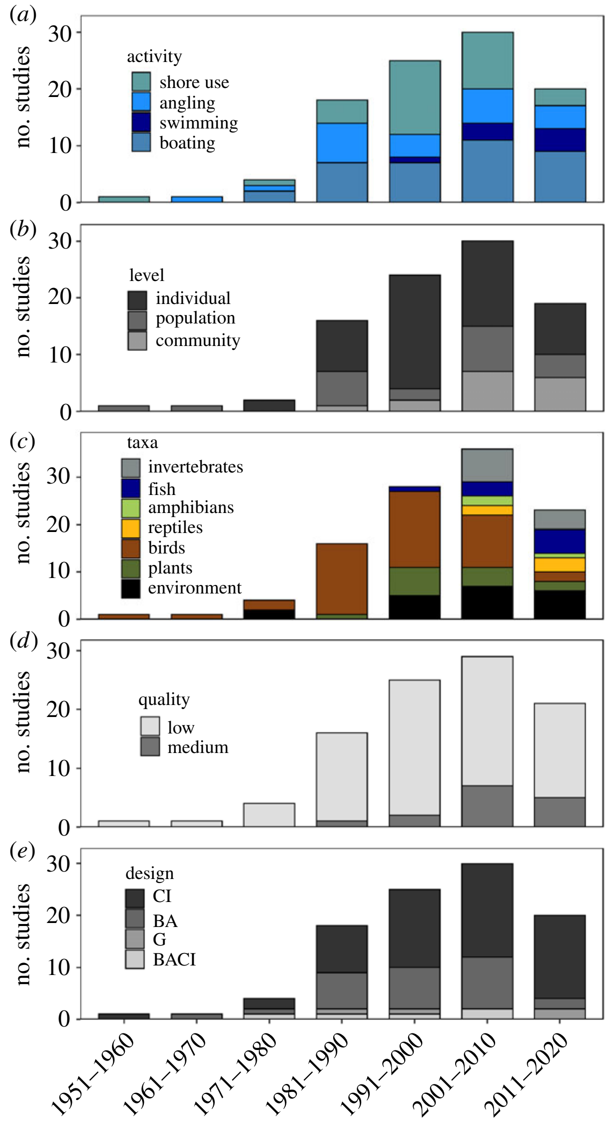

Figure 2. Number of studies over decades per (*a*) recreational activity, (*b*) level of biological organization, (*c*) taxon, (*d*) study quality and (*e*) study design (CI = control versus impact, BA = before versus after impact, G = gradient (correlation)) and BACI = before–after–control–impact design). (Online version in colour.)

table S2) included in the meta-analysis, those emphasizing the impacts of recreational activities on individuals were most prevalent, especially in the early literature (figure 2*b*). During the last two decades, the number of studies targeting impacts on populations and communities has increased, evening out the distribution of studies across the three levels of biological organization that interested us. Forty-eight out of 94 studies analysed focused on recreational impacts on birds (figure 2*c*). The quality of studies in our meta-analysis was mainly rated low (figure 2*d*). However, the proportion of studies with medium study quality increased over time. No studies of high quality could be identified using a fully controlled experimental approach in the wild.

(a) Ecological impacts of freshwater recreation overall and by recreational type

The overall summary effect size of all 94 studies was −0.62 [−0.83;−0.41] (mean, 95% confidence interval) for ecological impacts of water-based recreation. That means the ecological impacts of freshwater-based recreation were significantly negative pooled across all taxa, levels of biological organization and types of recreational activities. Most variability of the pooled effect sizes originated from random effects where the response variable was nested in taxa and study ($\sigma^2 = 0.26$), followed by study ($\sigma^2 = 0.11$) and taxa nested in the study ($\sigma^2 = 0.02$).

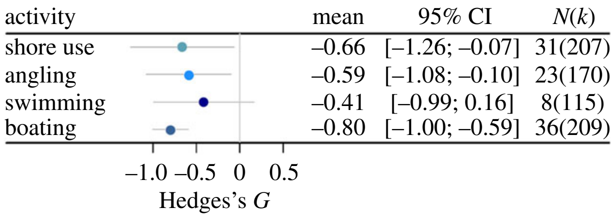

Figure 3. Forest plot with mean effect sizes of recreational activities. Shown are mean summary effect sizes (mean), 95% confidence intervals (95% CI), number of studies (*N*) and number of effect sizes (*k*). Effects are significant if 95% CI (horizontal lines) do not overlap the vertical zero line. (Online version in colour.)

Across taxa and levels of biological organization, the four subgroups of recreational activities studied did not differ in their pooled effect size, as indicated by overlapping confidence intervals (figure 3). The pooled effect sizes were significantly negative for three of the four types of recreational activities, indicating rather negative ecological impacts of aquatic recreation. In line with expectations, boating showed the strongest significantly negative pooled effect size, followed by shore use and recreational angling (figure 3). Although swimming also showed on average a negative summary effect size, confidence intervals overlapped zero (figure 3), indicating non-significance. However, the sample size was particularly small for swimming.

(b) Ecological impacts of freshwater-based recreation across levels of biological organization and on the environment

At all three levels of biological organization (individuals, populations and communities) the summary effect size of freshwater-based recreation was negative for all four recreational activities, specifically for boating and shore use, but effects were not always significant for recreational angling and swimming (figure 4). Specifically, the negative ecological effects of angling activities were significant at the population level but not at the individual and community level. The summary effect sizes of swimming were significantly negative at the population and community level, but the latter effect size originated from a single study and thus remains uncertain. Swimming impacts at the individual level were close to zero and not significant. Moderator analysis showed that for all recreational activities, the level of biological organization were not a significant moderator, either as a continuous (levels 1–3, with 1 = individual level, 2 = population level and 3 = community level) or categorical variable (*Q*-test, $p > 0.1$). Ecosystem and habitat effects were significant only for shore use, while effects were not significantly different from zero for angling, boating and swimming.

(c) Ecological impacts of freshwater-based recreation across taxonomic groups

The summary effect size of recreational impacts on each taxonomic group was, on average, negative but not always

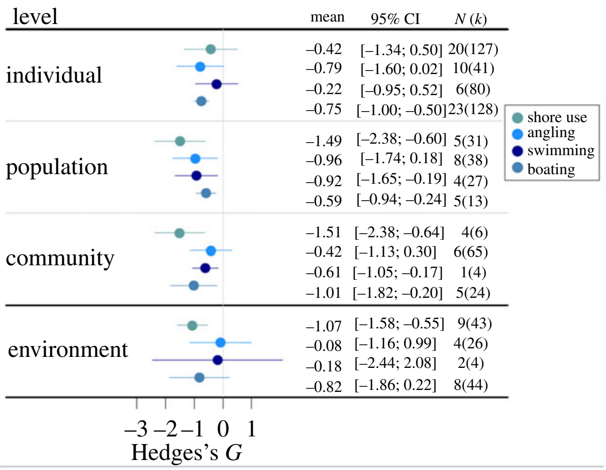

Figure 4. Forest plot with mean effect sizes per level of biological organization (individual, population, community and ecosystem) of recreational activities. Shown are the mean summary effect sizes (mean), 95% confidence intervals (95% CI), number of studies (N) and number of effect sizes (k). Effects are significant if 95% CI (horizontal lines) do not overlap the vertical zero line. (Online version in colour.)

significant (figure 5). The most negative effect sizes were observed for recreational impacts on invertebrates and plants, particularly for shore use and boating. Regarding shore activities, significantly negative ecological impacts were documented for invertebrates, birds and plants. The most significant negative summary effect size of recreational angling was observed in amphibians. Other significant impacts of angling were found for birds and reptiles (only one study), and less pronounced and sometimes non-significant for other taxa (e.g. invertebrates and plants). Significantly negative impacts of swimming were reported only for invertebrates and fish, with summary effect sizes for invertebrates being close to zero and for fish close to significance. Negative ecological impacts of boating activities were revealed for invertebrates, fish, reptiles, birds and plants. All summary effect sizes of boating impacts were significant except for plants. Despite some significant differences in effect sizes between taxonomic groups for shore use and boating, there were only moderate differences in ecological impacts of different recreational activities within taxonomic groups, as indicated by largely overlapping confidence intervals and mostly negative effect sizes.

(d) Ecological impacts of freshwater-associated recreation on birds

The impacts of shore use on individual birds (e.g. flight reactions) and bird populations (only one study) were significantly negative (figure 6). Given the lack of suitable studies, no summary effect size could be calculated for the impacts of shore use on bird communities ($k = 1$). The summary effect size of boating on birds was negative and significant at the individuals level. Two single effect sizes derived from studies of boating impacts on bird populations were both slightly negative, but at the community level, the summary effect size was non-significant (only one study). The impacts of recreational angling on individual birds were, on average, more negative than the population effects, but not significant at both levels and less pronounced at the bird community level. No studies of swimming impacts on birds were identified in our meta-analysis.

(e) Moderator analysis

The analysis of moderators to explain heterogeneity in effect sizes revealed no significant influences of water type (lentic and lotic) in studies on the impacts of shore use, angling and boating. Swimming in lentic waters tended to have more negative effect sizes than in lotic waters (Q-test, $N = 6$, $k = 66$, QM = 3.55, $p = 0.06$), but the sample size was low (three effect sizes out of two independent studies for lentic and 63 effect sizes from four studies for lotic waters). Habitat type as a moderator tended to influence impacts of shore use (Q-test, $N = 20$, $k = 131$, QM = 10.38, $p = 0.07$) and boating (Q-test, $N = 32$, $k = 185$, QM = 6.64, $p = 0.08$) with beach and benthic regions being the most affected habitat types, respectively. By contrast, habitat type was not a significant moderator of angling. The sample size for habitat impacts from swimming was too low to test habitat type as a moderator.

The scale of the study design (comparison of water bodies versus comparison of different zones within a water body) was not a significant moderator for the ecological impacts estimated for shore use, angling and swimming ($p > 0.1$). However, there was a trend for boating impacts being less negative in studies of different waters compared to studies of different zones within one water ($N = 34$, $k = 198$, QM = 3.66, $p = 0.06$). Only 22 studies examined more than one water body as control and more than one water body as treatment of recreational use. Forty-one studies simply compared different zones within the same water body. There was no influence of the study scale on the impacts of shore use and angling ($p > 0.1$).

Peer review was a significant moderator for the studies on impacts of angling ($N = 20$, $k = 135$, QE = 4526 ($p = 0.00$), QM = 6.69 ($p = 0.01$)), with peer-reviewed articles showing less negative effect sizes than non-peer-reviewed studies. By contrast, year of publication and publication type were not significant moderators for any of the four recreational activity categories ($p > 0.1$).

We compared the effect sizes of studying the impact of the presence of a recreational activity compared to sites without recreation (control versus impact) and the impact of an increase in the intensity of recreational activities (low versus high impact). The aggregated effect sizes of these two different approaches were very similar (see electronic supplementary material, figure in S1). The ecological impacts of increased intensity of recreational activity (low versus high impact) appeared slightly stronger than effects of those calculated from studies comparing the presence versus absence of water-based recreation (except for swimming, where the summary effect of low versus high impact relied on only one study).

(f) Considerations of study quality

We conducted rigorous tests on whether the weighting procedure affected the study findings. For all four types of recreational activities, our quantitative measure of study quality (table 1) did not explain variation in effect sizes (Q-test; shore use: QM = 0.71, $p = 0.40$; angling: QM = 2.85, $p = 0.09$; swimming: QM = 0.34, $p = 0.56$; boating: QM = 0.76, $p = 0.38$). Weighting according to study quality yielded slightly less negative effect sizes for impacts of shore use, angling and swimming (without changing the level of significance) and created slightly more negative effect sizes for impacts of boating compared to default weighting by inverse variance (electronic supplementary material, figure in S2). Low and medium study

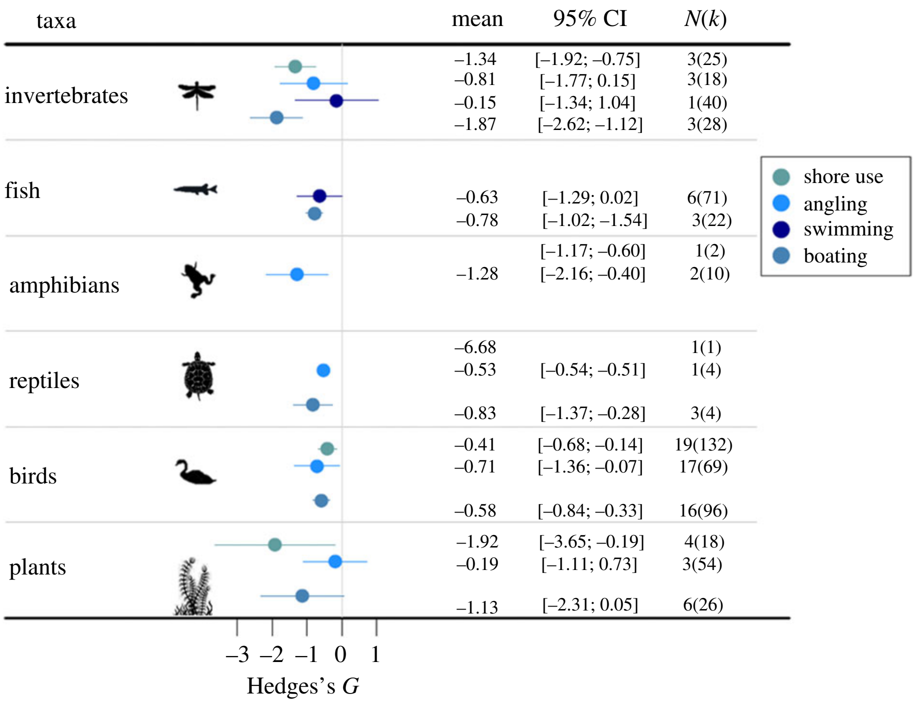

Figure 5. Forest plot with mean effect sizes per taxon of recreational activities. Shown are the mean summary effect sizes (mean), 95% confidence intervals (95% CI), number of studies (N) and number of effect sizes (k). Effects are significant if 95% CI (horizontal lines) do not overlap the vertical zero line. Values based on low sample size ($N < 2$ or $k < 3$) are shown in grey. If $k = 2$ the two effect sizes are given instead of 95% CI. If $k = 1$ the one effect size is given instead of mean summary effect size. (Online version in colour.)

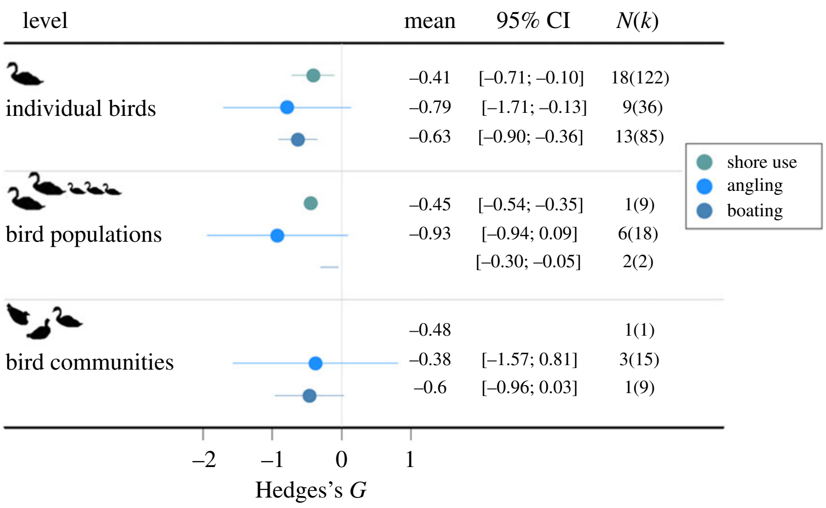

Figure 6. Forest plot with mean effect sizes per level of biological of birds (individual birds, bird populations and bird communities) of the four recreational activities. Shown are the mean summary effect sizes (mean), 95% confidence intervals (95% CI), number of studies (N) and number of effect sizes (k). Effects are significant if 95% CI (horizontal lines) do not overlap the vertical zero line. Values based on low sample size ($N < 2$ or $k < 3$) are shown in grey. If $k = 2$ the two effect sizes are given instead of 95% CI. If $k = 1$ the one effect size is given instead of mean summary effect size. (Online version in colour.)

quality also did not explain the variation of effect sizes ($p > 0.1$). However, descriptive visualization of low quality and medium quality as subgroups revealed that summary effect sizes of medium-quality studies showed less negative mean effect sizes than summary effects of low-quality studies in all four recreational activities (electronic supplementary material, figure S2). In addition, summary effect sizes for the impacts of shore use, angling and boating were only significant in low-quality studies but not in medium-quality studies, indicating that low-quality studies overrepresent negative impacts of recreation.

(g) Examining publication bias

Egger's test revealed a highly significant publication bias in each of the four recreation categories (shore use: QM = 17.11, $p < 0.01$; angling: QM = 6.52, $p = 0.01$; swimming: QM = 19.30, $p < 0.01$; boating: QM = 7.79, $p = 0.01$). The FSN indicated that even if a publication bias affected the meta-analysis, the true effect sizes of shore use, angling and boating would be significant because the FSN was greater than $5k + 10$ (shore use: 49 081 (greater than 1045); angling: 42 167 (greater than 870); boating 70 511 (greater than 1055)). The results can, therefore, be considered quite robust against publication bias, except the summary effect size of swimming (FSN: 89 (less than 585)).

4. Discussion

We found mixed support for the first study hypothesis that the ecological impacts of freshwater-related reactions vary with the type of activity. When aggregated across taxa and levels of biological organization, all four examined freshwater-related recreational activities were found to have significant negative ecological impacts. By contrast, impacts on the environment were only significant for shore use. Examining recreational impacts in more detail for specific taxa and levels of the biological organization revealed differences in effect sizes and levels of significance among the four recreational types. Although the impacts of boating were consistently negative, we rejected the second hypothesis as we could not reveal a consistent signal that increasing interaction strength with the aquatic ecosystem from shore use to boating also increased the ecological impact. In fact, impacts varied with the taxon and the level of biological organization, suggesting the potential for strong contextual effects. It is also possible that our categorization into four distinct recreational types failed to properly capture the specific disturbance potential of a given recreational activity (e.g. degree of water body affected, sound levels, number of people involved). We were unable to derive quantitative information on user densities and other exact metrics of disturbance, which is why we opted for a broad classification of recreational types. Finally, we did not find support for the third hypothesis, that the ecological impacts of aquatic recreation should be strongest at the individual level and decay towards the population and community levels. In general, and despite the evidence for publication bias and low study quality, we conclude that aquatic recreation can be expected to negatively affect ecological traits, but the effects depend upon context, activity, taxa and most likely use intensity and thus should not be generalized.

(a) Ecological impacts of specific recreational activities

Aggregated across all response variables and taxa, all four recreational types exerted similarly negative ecological impacts. However, when examining specific taxa and ecological responses, individual activities varied in their ecological outcomes. In some cases, study numbers were not sufficient to estimate effect sizes or confidence intervals overlapped zero, indicating that the current body of literature would not support general conclusions. Other findings were unequivocal. For example, shore use consistently caused negative trampling effects on riparian soil and vegetation, which can lead to decreased plant height and cover and a shift in species composition towards tolerant plant species and thus affected the environment as a whole [15]. There was also strong evidence that shore use disturbed mobile taxa such as birds. This finding can be explained by riparian and near shore areas being preferred breeding, foraging and migratory stopover habitats of many birds [52] while at the same time being preferred recreation sites. Even though intensities of shore use are expected to increase on warm and sunny days [2], some of the shore uses, such as dog walking, are less seasonal. Shore activities might, therefore, be a prevalent activity along freshwaters and during sensitive periods, such as territory establishment and spring breeding season [53]. We suggest that the best outcomes for conservation may be achieved by temporal zoning. By contrast, selectively constraining or banning single activities while allowing others will unlikely generate substantial conservation gains but fuel stakeholder conflicts instead.

Although (shoreline) angling caused overall significant ecological impacts across all taxa when effect sizes were pooled, these impacts were not consistent across the three biological levels and across taxa and were not significant for environmental response variables. While anglers have been proposed to be a particularly salient source of ecological disturbance, especially for sensitive bird species, because of their long stays in sensitive riparian habitats and their presence overnight [29], we found that the impacts of angling consistently less negative and generally milder than those of (non-angling) shore uses. One explanation might be that most anglers practise fishing in a rather solitary and relatively quiet fashion, thereby minimizing disturbances [54]. Angling restrictions to reduce wildlife disturbance might, therefore, not be as effective as commonly believed. The greatest impacts of angling were observed for amphibians, but these impacts can probably be explained as indirect effect from predation by fish [55]. Angler-managed lakes tend to host a more diverse fish community, including many larger-bodied individuals that predate on tadpoles [55], than unmanaged lakes [46]. Impacts related to recreational angling that were not observed for other recreational activities were mortality and injuries in wildlife related to angling gear [47,56]. Although littering is of the general concern in recreation [57], angling gear exposes particular threat to wildlife because of the use of hooks, non-degradable fishing lines and toxic material such as lead [47,56]. Less environmentally harmful angling gear alternatives (e.g. degradable fishing lines and lead-free weights) can be recommended from a conservation perspective.

The ecological impacts of swimming were generally not well documented, probably because of the difficulties in studying the impacts of swimming isolated from the multiple recreational activities happening jointly [58]. Studies of swimming as an isolated impact often concentrate on the toxicity of sunscreen compounds on biomass and mortality of e.g. molluscs [59]. Human discharge is an additional swimming-related impact source that can affect water quality by nutrient excretion or pathogens (not covered here). Surprisingly, we did not find literature on the disturbance effects of swimming on birds or mammals. When resting at banks or shore swimmers should have similar disturbing effects like other shore users. More studies on the impacts of swimming, snorkelling and diving are recommended to fill the knowledge gaps, especially because in temperate regions some lakes experience very high swimming uses during warm summers [2].

Boating showed the strongest and most consistent ecological impacts of the four activity types examined. We attribute our findings to the speed and noise levels, as well as wave actions and anchor impacts, associated with boating activities. Even though there are comparatively slow-moving and less noisy boating forms, such as paddling, many boating activities include methods of propulsion. Both speed and noise increase disturbance impacts [60] and explain the strong impacts of boating activities documented across all levels of biological organization. Specifically, boat propellers and anchoring can lead to damage to hard sediments and macrophytes, sediment resuspension thereby increasing turbidity and cause injuries in wildlife [9]. Additionally, wake wash, anchoring and mooring effects [30] and the introduction and translocation of invasive species by boats [31] are common ecological impacts associated with boating [9]. Reducing speed, noise and wake wash, as well as the use of zoning, might be effective in mitigating boating effects.

(b) Impacts of recreational use of freshwaters across levels of biological organization

Early literature on the ecological impacts of recreational freshwater use focused on the individual level. In recent decades, ecological impacts at higher levels of biological organization (populations and communities) have also been increasingly studied. Methodological advances might have increased abilities to study the population or community effects of recreation. Importantly, ecological impacts at the population level might be more relevant for conservation than at the individual level [40], although highly threatened species provide exceptions for single individuals' protection. Therefore, from a normative perspective (figure 1) [22], recreation-induced impacts on the mortality or breeding success of animals may be considered more important than changes in behaviour, physiology or other individual-level traits. Therefore, we rejected hypothesis 3 that recreational impacts would dampen from individual to population and community level.

Our meta-analysis revealed no significant differences among the summary effects of water-based recreation impacts at different levels of biological organization (i.e. recreation had similar impacts at the individual, population and community level, but the impacts were not consistently negative and significant). Importantly, some activities had significant effect sizes at higher levels of the biological organization but not at lower levels. This finding was unexpected because, intuitively, ecological impacts should decrease in strength from the individual to community level (hypothesis 3). While angling showed mainly strong impacts on lower levels of biological organization, impacts on the community level were minor. For shore use and boating, impacts at the community level were similarly strong as those at other levels. These activities also showed very strong environmental impacts, such as increased turbidity by boat wakes, which in turn can affect individuals, populations and communities. In short, our review did not support that freshwater recreation mainly affects individual levels of biological organization, but impacts are context- and activity-dependent, and cannot be easily generalized.

(c) Ecological impacts of freshwater recreation across taxonomic groups

Our taxonomic analyses revealed impacts of freshwater recreation varying by taxon and most pronounced for invertebrates and plants. Invertebrate communities serve as sensitive biomarkers for the ecological status of freshwaters [61] and can be influenced by changes to riparian vegetation and macrophyte cover as well as fish predation [62,63]. Reduced plant cover significantly impacts other species and ecosystem traits, such as increased turbidity and sediment resuspension [64], reduced fish reproduction [65], increased planktivory by fish [84] and loss of epiphyton and periphyton communities [66]. A sustained change in vegetation, as well as invertebrate abundance and species composition in response to recreation, can ultimately affect higher trophic levels, such as birds and fish as predators [61]. Importantly, not all recreational activities will have similar impacts. For example, our study failed to find significant effects of recreational angling on invertebrates and plants, while the impacts of boating and shore use were strong and consistently negative on these taxa. Again, a key message of our work is that although recreational impacts on specific taxa are conceivable, they should not be generalized across all forms of recreation.

In birds, we detected high variation in effect sizes when comparing different recreational activities. This finding might be due to differences in species' susceptibility to human presence and local variation in habitat quality, cover and user behaviour [40]. Moreover, FIDs vary among species and individuals of the same species [67], and this popular metric to assess the individual-level flight reactions of birds is also sensitive to local habitat and habituation. Other reasons for inconsistent responses to individual recreational activities could involve large variation in life histories, diets, nesting preferences, etc. of bird communities in riparian and wetland areas. Despite their high variation in behavioural responses, birds are considered highly disturbance-sensitive taxa and of significant conservation concern, probably explaining why bird studies were initially dominant in the material that we reviewed. In addition, they are relatively easy to study, with large amounts of readily available data. However, experimental manipulations of birds in freshwater contexts are rare, and observational studies, especially those of low quality, were found to generate larger negative effect sizes than higher-quality studies. These patterns might explain why the impacts on birds are well documented and significant, but also quite variable and less strong relative to other taxa, especially when compared to impacts on plants and invertebrates.

(d) Study limitations and future research needs

Our work constitutes the first systematic, comprehensive and transparent meta-analysis that summarized the current evidence about freshwater recreation impacts on species, populations and ecosystems. However, we identified a series of limitations that are worth noting. Most of the studies identified used study designs that we scored being of low validity. In particular, most studies were observational without controlling for confounding factors, which might be one explanation for high variances in effect sizes observed for some taxa, levels of biological organization or recreation types. Although we were able to derive more than 700 effect sizes, it was not possible to generate effect sizes for all combinations of taxon and recreational use. We also found studies of lower validity tended to report stronger negative effects than studies with medium validity, which is another indicator of publication bias contributing to overreporting of recreational impacts [36]. Although we have strong evidence for publication bias in our dataset, our robustness checks (e.g. FSN) indicated that impacts would still be significant for shore use, angling and boating. These results can, therefore, be considered robust despite the study limitations identified. We strongly recommend more experimental studies and better reporting of even basic data in future studies to allow the pool of effect sizes to be enlarged in the future.

As another limitation most studies used a within-ecosystem design, comparing sites with and without recreation or along an activity gradient within in the same ecosystem. Such designs do not allow population- or community-level insights at the ecosystem scale. Even though the scale was not a significant moderator, there was a tendency that the ecological effects of recreation on the scale of whole water bodies were less pronounced than the effects on the scale of zones within the same water body. Thus, the interpretation of impacts at the scale of whole waters is limited. Experimental studies were generally very rare and very few used robust before–after–control–impact designs. This is a major shortcoming of the entire literature mainly relaying on observational data. Only experiments can identify true causalities and are thus strongly recommended for future studies.

Only 94 studies out of the 178 that were principally relevant could be used for this meta-analysis, because the rest did not allow the calculation of effect sizes as a result of missing data. We tried to be as inclusive as possible to maximize the sample size, by including studies with different scales and comparisons of different intensities, and used a series of robustness checks for our work. Importantly, we considered study quality using a weighting approach, which we found generated more conservative results and is thus considered superior to an unweighted approach. In this manner, we also addressed the problem of pseudoreplication in many studies by incorporating the number of studied water bodies in our validity measure. Nevertheless, the sample size for specific taxa and recreation type combinations was low and those average effect sizes should be treated with caution. In addition, the large number of bird studies compared to other taxa might have biased the overall summary effect size towards less negative. The detection of statistically significant but weak effects is typical of large sample sizes. Thus, many less prominent (as currently covered by literature) but nonetheless important ecological impacts might remain undetected because of low sample sizes. We strongly recommend performing more studies and engaging in more complete reporting to facilitate the extraction of data needed to calculate effect sizes in future research.

Even though this work can be considered a global meta-analysis because it incorporates studies from almost all continents (except Africa and Antarctica), the studies were conducted primarily in the Northern Hemisphere and mainly in only three countries. This might have introduced spatial and interpretative biases into the analyses that could not be avoided. More research on underrepresented continents is recommended. The bias towards wealthier countries should be addressed by supporting research in the global south. In addition, the large sample size regarding bird studies, compared to low sample sizes for other taxa might have biased the overall summary effect size to be less negative. The detection of statistically significant but not strong effects is typical of large sample sizes, and indicates that many less prominent but nonetheless very real impacts are also being experienced by other systems, but they are below our detection due to much smaller sample sizes. Further research is especially needed to study the impacts on reptiles, amphibians and in general population and community levels of all taxa. Emerging methods that might facilitate such research include drones, citizen science, remote cameras and sensor networks.

(e) Conclusions and implications for conservation policy

Our synthesis revealed that recreation impacts on freshwater ecosystems are often negative, potentially widespread, but vary by recreational type, taxon and ecological response variable. Hence, ecological impacts of recreation can be expected, but they are context-specific and cannot be easily generalized. Therefore, policymakers and conservation managers need to engage in nuanced and contextualized evaluations about the impact of recreation rather than to bluntly assume that aquatic recreation necessarily constrains biodiversity or ecosystem status. Policymakers and managers are also recommended to carefully define conservation objectives, be explicit and transparent about the underlying normative decision framework, and engage proactively with stakeholders before implementing actions. Specifically, we recommend carefully defining which level of biological organization is considered ecologically or legally relevant when motivating conservation action, because our work has shown that outcomes of recreation are in some cases activity specific and vary from individuals to ecosystems. While individual-level conservation might be necessary for threatened species facing the risk of extinction, in most conservation contexts, conservation of population size, community integrity or habitat status is more relevant. Our work showed that ecological impacts of outdoor recreation may not be present in certain taxa and for certain levels of biological organization. In these situations, constraining recreation with the hope of achieving conservation gains may be an illusion that negatively affects human welfare without supporting conservation. Additionally, as the aggregated effect sizes of the various recreation types were often quite similar, we warn against conservation policies that are tailored to just one type of recreational use. Constraints on single-user groups may have no conservation benefit as long as other activities continue to use local ecosystems. In cases where decision-makers deem conservation action to be relevant, our work suggests that removing recreation and other human uses entirely from selected ecosystems may be most promising, followed by variants of spatio-temporal zoning of all uses. Clearly, removing access temporarily or permanently will strongly negatively affect human welfare, which has to be explicitly considered in the design and implementation of conservation policies to ideally achieve net gains for conservation and human welfare (e.g. by improving infrastructure in non-protected ecosystems as a compensatory measure). Any conservation measure should be carefully monitored, ideally using before–after–control–impact designs to generate the applied evidence base on whether managing recreation has the intended conservation benefits. In particular, monitoring the impacts of zoning and reduced access on the scale of whole waters is strongly recommended, as this practically relevant knowledge for conservation management is currently lacking.

Data accessibility. Data and R script are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h18931zm3 [68]. Supplementary information are provided in the electronic supplementary material.

Authors' contributions. M.S., R.A. and C.W. conceptualized and designed the meta-analysis and the systematic review. Acquisition of data, literature screening and extraction of relevant information for effect size estimation was performed by M.S. with support from B.W. and N.M. M.S. and R.A. performed the analysis and drafted the manuscript. Interpretation of results, critical revision of the manuscript for important intellectual content and final approval was performed by all authors.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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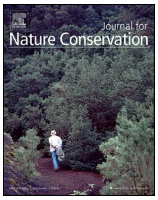

A day on the shore: Ecological impacts of non-motorised recreational activities in and around inland water bodies

Nora Meyer[a,*], Malwina Schafft[b,d], Benjamin Wegner[b,d], Christian Wolter[b], Robert Arlinghaus[b,d], Markus Venohr[c], Goddert von Oheimb[a]

[a] *Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Pienner Str. 7, 01737 Tharandt, Germany*
[b] *Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany*
[c] *Department Ecohydrology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany*
[d] *Division of Integrative Fisheries Management, Department of Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany*

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ABSTRACT

With the increasing importance of recreational activities in and around inland water bodies, there is a need for sound knowledge about their ecological impacts. This narrative review summarizes and analyses the ecological effects of the land-based activities walking, biking, nature observing and relaxing on the shoreline as well as the water-based activities swimming, snorkelling, scuba diving, and canyoning. Searching multiple databases with standardized search terms retrieved twenty-six publications for further analyses. While walking was the most studied activity, birds were the most studied organism group, with a focus on individual time budgets and avoidance behaviour. Population-level analyses were exceedingly rare. The most frequently studied activity-effect combinations were walking and birds, walking and terrestrial plants and scuba diving/snorkelling and fishes. Aquatic plants, amphibians, reptiles, water chemical parameters and terrestrial and aquatic algae were underrepresented in the existing literature. No study on mammals was identified. Disturbance often led to temporary behavioural changes of birds and wildlife. Plants were more strongly impacted than animals, suffering from recreation-induced damage and dieback, which led to changes in community composition. The difference in intensity of impact between mobile and sessile organisms calls for different management strategies, depending on local conservation targets. Future studies should focus on underrepresented taxonomic groups and study population or community-level impacts, to collectively provide the sound scientific basis for the sustainable recreational use of inland water bodies, while minimizing or avoiding severe ecological impacts.

1. Introduction

Lakes, reservoirs and rivers cover just 2.3% of the Earth's surface, but are disproportionately rich in biodiversity (Dudgeon et al., 2006) and home to 9.5% of the Earth's known animal species (Reid et al., 2019). One third of all vertebrate species are confined to freshwater (Dudgeon et al., 2006). However, freshwater ecosystems experience substantially greater biodiversity losses than terrestrial ecosystems (Bongaarts, 2019; Dudgeon et al., 2006). Freshwater bodies are naturally in a receiver-position in the landscape, where they accumulate various catchment influences (Reid et al., 2019) and are thus potentially highly sensitive to the net effect of multiple anthropogenic stressors (Birk et al., 2020). Climate change places additional stress on already burdened freshwater bodies (IPCC, 2013; Scheffers et al., 2016).

The numerous impacts on biodiversity resulting from multiple anthropogenic uses of freshwater bodies are well recognized and for some taxa well reported (e.g. Díaz et al., 2019; Grizzetti et al., 2019; Jackson et al., 2016). A plethora of studies have found significant drivers of biodiversity change, such as urbanisation (Chen & Olden, 2020), land use change (Radinger et al., 2016), water abstraction (Boddy et al., 2020), hydropower production (Schwarz, 2019), river regulation (Peipoch et al., 2015), and inland navigation (Zajicek & Wolter, 2019). However, these commercially-centred analyses of anthropogenic impacts on aquatic ecosystems largely ignore an increasing non-commercial recreational use. In the developed world, recreational activities have gained considerable importance due to substantial changes

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[*] Corresponding author at: Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Pienner Str. 7, 01737 Tharandt, Germany.
E-mail address: nora.meyer@tu-dresden.de (N. Meyer).

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in many people's living conditions (Arlinghaus et al., 2021; Venohr et al., 2018). Recreational activities are defined as activities that offer a contrast to work-related activities and the possibility of constructive, restorative and pleasurable benefits (Cole & Hammitt, 1998). The impacts of recreational and tourist activities are best studied in forest and marine systems (Larson et al., 2016). In marine systems, studies have focused, for example, on the impacts of ecotourism on cetacean species (Lusseau, 2004; Trave et al., 2017), or scuba diving on coral reefs (Samia et al., 2019).

Since 1950 there has been a rapid urbanisation process, resulting in as much as 55% of the worlds population now living in cities (United Nations et al., 2019). Hazards to health related to urban lifestyle are on the rise in industrial countries (Béjean & Sultan-Taïeb, 2005; Godfrey & Julien, 2005). At the same time, work strain (Morschhäuser et al., 2010) and dissatisfaction with work schedules has risen (Roberts, 2007). Outdoor recreational activities are seen as a cure for the mental and physical stress of people in ever-growing cities (Frumkin et al., 2017; Morita et al., 2011; Ryan et al., 2010; Wolsko et al., 2019). As water is as much cultural object as material substance (Watson, 2019), even a little waterbody in an urban surrounding can be the core for environmental education and recreational activity (Gunn et al., 1972; Meyerhoff et al., 2019). Inland waters are a popular destination for people in need of a break or a cool-down, because for most people they are easier to reach than marine waters. Small lakes, some of anthropogenic origins, like gravel pits are particularly important locations not only for recreational activities of urban residents (Meyerhoff et al., 2019) but also for environmental education (Gitau et al., 2019), because they are highly abundant and close to many people's home. Spending a day on the (lake-) shore relaxing, walking, biking or swimming are all popular activities (Kochalski et al., 2019). Especially in forests, ponds and water surfaces attract visitors and increase visitor numbers (Janeczko, 2009). Monitoring the impacts of these activities is difficult as they are usually performed by individuals rather than clubs or other organisations and because the widespread nature of a large number of small lakes scattered in the landscape. However, a growing demand for access to surface waters may cause temporary or permanent damage and endanger precisely the scenic beauty which is sought by visitors and consequently also represents a threat to aquatic habitats for flora and fauna (Andrés-Abellán et al., 2005).

The ecological impacts of recreational activities on freshwater bodies have not yet received much academic attention, although the degradation of natural wildland areas by human recreational activities was identified already in the 1990s (Cole & Hammitt, 1998), and first studies about recreation-induced ecological changes were already published in the 1970s in the USA (Liddle, 1973; Liddle, 1975). There are many ways in which recreational behaviour directly impacts the environment, such as disturbing wildlife (Shannon et al., 2017), compacting or degrading soil (Andrés-Abellán et al., 2005) and breaking off parts of plants (Bowles & Maun, 1982). Recreational activities can also cause degradation or loss of habitat and, thus, thereby impact the diversity, composition and abundance of freshwater organisms (Venohr et al., 2018). The term ecological impact suggests an undesirable change as a result of anthropogenic use (Cole & Hammitt, 1998), but is a more precise term than disturbance (Stock et al., 1994) because the term disturbance is value loaded. Ecological impact is therefore the term used in this analysis. The (ecological) impact of visitors on natural areas depends not only on the overall number of visits, but also on the duration and type of activities and the fragility of the respective ecosystem or organism group under consideration (Cole, 1995; Cole & Marion, 1988).

Many inland water bodies are particularly sensitive ecosystems (Dudgeon et al., 2006; Ormerod et al., 2010), with recreational activities found both at the shoreline and in the water. On and in open waters, human presence can damage water plants and disturb aquatic wildlife, for example nesting waterfowl, which may lead to lower reproductive success (Keller, 1989; Yalden & Yalden, 1990). Another threat may be the release of nutrients and chemicals from humans into the water (Poiger et al., 2004), potentially affecting fish (Blüthgen et al., 2012) or invertebrates (Schmitt et al., 2008). Invertebrates are commonly used for monitoring changes in quality of freshwater ecosystems (Hodkinson & Jackson, 2005). Especially benthic invertebrates are used to determine water quality (Carew et al., 2013) and have been studied in recreational contexts to index anthropogenic impacts (Brauns et al., 2011; Hardiman & Burgin, 2011a, 2011b).

Given the increasing importance of recreational activities in and around inland water bodies and the applied need for a sound knowledge base to manage the various demands while conserving and enhancing biodiversity, we conducted a systematic literature review on the ecological effects of recreational activities which take place near or in inland waters. Previous reviews on the effect of recreational activities on nature which bear reference to freshwater systems exists (Table 1). Walking is one of the most common recreational activities on land; accordingly, this activity and the effects of trampling are well studied. Liddle (1975) and Cole & Bayfield (1993) laid the foundations for this research field. Obedzinski et al. (2001) summarised the effects of camping, walking and vehicles on woody vegetation. Anderson et al. (2015) studied the effect of walking on the spreading of non-native species. Other systematic reviews have compared effects of aquatic recreation on wildlife (Larson et al., 2016). Anderson et al. and Larson et al. were the only ones using meta-analytical techniques. Few studies have been published on the ecological effects of non-consumptive land-based activities, such as biking (Nyhof & Trulio, 2015), relaxing on the shore (Bowles & Maun, 1982) and nature observation (Wilkins et al., 2017). Non-comprehensive summaries on recreation-induced effects on freshwater systems exists as well (Venohr et al. 2018).

Yet, the recreational activities swimming, diving, snorkelling and canyoning remain insufficiently studied. In a global systematic review, Larson et al. (2016) analysed, among other publications on different topics, 25 studies dealing with swimming, unfortunately without stating how and which species were impacted. Another review by Brausch & Rand (2011) focused on the influence of chemical components of personal care products on aquatic organisms such as fish, algae or plants without analysing the paths of products into the water, but did not particularly focused on recreational activities as a source. In general, swimming, diving, snorkelling and canyoning are expected to have effects on organisms located in the open water and on the shoreline, but this has not yet been systematically assessed.

Most previous reviews of recreation in freshwater ecosystems did not focus on one specific activity (Table 1) but concentrated on disturbance in general (Blumstein et al., 2005; Cayford, 1993; Price, 2008) or on recreational use in general (Blanc et al., 2006; Carney & Sydeman, 1999; Cole & Landres, 1996). In a more specific approach, Gerba (2000) reviewed the shedding of enteric pathogens during recreational swimming, without, however, linking the amount of material shed by bathers to the effect on aquatic organisms. We are not aware of reviews on the ecological effects of swimming, snorkelling, scuba diving, canyoning, walking, biking or relaxing close to an inland water body.

This study provides the first comprehensive review of recreational activities and their ecological effects, with particular focus on largely unregulated, private activities on the banks and in the littoral zone of freshwaters. In particular, we focus on the land-based activities walking, biking, nature observation and relaxing on the shoreline and on the water-based activities swimming, snorkelling, scuba diving and canyoning. Our literature review focuses on publications that clearly link the impact of a specific activity with a response of organisms or a change in soil or water characteristics. We used material identified with a standardized literature search to determine:

(a) which combinations of activities and impacted organisms were studied,
(b) which aspects of these activities were observed to have an effect and
(c) how severe the observed ecological impacts were.

Table 1
Summary of all reviews found with the search-terms matching the topic of water-related recreation (n = 11).

Activity/ Target Organism	Camping	Disturbance	Recreational use	Personal Care	Vehicles	Walking
Algae				Brausch & Rand, 2011		
Amphibians				Brausch & Rand, 2011		
Animals			Larson et al., 2016			
Aquatic plants				Brausch & Rand, 2011		
Benthic invertebrates				Brausch & Rand, 2011		
Birds		Blumstein et al., 2005 Cayford, 1993 Price, 2008	Carney & Sydeman, 1999			
Fishes				Brausch & Rand, 2011		
Non-native Species						Anderson et al., 2015
Vegetation						Root-Bernstein & Svenning, 2018
Wilderness ecosystems			Cole & Landres, 1996			
Wildlife			Blanc et al., 2006			
Woody vegetation	Obedzinski et al., 2001					Obedzinski et al. 2001

2. Methods

The literature databases and search engines BioOne, AFSA, Web of Science Core Collection, Scopus, Conservation Evidence, Base and Natursport were used with search terms matched to their individual specification and focus (see search terms provided in S1-S8). To detect publications that focus on recreational activities, the search terms “recreation”, “leisure”, “sport”, “tourist” and “outdoor activity” were used. Terms that were used to refer to a water-based location were for example “lake”, “river”, “freshwater”, “marine”, “littoral” etc. To ensure a measured impact of some kind, terms like “reaction”, “impact*”, “disturb*”, “effect” or “change” were employed. The ecological aspects were addressed with terms like “animal”, “vegetation”, “biodiversity”, “water” and the main taxonomic classes of the animal kingdom (for details see Tables S1-S8). Google and Google Scholar were used as additional sources with reduced search terms (S5). The German literature base “Natursport” was used to identify grey literature. The search was not limited to studies published in specific years. But as the last query was performed in February 2019, no studies published after this were taken into consideration for analysis.

The search terms yielded over 13,000 records. These were filtered automatically in EndNote by the second author to omit duplicates. Then some of us screened titles and abstracts for the recreational activities of interest. This systematic review represents an in-depth analysis of a

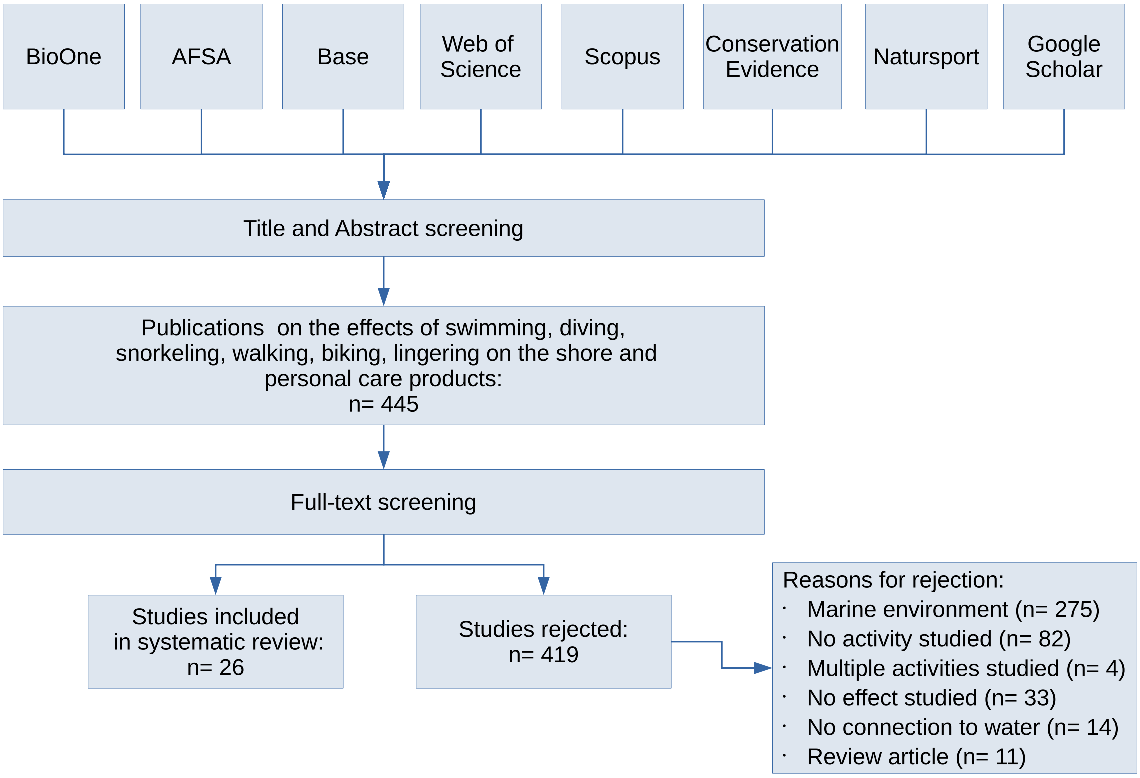

Fig. 1. Flowchart for literature acquisition.

subsample of all recreational activities carried out in freshwater ecosystems. The activities analysed here include biking, relaxing at the shore, nature observation, swimming, snorkelling, scuba diving and walking on land or in a stream (canyoning). Literature about consumptive activities (e.g. angling and hunting) and boating activities were excluded. This selection yielded 445 publications (Fig. 1). After full-text screening performed by the first author we excluded papers for the following reasons: from marine environments (275), no reference to specific activities or laboratory studies (82), reporting cumulative effects from several activities (4), no reference to impacts (33) and reviews. Elven of the excluded reviews were further referred to in introduction and discussion. Additionally, nine of the 419 publications that were discarded from the main-analysis, because they did not meet the quality criteria, were used in the discussion. The main analysis consists of 26 publications.

The information provided by the retrieved papers was manually extracted and saved in a standardized form according to Table 2. Setup information included study duration and location, study design and number of replicates. Organisms studied and species' identity were coded along with the response measured and the response specification. Animals were categorised into the main groups birds, mammals, amphibians, reptiles, invertebrates and fishes. Plants were differentiated into macrophytes and algae. Soil characteristics comprised density and content and water characteristics included water clarity, pH and nutrient load.

For every effect reported, the level of biological organisation at which the study object was affected was determined. As effects on the individual level we defined changes in behaviour, such as statements on time budgets (for example, time spent foraging, vigilant or in comfort), and physical reactions such as damages, injuries or heart rates. An effect at the population level was present when measurements of abundance allowed statements on the relative size of the population or when reproduction was affected. Community composition was impacted when changes in biodiversity or species composition were observed. We defined the ecosystem as the highest level of biological organisation. Changes in habitat structures, such as vegetation cover, in water quality and the compaction of soil fall into this category.

The specific aspect of each activity that had an impact on the environment was noted. In most studies, it was not clearly stated whether the visual, acoustical or olfactory aspect of human presence caused a reaction in the affected animals. Then, presence was noted as the specific aspect of the activity. If mentioned, the visitor number or density was extracted to gain insight on the intensity of human pressure that led to an ecological impact.

3. Results

3.1. Quantity and quality of publications

After filtering, 26 articles remained for our analyses. Of the overall limited number of studies, a clear concentration of locations on the northern hemisphere was found. Most studies were carried out in the USA (n = 7) and Germany (n = 6). The remaining 13 studies were performed in nine countries; two studies each in Australia, Brazil, Great Britain and Spain, and one each in Canada, France, Russia, Switzerland and Turkey. The most frequently used study-design was a comparison of control and impacted sites (CI, n = 15). Five studies reported the impact of a recreational activity (A, after impact only), while another five also considered the status before an impact (BA, before vs. after). Only one study used the most comprehensive BACI design comparing before and after observations of both impacted and control plots. Birds were the most frequently studied (9 publications), followed by invertebrates (6), plants (4), soil (4), fishes (3), water (2), amphibians (1), reptiles (1) and algae (1) (Fig. 2). Multiple groups were analysed in four studies. The studies on animals and plants focused on time budgets and abundance rather than biodiversity and reproductive success. Most studies (n = 17) referred responses to recreational activities at the individual level. Effects at population, community and ecosystem level were reported by five, six and four studies, respectively.

Table 2
Parameters and details retrieved from the literature.

Coded Parameter	Variables
Identifier	Authors
	Publication type
	Journal
Study type	A - after impact only
	CI - control vs impact, no before data
	BA - before vs after without control
	G - gradient response model
	BACI - Before /after control impact
Study design	temporal randomised
	spatial randomised
	temporal not randomised
	spatial not randomised
Biotope	Lake
	River
Taxon / Physics	Invertebrates
	Fish
	Amphibia
	Reptiles
	Birds
	Mammals
	Plants
	Algae
	Soil characteristics
	Water characteristics
Activity	Walking
	Dog walking
	Biking
	Swimming/Bathing
	Snorkelling
	Diving
	Camping
	Wildlife observation
Impact	Presence
	Noise
	Trampling
	Paddling
	Pollution/Toxicity
	Damage/Injury
	Extraction/Consumption/Mortality
Response measured	Avoidance
	time budgets
	Physiological
	Abundance
	Reproduction
	Community
	Biodiversity
	Water chemistry
	Pollution
	Soil compaction
Level of biological organisation	Individual
	Population
	community composition
	Ecosystem
Outcome	Positive effect
	Negative effect
	Change
	No effect
Visitors	Density
	Number

Effects of recreational activities on soil and water characteristics were addressed in four and two studies, respectively (Fig. 2). Two studies each focused on soil compaction and the abundance of certain chemical elements in the soil and two focused on water chemistry. Walking was the most frequently studied activity followed by relaxing on the shoreline and scuba diving, while all other activities were examined in one study each. The most investigated impacts were human presence and trampling, while water pollution and noise were only addressed in the swimming and dog walking study, respectively.

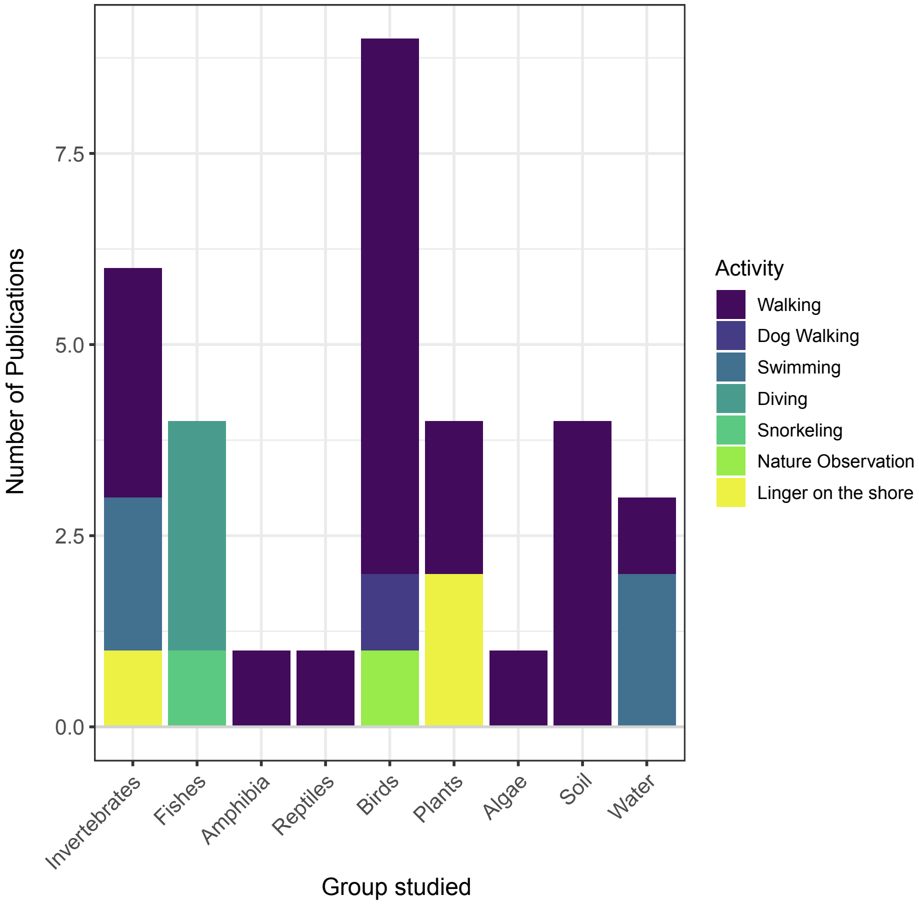

Fig. 2. Bar chart displaying the number of publications studying each combination of study object (Group) and activity. As six publications reported on more than one combination, the total is n = 33.

Most studied habitats were located in or around lakes (n = 17), primarily at the shore (n = 8). The studies relating to rivers (n = 11) concentrated mainly on the river banks (n = 8). One publication studied the benthos of a river.

Human presence was the most studied impact; however only five studies provided information on visitor numbers in their respective study areas. Two of these publications reported results for experimental disturbance. Schmidt & Gassner (2006) tested the influence of two scuba divers on the behaviour of fish, and Hardiman & Burgin (2011a, 2011b) studied the impact of different trampling intensities on invertebrates in a canyon stream. Guillemain et al. (2008) reported one guided tour nearly every day in their study area and the study area of Serengil & Özhan (2006) was visited by 10,000–50,000 people per year. Caires (2007) reported an observed threshold relationship between canyoning and invertebrate drift, where four walkers per 30 min interval led to a significant increase in invertebrate drift. Yalden (1992) reported a peak of 7.8 people per km shoreline. The low number of publications reporting visitor numbers and the differing ways of reporting them impedes a comparison of the recreational usage intensities in terms of impact thresholds.

Another factor for estimating visitor densities is the size of the impacted area. This information was included in eight publications, mainly as the lake surface area or the length of the river section under observation. However, no generalisations can be generated from this information since the output forms were too different across studies.

3.2. *Terrestrial organisms and soil*

3.2.1. *Birds*

Birds were the most commonly studied group, with nine publications. The focus was on responses at the individual level (n = 7). In three cases, effects on the community level were reported. One publication focused on two different levels of biological organisation (individual: individual short term abundance, and community level: species diversity (Fletcher et al., 1999)).

In one study, birdwatching tours did not significantly affect the abundance of waterfowl but induced behavioural changes (Guillemain et al., 2008). The birds spent less time in comfort and increased the time spent foraging and in movement. Guillemain et al. (2008) assumed that waterfowl increased the time spent foraging to compensate for energy loss caused by disturbance. They proposed that the birds became accustomed to disturbances to some extent, so that they did not leave disturbed lakes. However, the waterfowl did not become fully habituated to the disturbance, so that behavioural responses remained visible. This is consistent with findings of a walking experiment showing that waterfowl in a preserved area did not increase tolerance towards pedestrians over the course of one season (Trulio & White, 2017). In another study on waterfowl, the presence of pedestrians increased the time spent vigilant (Fernández-Juricic et al., 2007), while sleeping time was significantly reduced (Bellebaum, 1999; Fernández-Juricic et al., 2007). Birds seemingly not only react to visual stimuli but also recognise danger by acoustic signals. The time spent vigilant significantly increased after the playback of dogs barking, as would occur during dog-walks (Randler, 2006). A similar effect was observed by Randler after a playback of alarm calls of coots. Birdwatching led to a significantly longer vigilance in sandhill cranes, and the time spent foraging was longer than in undisturbed areas (Wilkins et al., 2017). However, human activities explained less than 20% of the variation in crane behaviour at impacted sites compared to undisturbed sites. Wilkins et al. (2017) suggested buffer zones between humans and birds as a management measurement. This was also proposed by Fernández-Juricic et al. (2007) for areas that provide suitable habitats for birds.

Fletcher et al. (1999) did not only focus on the individual-level but also at the level of community and found a higher species richness of raptors, along with a higher number of individuals in control sites along riparian corridors than in sites with a path next to the river. However, the abundance of red-tailed hawk (*Buteo jamaicensis*), known to be insensitive to urbanisation, was not influenced by pedestrians. Overall, there is limited evidence that entire populations of waterfowl or water-related birds are affected by shore use so far.

Yalden & Yalden (1990) detected a sensitivity of golden plovers (*Pluvialis apricaria*) to the presence of people in the pre-incubation period. The parents took more time returning to incubating when people were around, risking the survival of their offspring. Territory fights occurred when the parents tried to lead the flock away from the pedestrians on the shore (Yalden, 1992; Yalden & Yalden, 1990). Yalden (1992) observed a significantly lower number of territories of common sandpipers (*Actitis hypoleucos*) in lake sections with recreational disturbance. Surprisingly, a higher percentage of hatched eggs and fledged chicks was found in the disturbed territories, but the difference was not significant (Yalden 1992). However, the pronounced avoidance of disturbed areas by common sandpipers resulted in an overall smaller population size at the studied lake (Yalden, 1992).

3.3. Amphibians and reptiles

Amphibians and reptiles were considered together in our analysis. Negative impacts of walking, e.g. lower numbers of amphibians in areas with recreational activities (Rodríguez-Prieto & Fernández-Juricic, 2005), avoidance behaviour such as abandoning basking (Nyhof & Trulio, 2015), and longer periods of time taken to return to a disturbed area (Rodríguez-Prieto & Fernández-Juricic, 2005) were reported in three publications. One publication reported the effects of multiple activities (camping, boating, fishing and hiking) on turtles, showing minimal changes in turtle behaviour (Laverty et al., 2016). Rodríguez-Prieto & Fernández-Juricic (2005) found that frog abundance decreased with proximity to recreational areas. Generally, more frogs were found in less visited areas, indicating that recreational activities influenced frogs at a population level. The authors deduced that the responses of frogs to humans may vary with habitat structure because frogs flushed earlier in areas with less vegetation cover.

The basking of turtles was interrupted by walking in 5% and biking in 6% of all events (Nyhof & Trulio, 2015). This value was much higher for cars (45%). Sun basking is crucial for turtles' thermoregulation (Nyhof & Trulio, 2015) and this might ultimately affect the survival of an individual. Laverty et al. (2016) detected minimal effects of recreational activities on the daily movement patterns, annual home range sizes or health of Eastern Musk Turtles (*Sternothernus odoratus*). Yet, a higher number of dead turtles was found on impacted sites compared to non-impacted sites. However, the differences in mortality were not statistically significant.

3.3.1. Algae

Dubovik et al. (2007) studied the impact of walking on algal species diversity in soil. The authors noted a lower abundance and diversity of algal species in impacted areas. In addition, a simplification of taxonomic and biological structure was found. The abundance of one species, *Nostoc commune*, increased with the visitor impact. According to Dubovik et al. (2007), this species is an indicator of pasture loads.

3.3.2. Macrophytes

Four studies focussed on the ecological impacts of recreational activities on terrestrial macrophytes close to water bodies. The trampling associated with walking resulted in a reduced vegetation height (Gremmen et al., 2003), density (Andrés-Abellán et al., 2005; Bonanno et al., 1998) and number of individuals (Bowles & Maun, 1982) as well as in a lower plant species diversity (Andrés-Abellán et al., 2005).

Ninety percent less plant species were found in the most walked-on compared to the least walked-on plots at an waterfall in Spain (Andrés-Abellán et al., 2005). Recreational use, in particular trampling changed the plant species composition towards more resistant and nitrophilous species. The ongoing trampling observed in that study affected the area at an ecosystem level.

Freshwater dunes are sensitive ecosystems, which suffer from the trampling of pedestrians and swimmers. Bowles & Maun (1982) found human activities in dunes to impact plants at the individual level by causing physical damage such as broken leaves and branches, while Bonanno et al. (1998) found lower plant densities and lower species richness both in the ground and tree layer, representing an impact at ecosystem level. Both studies also found that trampling severely affected the ecosystem by reducing the flowering shots and delaying dune stabilization. These effects occurred in both studies at high and low levels of use, indicating that the best way to protect this sensitive ecosystem would be a spatial restriction of access.

3.3.3. Soil characteristics

Four publications analysed the ecological impacts on soil characteristics. Observed effects were the occurrence of bare ground (Andrés-Abellán et al., 2005; Fletcher et al., 1999), soil compaction (Andrés-Abellán et al., 2005; Serengil & Özhan, 2006) and the reduction of the organic matter concentration in the soil (Andrés-Abellán et al., 2005; Serengil & Özhan, 2006). The organic matter and organic carbon contents decreased slightly with increasing intensity of use (Andrés-Abellán et al., 2005). Andrés-Abellán et al. (2005) and Serengil & Özhan (2006) reported an increase in the sand fraction content as well as an increase in the pH value of the soil.

3.4. Aquatic organisms and water characteristics

3.4.1. Invertebrates

Five publications focused on invertebrates; in particular on the abundance of different species in various zones of the shore (Brauns et al., 2011), a higher drift density (Caires, 2007), and changes in the community composition (Hardiman & Burgin, 2011b; Zumkowski & Xylander, 1994). Three publications dealt with, canyoning (walking in the bed of a lotic waterbody). This activity differs from walking on land because it is performed exclusively in the bed of a stream or canyon (Hardiman & Burgin, 2011a, 2011b). A trampling experiment by Hardiman & Burgin (Hardiman & Burgin, 2011b) revealed that the macroinvertebrate abundance immediately after the disturbance was about 70% lower in trampled than in untrampled plots in a canyon stream. However, the macroinvertebrate communities recovered rather quickly, and 15 days after the disturbance no differences were found between trampled and untrampled plots. The community composition recovered to a diversity level similar to that before the disturbance, so that no long-lasting effect on invertebrate populations was visible from on time in-stream trampling. The authors also found that after the disturbance event the abundance in untrampled plots dropped below that in trampled plots. Hardiman & Burgin (2011b) reasoned that the trampling impacted the macroinvertrebrate community but that it rapidly recovered due to recolonisation from neighbouring plots. In an in-situ study on the effect of trampling on stream macroinvertebrates, Hardiman & Burgin (2011a) found no significant relationships between the macroinvertebrate assemblage composition and the visitation level of the canyons. Significant differences were only detected between different canyons. Hardiman & Burgin (2011a) concluded that, the current level of recreation did not lead to a significant negative impact on the macroinvertebrate assemblage. This was perhaps due to the location of the streams in a remote wilderness setting and to a resilience that the macroinvertebrates had developed under conditions with unpredictable natural disturbances. This resilience manifested in high mobility, fast recolonisation or year-round breeding.

Caires (2007) determined a threshold relationship between canyoning and invertebrate drift (four walkers per 30 min interval). This study found an increase in drift density with hiker numbers, but only in four of eight studied taxa. No difference in total benthic invertebrate abundance among sites of different use levels was found. This suggests a rapid recolonisation process.

Brauns et al. (2011) found a more negative impact on macroinvertebrates of artificial beaches for relaxing on the shore than Caires (2007) and Hardiman & Burgin (2011a, 2011b) found for canyoning. Of course, creating a long-lasting beach site is more severe compared to temporary canyoning impact, explaining the difference. The effect of the beach was evident in terms of lower species richness and lower relative abundances of *Coleoptera*, *Crustacea*, *Gastropoda* and *Trichoptera*. Brauns et al. (2011) concluded that the reduction of habitat complexity of the littoral led to unfavourable habitat conditions for the macroinvertebrates and thus to a reduction in abundance. Because artificial beaches had low structural complexity, no characteristic species or a distinct associated community for this shoreline development type exists.

Zumkowski and Xylander (1994) observed drastic changes in the amount and the community assemblage of heteroptera and choleoptera in gravel pit lakes that were used both for swimming and surfing. The differences between impacted and non-impacted areas changed with seasons: at impacted sites individual and species numbers dropped with the beginning of the bathing season in summer and increased again in autumn. At non-impacted sites, constant numbers were observed for all seasons.

The effects of water-based activities on fish were analysed in three publications. The observed effects on fishes of swimming, bathing or snorkelling were mostly negative, particularly concerning their avoidance behaviour (Schmidt & Gassner, 2006), lower abundances (Bessa & Gonçalves-de-Freitas, 2014; Teresa et al., 2011) and lower reproduction (Bessa & Gonçalves-de-Freitas, 2014; Teresa et al., 2011). One publication mentioned positive impacts of recreational activities on the abundance of certain species (Teresa et al., 2011). Abundance of individuals after a disturbance was the factor most often measured. Schmidt & Gassner (2006) measured the direct effect of two scuba divers on fish densities and found a significant difference in densities before and immediately after the dive as well as before and 30 min after the dive. Schmidt & Gassner (2006) noted that the fish stayed in the same horizontal layer when fleeing from the divers. They identified light as the main factor triggering avoidance behaviour. The fishes also returned quickly to their original position after the divers had stirred up sediments. The influence of human presence on the reproduction of fishes was ascertained in a lower number of nests of *Crenicichla lepidota* in highly frequented areas (Bessa & Gonçalves-de-Freitas, 2014) and in a lower number of individuals engaging in reproductive activities (Teresa et al., 2011). Despite some effects of recreational activities on fish observed, spawning habitat destruction remained the most significant reason for the decline of *Crenicichla lepidota* and *Hyphessobrycon eques*.

Teresa et al. (2011) concluded that the species whose abundance was positively affected by disturbance were those that profited from sediment suspension, according with the findings of Schmidt & Gassner (2006). Another study found that, in areas with unregulated snorkelling tourism, the behaviour of territorial fishes was more strongly impacted by the visitors than in areas with controlled tourism (Bessa & Gonçalves-de-Freitas, 2014). These authors concluded that human behaviour in areas with uncontrolled tourism led to reduced aggression of territorial fish, implying a habituation effect.

3.4.2. *Water characteristics*

Four publications were containing information on some kind of water quality characteristics. No effect of walking on water quality (Hardiman & Burgin, 2011a) or camping on pH-value (Laverty et al., 2016) were found. Two publications found increases of sunscreen compunds in waterbodies used for swimming (Gondikas et al., 2014; Poiger et al., 2004). Hardiman & Burgin (2011a) reported no measurable effect of canyoning on water quality and. They concluded that the levels of recreational pressure in their study area were too low to impact the water quality and therefore thethe river-ecosystem. Poiger et al. (2004) found that the concentrations of UV-filters used from in sunscreen products to increases in the water with increasing visitor numbers. As expected by the authors, the concentration of UV-filters in lakes generally increased in the summer months. Their results indicate a potential of bioaccumulation of UV-filters in recreational waters, due to the lipophilic nature of the compounds. However, the release of sunscreen from the skin while swimming was lower than predicted from input estimates, with an assumed wash-off of less than 50%. Laverty et al. (2016) found no differences in the pH- value of the water of impacted and non-impacted sites in their study area.

A particle analysis showed that titanium dioxide (TiO_2)-contents in the water of a heavily used lake increased during the summer months (Gondikas et al., 2014). This could be addressed by the wash-off of sunscreen, which can contain TiO_2-particles, from the skin of swimmers and people performing water sports. However, this study could not clearly link the increase in TiO_2 in the water to recreational activities, as the particles could be released into the water also through other ways such as facade-paint runoff or natural causes.

3.4.3. *Summary*

Fig. 3 shows that the studied groups can be devided into two categories. Mobile organisms such as birds, fish, amphibia and reptiles were mainly studied on the individual level. The studies reported abundance, behavioural changes or densities, which does not allow conclusions on the community or the entire ecosystem. Most effects reported for this category seemed not relevant for the survival of the population. Algae, macrophytes and soil were mostly studied on the community- or ecosystem-level and the effects such as simplification of taxonomic structure or reduced biodiversity are of greater ecological importance.

4. Discussion

Despite our systematic search we found only a very little amount of studies investigating potential ecological effects of recreational activities. This holds true for both understudied activities and taxa and it confirms our first assumption that certain combinations of activities and affected organisms are better studied more deeply than others couldan be confirmed for thethe selectedion kinds of activities in our studystudied here. The impacts of swimming on aquatic animals or plants were assessed rarely studied.

Birds were negatively impacted by recreational activities in most analysed studies, but mainly at the individual level. The main studied aspect were behavioural changes. Even though disturbance-induced reduction of rest- and feeding-time might threaten individual fitness, such measures are ecologically less relevant as long as population size or reproduction failures are not measures too (Bateman & Fleming, 2017). Specifically, impacts on the reproduction of birds were comparably rarely studied, precluding generalized insights, although birds are highly relevant in nature conservation frames. The two publications on bird reproduction reported negative effects of recreational activities on reproductive success, but it remained unclear whether these effects affected population abundance. Even though waterfowl and birds next to water are relatively intensively studied, publications on effects of shore based recreation at higher biological levels and with a greater significance to population survival are currently lacking.

Similarly, studies on amphibians and reptiles found avoidance

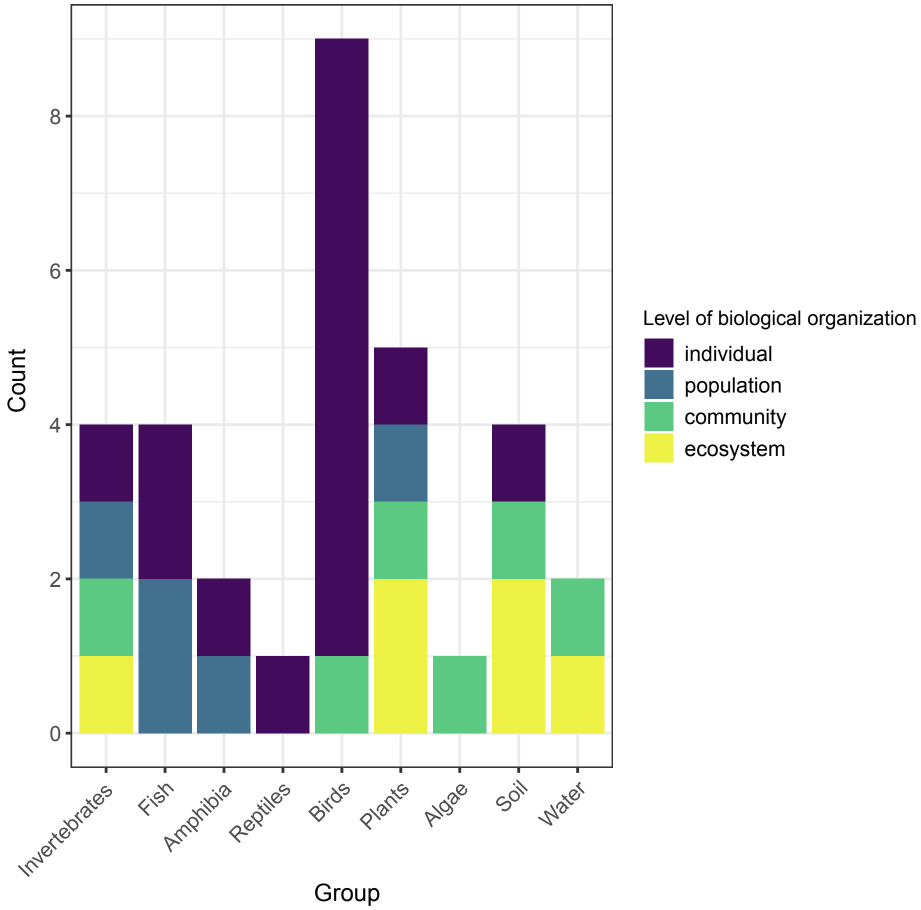

Fig. 3. Level of biological organisation of studied groups.

responses to recreational activities. Whether recreational uses have a long-lasting effect on turtle behaviour was found to depend largely on the density and frequency of the activities (Nyhof & Trulio, 2015). The non-significant difference in home range sizes and mortality in Laverty et al. (2016) might be due to the comparably low user intensity in their study area. Additional studies on the effects of various recreational activities are thus needed to identify thresholds and the behavioural adaptation as well as more severe effects on health and population survival of amphibians and reptiles. Taking into consideration that almost half of the amphibian species and one out of five reptilian species are threatened (Böhm et al., 2013; Stuart et al., 2004), effects of recreation on these two groups should be studied more intensely in general as well as in aquatic, shore-based contexts. If research continues to show effects on populations, as a management method, Rodríguez-Prieto & Fernández-Juricic (2005) proposed the zonation of stream banks. lakes. Low quality areas should then of course be held open to visitors, while high quality areas with an additional buffer zone could be reserved for conservation.

The amount of studies found on aquatic and terrestrial macrophytes was also comparably low, which was surprising given that studying these non-mobile organisms is perhaps easier than for example studying fish under water and effects of shore use seem obvious through trampling effects as revealed in terrestrial studies (Cole & Bayfield, 1993; Liddle, 1975). Especially aquatic vegetation was not studied in the publications found. Results on riparian vegetation however show severe impacts of recreational activities on vegetation growing on the shoreline by reducing abundance and diversity and changing species composition. Thus, we conclude that impacts of shore-based lake use most likely impacts riparian plants, particular herbs.

Other than expected, of the most common aquatic recreation activities swimming, snorkeling and scuba diving, no effects on aquatic algae or aquatic macrophytes were reported. Obviously, nutrient inputs with potential impacts on macrophytes of these recreational activities are of minor importance compared to e.g. land use. In addition, macrophyte-rich waters might be of little attraction for swimmer and snorkeler, which reduces spatial overlap and thus, potential impact. One publication in German found no additional damage caused by diving in lakes that were already used for other activities (Lutz, 1996).

One study found severe impacts of walking on the abundance, diversity and structure of algal communities in soils next to water (Dubovik et al., 2007). This is consistent with findings in algal communities on rocks under water influenced by hikers (Smith, 2009). However, algal growth depends on a combination of factors and the nutrient input by recreationists seems minor compared to the input of agriculture (Chakraborty et al., 2017), wastewater (Chen & Olden, 2020) and the effects of temperature and light (Singh & Singh, 2015).

Soil and its degradation are strongly linked with the status of the vegetation cover. Frequent trampling results in the disappearance of vegetation and this might lead to areas with bare soil prone to erosion and unfavourable for the reestablishment of vegetation. Therefore, management aiming at the protection of vegetation will simultaneously include protection of soil. This can be relatively easily managed by restricting access to existing pathways and areas for access to the water.

The results on the effects of recreational activities on invertebrates can be sorted into two groups. The first contains species located in streams and rivers being impacted by canyoning (Caires, 2007; Hardiman & Burgin, 2011a, 2011b). Drift density was the most common response variable for this group. However, this variable does not imply a lower chance of survival or reproduction of the impacted invertebrates. A rapid recolonisation was reported in all four studies. This shows the non-severity of the reported effects of canyoning on macroinvertebrates. The second group consists of invertebrates in lakes and ponds that are affected by swimming (and surfing) (Brauns et al., 2011; Zumkowski & Xylander, 1994). The landscaping needed for beaches for relaxing on the shore and entering the water as well as swimming which is more locally concentrated seemed to have a stronger and more fundamental impact on invertebrate communities. So far it remains unclear, how many invertebrate species are capable of avoiding threats by migrating and to what extent populations of invertebrates are impacted by recreation alone.

The findings on fish show that they are not only impacted by swimming, snorkelling and diving at an individual level but in some cases also through their reproduction, which in extreme cases could have population level effects (Gwinn & Allen, 2010). Here, similar to the results reported for invertebrates, habitat destruction, especially aquatic macrophytes, through recreational activities is a relevant threat to some fish species if the extend of recreational-induced habitat change is severe and long-lasting. There is no data to support this claim, as the studies reported mainly experimental interventions. However, not only the degradation of banks and fish refuges through activities in the water is a threat to fishes (Schulz, Śmietana, & Schulz, 2006). Also camping on the shore can potentially increase the input of chemicals and nutrients into the water (King & Mace, 1974; Laverty et al., 2016), but there is no hard data how this affects fish in the wild.

The presence of humans in the water can lead to behavioural responses of fishes, but also the sound of underwater breathing apparatuses, which produce sounds in a range that the hearing organs of fishes and decapod crustaceans are most sensitive to, can be problematic (Radford, Kerridge, & Simpson, 2014). Even activities without electric or motor-driven equipment like swimming or muscle driven boats can generate underwater noise as proven in an experiment by Erbe et al. (2016) that could interfere with the acoustic communication of fishes and thereby have an impact on mating success and reproduction (Zelick et al., 1999). Yet, currently it is highly speculative if such effects materialize at the population level as no research has quantified this.

The increasing concentration of UV-filters in the water alone is not a real ecological effect and was not linked to threats to organisms in the studies of Poiger et al. (2004) or Gondikas et al., (2014), experimental studies in the laboratory suggest negative ecological effects of UV-filters. For example, Kaiser et al. (2012) discovered a toxic effect of some UV-filters on the reproduction of snails, and Blüthgen et al. (2012) showed accumulation of the filters in zebrafish and an alteration of their gene expression. However, knowledge of the extent to which UV-filters are released from the skin of bathers into the water, the resulting concentration of UV-filters in a water body, as well as the link to the actual damage to aquatic organisms still lacks. To make matters more difficult, recreational activities are often not the only nor the most dominant source for chemical compunds in the water, for example TiO_2 is used in sunscreen and facade-paint (Gondikas et al., 2014). The direct link from recreational activities to changes in water quality might also be difficult as chemical characteristics of waterbodies will depend on the geology of the surrounding area and the morphology of the lake basin or river bed (King & Mace, 1974). The results of this study agree with Venohr et al. (2018) that the impacts of sunscreens on freshwater organisms are rarely studied, especially in-situ. Likewise, potential pollution of freshwaters through activities like swimming snorkelling or scuba diving is insufficiently studied. The mainly negative effects found in the results of this literature search as well as in additional material underline the importance of further in-situ studies on this topic.

The systematic literature search yielded an insufficient amount of material on the ecological effects of recreation on water quality. This might be due to a real lack of studies on this topic or partly due to the decision on not including publications with divergent keywords or titles. For example, Phillip et al. (2009) reported poor water quality as a result of swimming. But as the main focus of this paper was on hazards to human health and were therefore not mentioned as ecological impacts, it did not show up in the literature search. Although, the strict quality criteria yielded to a reduced number of material for the analysis, we believe that the rigorous sorting process led to a set of literature with a higher quality of the studies that met the criteria and the scope of our review.

A lack of studies on the effects of recreational activities on specific groups does not, however, mean that these are not impacted (Larson et al., 2016). Almost all species are sensitive to recreational activities in their habitat to some degree (Blanc et al., 2006). However, not all effects measured locally or at the individual level in the case of animals will scale up to affect populations or even ecosystem function. Our literature review showed that population or community-level studies of the impact of outdoor recreation at the shores are rather rare and effects are limited to a few studies. This does not mean there are no effects of recreation, but the current body of literature mainly supports the evidence that plants as sessile organisms (e.g., terrestrial plants) seem to be the most impacted by shore based organismsactivities and that mobile organisms such as birds, fishes or invertebrates tend to respond individually, but show compensatory response that limit the long-term impact at the population level or allow rapid recovery after the disturbance. The groups studied in the available literature might reflect the interest of researchers and the ability of researchers to study effects rather than the threats that these groups face (Blanc et al., 2006). Overall, our work revealed a substantial need for more research, especially experimental in-situ work to study cause-and-effect as most study designs employed in the literature employed observational data and basic study designes such as BA and CI.

5. Conclusion

Our systematic review revealed a significant gap of data and research. Although recreational activities on and along freshwaters are of significant, growing importance their potential interference with environmental quality and conservation aim is little studied. Therefore, our results summarise first evidence for negative environmental impacts of selected recreational activities on some taxa, but they are far from being comprehensive. Globally, there is sufficient overlap between species ranges and recreational activities for all taxa in freshwaters, so that the detected lack of studies for most taxa leaves it open, whether there is no conflict or just lack of research and funding.

The analysis of the ecological impacts of recreational activities in and along water bodies collectively revealed that the responses of sessile and mobile organisms to human disturbance differ substantially. Mobile organisms were less affected by recreational activities than sessile ones. For instance, fishes and birds fled and changed their location or altered their behaviour in different ways as a reaction to disturbance through humans, and the literature on population-level impacts is largely absent for these taxa groups. Similarly, mobile invertebrates reacted to temporary disturbance with migration to undisturbed areas and recolonization processes were observed thereafter. The data so far does not suggest strong and lasting population level effects, except when local habitats are altered in a strong fashing, e.g., due to beaches for macroinvertebrates. Sessile organisms, however, such as plants for which damage and dieback were reported, were impacted more severely by shore based recreation. Intact bank vegetation is crucial for the health of an ecosystem; it protects the shoreline and provides food and shelter for other organisms. The studies on water quality showed a variety of results, ranging from no effects to the accumulation of UV-filters in the water. However, the number of studies on water quality and other water characteristics was so low that no generalized statements on this topic could be made.

Whether the use of natural or near-natural inland waters for recreational activities always leads to negative impacts cannot be definitively answered by the findings presented here. The strict quality criteria resulted in an overall small dataset and in a low number of studies on topics that are already known to be under-published like the impacts on water quality. Subsequently, only high quality studies with strong and clear evidence were analysed. Yet, sticking to the systematic process led to a reproducible and up-to-date review on the current literature on the ecological effects of shore- and water-based recreational activities.

Our research suggests that shore based recreation can under some situations have lasting ecological effects, particularly on plants. Under these conditions and depending on local recreational use intensity, management of access or zonation can be a measure to avoid negative ecological impacts caused by people seeking relaxation at the water. However, other measures, such as environmental education should also be considered first to harmonise the interactions between recreational activities and the environment they make use of. Future studies should include underrepresented organism groups to close knowledge gaps and provide a broad and robust knowledge base for informing sustainable management of outdoor recreation. In particular, more studies at the population level and with robust BACI designs are needed because population level or community level impacts of recreation are perhaps more relevant from a conservation perspective than studies that for example studies individual behavioural displacements in birds or fishes that have no consequences for the population as a whole. Thus, rather than local studies, a focus on whole lake studies and whole populations is recommended for the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2021.126073.

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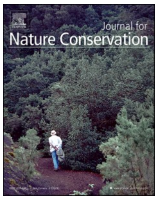

Impact of water-based recreation on aquatic and riparian biodiversity of small lakes

Malwina Schafft[a,b,*], Robert Nikolaus[a], Sven Matern[a,b], Johannes Radinger[a], Andreas Maday[a,c], Thomas Klefoth[d], Christian Wolter[a], Robert Arlinghaus[a,b]

[a] *Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany*

[b] *Division for Integrative Fisheries Management, Thaer-Institute of Agricultural and Horticultural Sciences, Faculty of Life Sciences, Humbolt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10155 Berlin, Germany*

[c] *Angler Association of Lower Saxony, Brüsseler Straße 4, 30539 Hannover, Germany*

[d] *Ecology and Conservation, Faculty of Nature and Engineering, Hochschule Bremen, Neustadtswall 30, 28199 Bremen, Germany*

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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 recreation-induced impacts on freshwater and terrestrial environments (Bateman & Fleming, 2017; Birk et al., 2020; Buckley & Keto, 2022; Schafft et al., 2021).

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[*] Corresponding author.

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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 (P. B. 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 (P. B. 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 (P. B. 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 meta-analysis 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 (A.N. 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:

(1) 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 recreation-induced 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

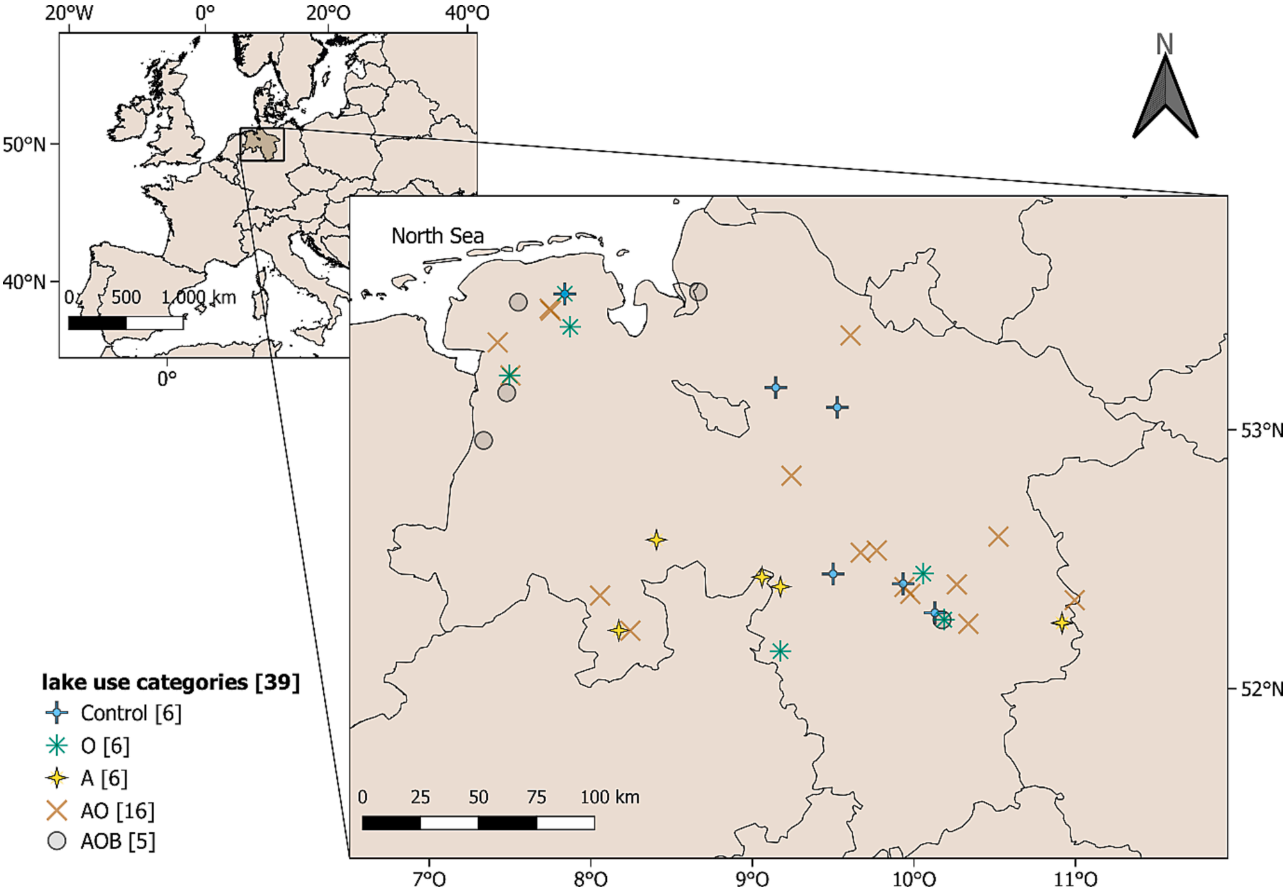

Fig. 1. Map of the sampling area in Lower Saxony, Germany, indicating the sites of the 39 gravel pit lakes of the 5 predefined lake use categories (Control = no use, O = no angling but other usage, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating). Number of sampled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

added lakes with specific, potentially outstanding recreational human 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®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 × 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

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	O	13.6	9.6	23.0	47	0.06	29.2
8	Hänigsen	O	6.2	7.7	12.3	27	0.02	9.8
9	Hopels	O	5.5	6.7	14.5	37	0.01	4.8
10	Kiessee Isums Groß	O	2.8	5.2	11.3	21	0.05	5.3
11	Pfütze	O	10.6	4.3	7.3	32	0.01	5.7
12	Westerhammerich	O	16.5	7.4	17.42	35	0.01	4.9
13	Buschmühlenteich	A	3.0	0.6	1.1	41	0.04	9.2
14	Donner Kiesgrube 3	A	1.0	3.3	5.2	40	0.03	8.9
15	Mergelgrube	A	0.7	1.4	2.3	38	0.02	3.6
16	Röhrs Teich	A	6.2	2.7	4.4	61	0.44	89.8
17	Stockumersee	A	10.4	3.9	10.3	48	0.04	31.8
18	Vereinsteich Heede	A	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 was measured and litter was collected at a random set of 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 + non-angling) + 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 non-mobile (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 × 23 cm × 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^2 plots. Trees taller than 2 m were identified and counted along these transects, and herbs were assessed within the 1 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.rote-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^2 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^2). Although Matern et al. (2019) did not find significant differences in fish biomass between managed and unmanaged gravel pit lakes, we used

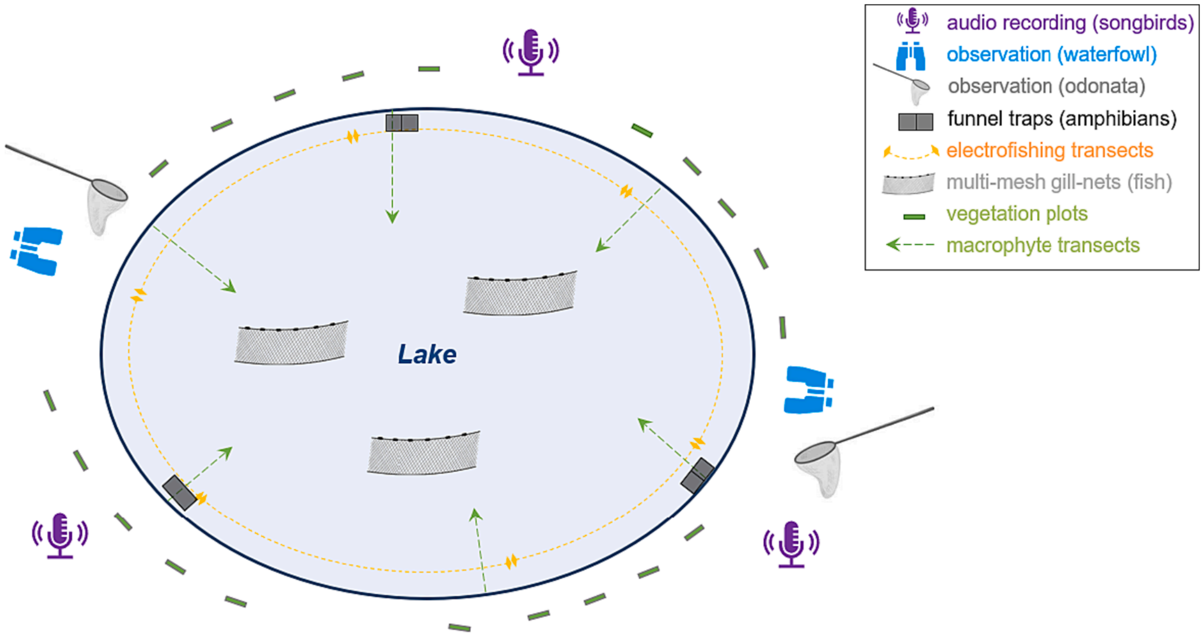

Fig. 2. Schematic visualization of the biodiversity sampling.
Adapted from Nikolaus et al. (2022)

BPUE to control for potential fish-induced effects (e.g. predation) on other taxonomic groups (Trovillion et al., 2023). Lake's submerged macrophyte coverage was calculated by extrapolating the transect-based 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).

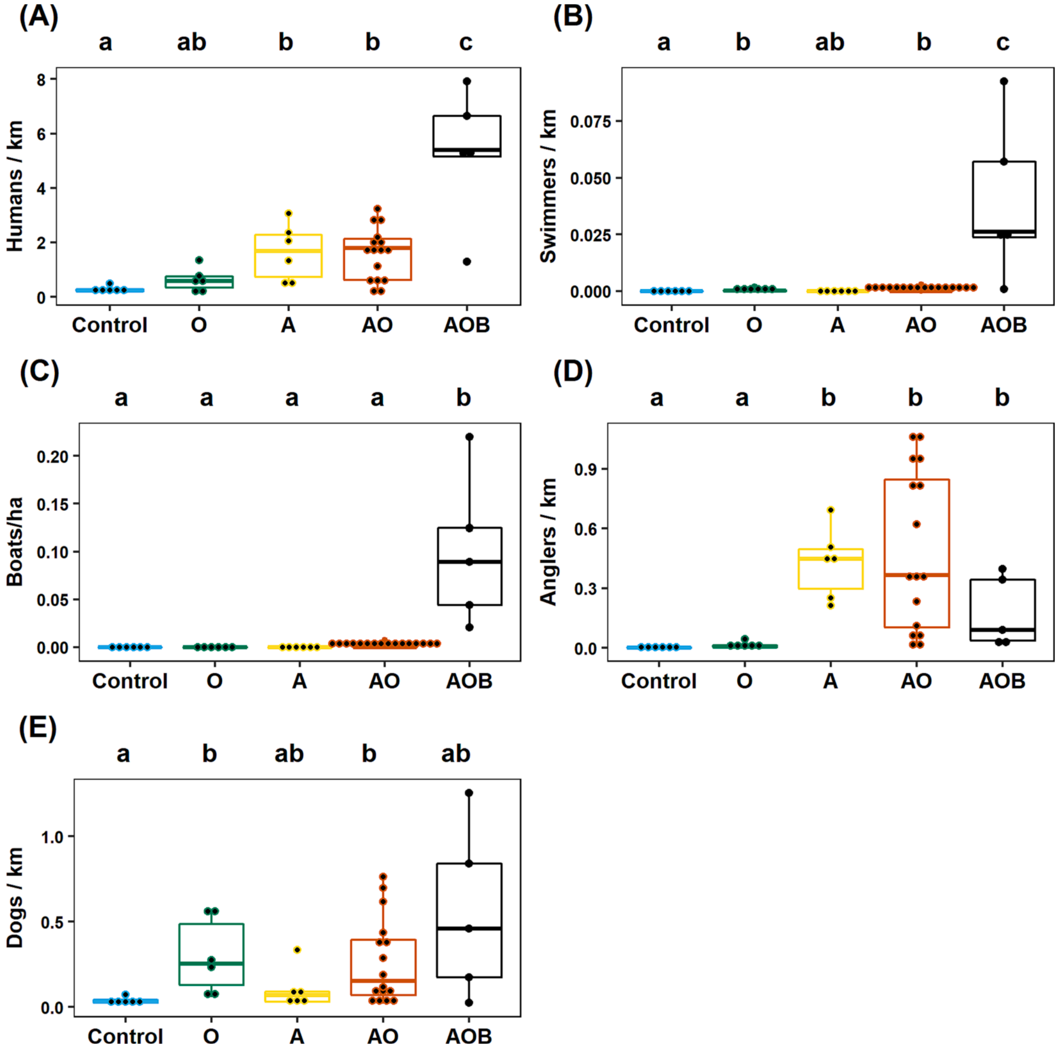

Fig. 3. Use densities of humans (A), swimmers (B), boats (C), anglers (D), and dogs (E) based on standardized counts per lake use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating). Densities are shown per ha lake area 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).

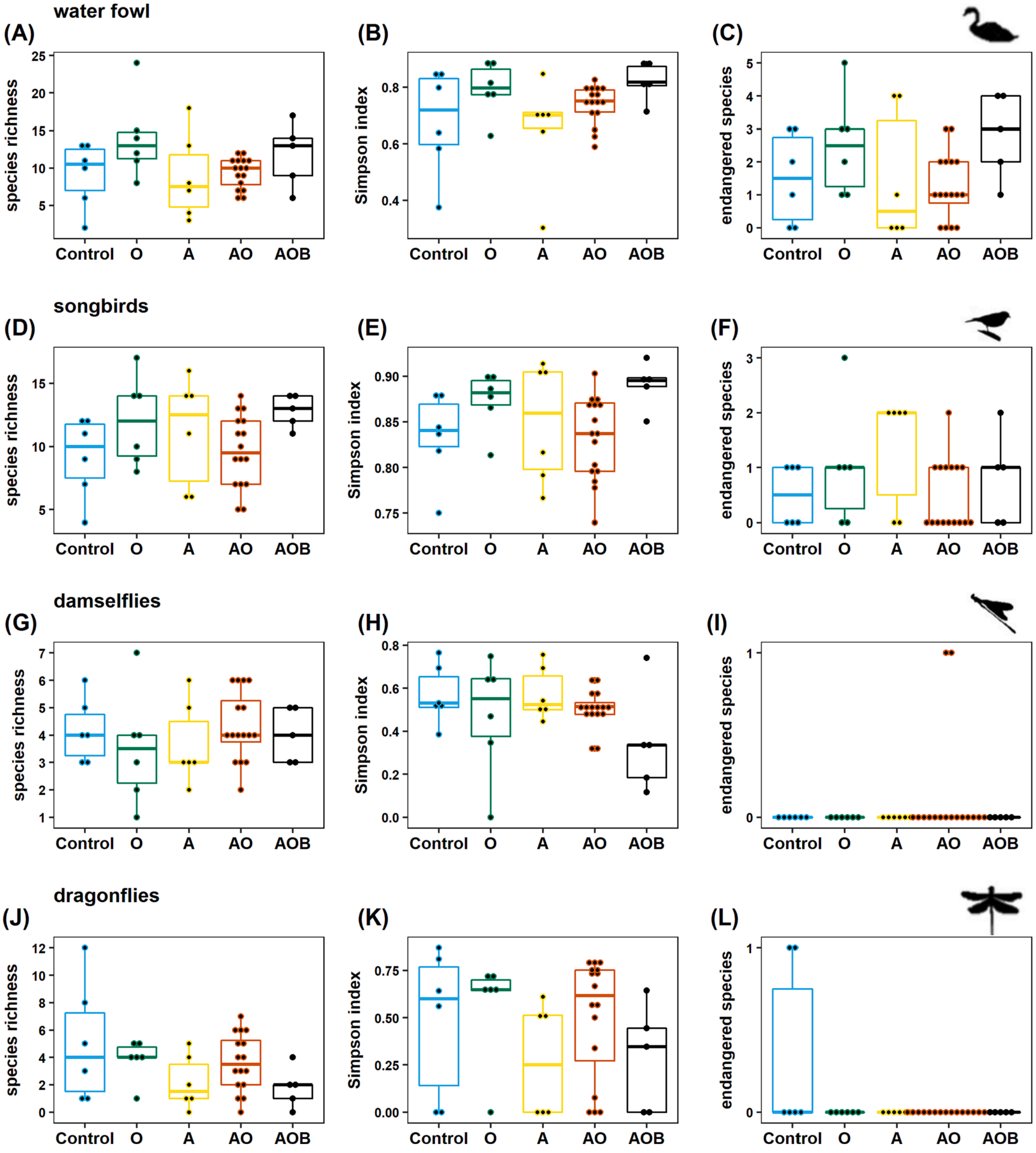

Fig. 4. Boxplots of species richness, Simpson diversity index and number of endangered species per lake use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating) for waterfowl (A, B, C), songbirds (D, E, F), damselflies (G, 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.

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.

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 songbird diversity indices between the five lake categories (Fig. 4, Appendix Table A6). However, the multivariate regression analysis indicated 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 songbirds ($p = 0.01$). By contrast, human use intensity tended to be positively related to the Simpson diversity index of songbirds, although 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

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).

	waterfowl			songbirds			damselflies			dragonflies			amphibians			fish			macrophytes			riparian herbs			riparian trees			A priori expected relations 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	
Mean depth (m)													x	x	x	x	x	x	x	x	x							+ fish^{1}; - amphibians^{2}
Lake area (ha)	+	+	x																									$+^{3}$
Shoreline length (m)				+	+	x	x	x	x	-	x	x										(+)	x	(+)	x	x	x	$+^{3}$
Relative depth ratio													x	x	x				x	x	x							$+^{6}$
Shoreline development factor	+	x	(+)	x	x	x	x	x	x	+	x	x	x	x	+	x	x	x	(+)	x	x	x	x	x				$+^{4}$
Total phosphor (mg/l)							x	x	x	x	x	x				x	+	x	(-)	x	x							+ fish^{5}; - all except fish^{2,6,14}
Total organic carbon (mg/l)							x	x	x	-	x	x																- odonata^{14}
Nitrate (NO_3 mg/l)																			-	x	-							$-^{6}$
pH-value																			x	x	x							$-^{7}$
Secchi depth																			+	x	x							$+^{6}$
Macrophyte coverage (%)	(-)	x	-				x	+	x	x	x	x	x	x	x	x	x	x										$+^{2, 10,13}$
Reed (%)	x	x	x	x	x	x	x	-	x	x	x	x				x	x	x										$+^{2, 10,16}$
Age (years)				x	x	x										+	x	x	x	x	x	x	x	x	x	+	x	$+^{5,6,8}$
Urbanisation (%)																									x	x	x	$+^{12}$
Agriculture (%)	x	x	x	x	x	x	x	x	x	x									(+)	x	(+)	+	x	x	x	x	x	+ birds; - odonata, plants^{7,12,14}
Forest (%)				x	x	x							x	x	(-)										x	x	x	+ all $^{2, 8}$
Wetland (%)							x	x	x	+			x	x	x													$+^{2,14}$
Distance to lentic water (m)	x	x	x										x	x	(+)	x	x	x	x	x	x							$-^{2}$
Distance to street (m)				x	x	x																						$+^{8}$
Distance to settlement (m)																						-	x	x	x	x	x	$-^{12}$
Open sites/m																			x	x	x	-	x	x	x	x	x	+ herbs, macroph.^{6}; -trees
Trail length/shoreline length																						x	x	x				
Angling use/km	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	(+)	x	x	x	x	x	x	x	x	x	x	- all except fish^{2,10}, + fish^{5}
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	x	x	x	(+)	x	x	-	x	x	x	x	x	x	x	+	x	x	x	x	x	+	x	x	x	x	x	- all except herbs^{2,9,10}; plants^{9}
Fish biomass (g /100m^{2})	x	x	x				x	x	x	-	x	x	x	x	x													+ birds^{15}; - others$^{2, 13}$
Number of lake visits	x	x	x																									+

+/- = significant, $p < 0.05$ **(+/-)** = trend, $p < 0.1$ x = in model, but $p > 0.1$ x = not in final model, but predictor in full model

[1]Brucet et al. (2013); [2] Hecnar and M'Closkey (1997); [3] He and Legendre (1996); [4] Wetzel (2001); [5] Matern et al. (2022); [6]Hilt et al. (2022), [7]Coutris et al. (2011), [7]Vestergaard and Sand-Jensen (2000), [8] Rashidi, Chamani, and Moshtaghi (2019); [9]Nikolaus et al. (2022); [10]Müller et al. (2003); [11]Sime (1999), [12]Deutschewitz et al. (2003), [13]Knorp and Dorn (2016), [14]Holtmann et al. (2018); [15]Found et al. (2008); [16]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 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	Dragonflies	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), **$p < 0.01$**
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), **$p < 0.01$**
Area (ha)	0.18 (0.07), **$p = 0.01$**					
SDF	0.14 (0.05), **$p = 0.01$**		0.35 (0.14), **$p = 0.01$**		0.12 (0.06), $p = 0.05$	
Shorleline length (m)		0.19 (0.05), **$p < 0.01$**	−0.29 (0.14), **$p = 0.04$**			0.04 (0.02), $p = 0.08$
Distance to settlement (m)						−0.19 (0.03), **$p < 0.01$**
Agriculture (%)			−0.15 (0.10), $p = 0.15$		0.12 (0.07), $p = 0.06$	0.12 (0.02), **$p < 0.01$**
Wetland (%)			0.25 (0.10), **$p = 0.01$**			
TP/SRP (mg/l)					−0.24 (0.12), $p = 0.05$	
NO_3 (mg/l)					−0.17 (0.08), **$p = 0.04$**	
TOC (mg/l)			−0.38 (0.12), **$p < 0.01$**			
Age				0.19 (0.06), **$p = 0.01$**		
Secchi depth (m)					0.17 (0.07), **$p = 0.01$**	
Macrophyte cover (%)	−0.10 (0.06), $p = 0.09$‘					
Fish BPUE (g /100 m^2)			−0.33 (0.14), **$p = 0.02$**			
Open sites /m						− 0.19 (0.04), **$p < 0.01$**
N	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^2(Cragg - Uhler)	0.60	0.32	0.57	0.47	0.69	0.96

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.

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).

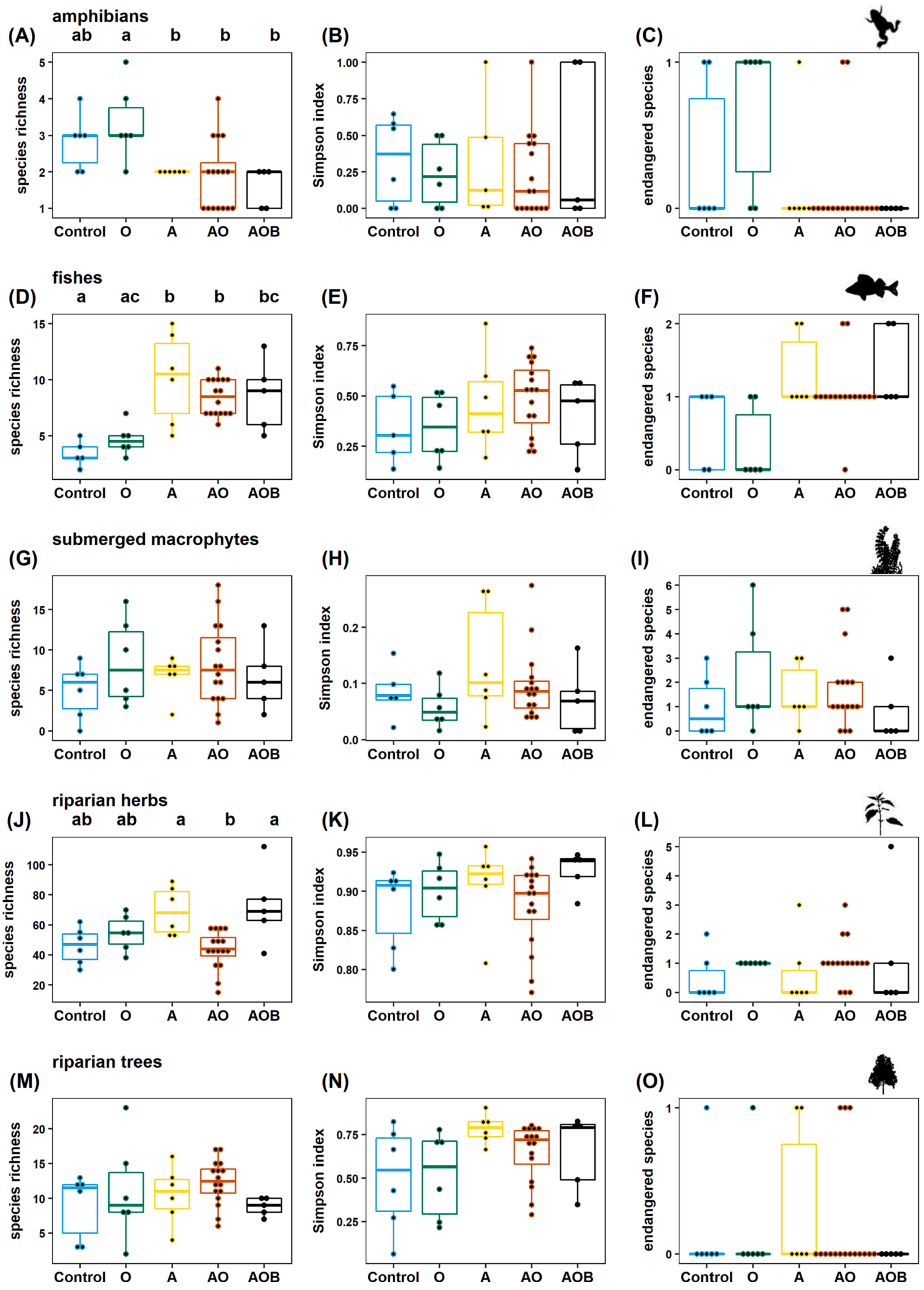

Fig. 5. Boxplots of species richness, Simpson diversity index and number of endangered species per use category (Control, O = other uses than angling, A = angling only, AO = angling and other uses, AOB = angling, other uses and boating) for amphibians (A, B, C), fishes (D, E, F), submerged macrophytes (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.

Macrophyte species richness was explained positively by the Secchi depth and negatively by nitrate (NO_3). 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 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 (P. B. 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 sand-specialized 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 trampling-resistant 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 (M. I. 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; A. E. Williams & Moss, 2001), even if most anglers highly value dense aquatic vegetation (A. E. 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 long-term 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

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available via via www.fred.igb-berlin.de (DOI: 10.18728/igb-fred-807.0) 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

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RESEARCH ARTICLE

WILEY

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

Robert Nikolaus[1] | Malwina Schafft[1,2] | Andreas Maday[1] | Thomas Klefoth[3] | Christian Wolter[1] | Robert Arlinghaus[1,2]

[1]Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

[2]Division for Integrative Fisheries Management, Albrecht Daniel Thaer Institute of Agriculture and Horticulture, Humboldt-Universität zu Berlin, Berlin, Germany

[3]Ecology and Conservation, Faculty of Nature and Engineering, Hochschule Bremen, City University of Applied Sciences, Bremen, Germany

Correspondence

Robert Nikolaus, Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, Berlin D-12587, Germany.

Email: nikolaus@igb-berlin.de

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Abstract

1. Humanity is facing a biodiversity crisis, with freshwater-associated biodiversity in a particularly dire state. Novel ecosystems created through human use of mineral resources, such as gravel pit lakes, can provide substitute habitats for the conservation of freshwater and riparian biodiversity. Many of these artificial ecosystems are subject to a high intensity of recreational use, however, which may limit their biodiversity potential.
2. The species richness of several taxa (plants, amphibians, dragonflies, damselflies, waterfowl, and songbirds) was assessed and a range of taxonomic biodiversity metrics were compared between gravel pit lakes managed for recreational fisheries (n = 16) and unmanaged reference lakes (n = 10), controlling for non-fishing-related environmental variation.
3. The average species richness of all the taxa examined was similar among lakes in both lake types and no substantial differences in species composition were found when examining the pooled species inventory. Similarly, there were no differences between lake types in the presence of rare species and in the Simpson diversity index across all of the taxa assessed.
4. Variation in species richness among lakes was correlated with woody habitat, lake morphology (surface area and steepness), and land use, but was not correlated with the presence of recreational fisheries. Thus, non-fishing-related environmental variables had stronger effects on local species presence than recreational fisheries management or the presence of recreational anglers.
5. Collectively, no evidence was found that anglers and recreational fisheries management constrain the development of aquatic and riparian biodiversity in gravel pit lakes in the study region; however, the conservation of species diversity in gravel pit lakes could benefit from an increasing reliance on habitat enhancement activities.

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

1 | INTRODUCTION

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

Artificially created aquatic habitats, such as gravel pit lakes or ponds, could maintain and increase native freshwater biodiversity by providing refuge and secondary habitats for rare or endangered species (Damnjanović et al., 2018; Oertli, 2018). The origins of artificial lake ecosystems are often relatively recent (less than 100 years of age; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2016), where artificial lakes are often created by mining for mineral resources (Saulnier-Talbot & Lavoie, 2018). More than 1×10^9 t of sand and gravel were excavated in more than 24,500 quarries and pits within the European Union in 2017 alone (European Aggregates Association [UEPG], 2017). The resulting numerous artificial lakes (for simplicity henceforth referred to as 'gravel pit lakes') have become common elements in many cultural landscapes across the industrialized world (Oertli, 2018).

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

Many gravel pit lakes located in central Europe are used for recreational fisheries (Matern et al., 2019; Zhao et al., 2016). In some regions of the world anglers are not only resource users but also managers of fish populations and habitats (Arlinghaus, Müller, Rapp, & Wolter, 2017). This particularly applies to Germany, where organizations of anglers, usually angling clubs and associations, are leaseholders or owners of freshwater fishing rights, and in this position are also legally entitled to manage fish stocks (Arlinghaus, Müller, et al., 2017). This includes the right to stock fish, to manage littoral habitat, and to introduce access and harvest regulations (Arlinghaus, Müller, et al., 2017). As the stocking of fish is particularly prevalent in freshwater recreational fisheries management, key impacts of the presence of recreational fisheries and associated management activities can be expected at the fish stock and fish community levels (Matern et al., 2019; Zhao et al., 2016). Angler-induced changes typically elevate fish species richness through the release and introduction of large-bodied 'game' fishes of high fisheries interest (Matern et al., 2019; Zhao et al., 2016). In turn, the altered fish community may affect submerged macrophytes (e.g. by the introduction of benthivorous fish that uproot macrophytes; Bajer et al., 2016) and other taxa (e.g. birds, Cucherousset et al., 2012; amphibians, Hecnar & M'Closkey, 1997; or invertebrates, Knorp & Dorn, 2016), through predation. In addition, anglers may modify littoral habitats to create access to angling sites, thereby affecting the species richness of plants (O'Toole, Hanson, & Cooke, 2009) and dragonflies (Müller et al., 2003), or affecting mobile taxa, such as birds, through direct contact and disturbances (Bell, Delany, Millett, & Pollitt, 1997; Cryer, Linley, Ward, Stratford, & Randerson, 1987). Indirectly, angler presence can also inadvertently kill non-targeted wildlife, such as through lost fishing gear that is ingested by birds or where birds become entangled (Franson et al., 2003; Sears, 1988). Therefore, anglers can be seen both as stewards of aquatic ecosystems (Granek et al., 2008) and as a potential threat to certain aquatic taxa, depending on the local angling intensity and other conditions (Reichholf, 1988).

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

In order to contribute to this continuing debate, the work presented here studied the taxonomic biodiversity associated with gravel pit lakes using a space-for-time substitution design, comparing lakes managed and used by recreational fisheries with lakes that do not experience recreational fisheries actions, and therefore lack angler impacts. The goal of the study was to examine the impact of recreational fisheries on the aquatic and riparian biodiversity detectable at typical gravel pit lakes in north-western Germany. The specific objective was to estimate the effect of recreational fisheries on species richness, faunal and floral composition, community diversity, and conservation value across a range of aquatic and riparian taxa (e.g. birds, amphibians, and dragonflies) that are protected by national and European conservation legislation. The absence of recreational fisheries in a given gravel pit lake does not mean that the ecosystem remains undisturbed from other recreational uses, such as swimming and walking. It was hypothesized, therefore, that the presence of recreational fisheries and associated management activities would, on average, not affect the species richness and conservation value of taxa that are not specifically targeted by anglers (Odonata, amphibians, submerged and riparian vegetation, waterfowl, and songbirds). This hypothesis was formulated as a statistical null hypothesis to be refuted by empirical data.

2 | METHODS

2.1 | Study area and lake selection

This study was conducted in the Central Plain ecoregion of Lower Saxony in north-western Germany (Figure 1), where natural lentic waters are scarce. Of 35,048 ha of total standing waters in Lower Saxony, 73% by area and more than 99% by number are artificial lakes. These artificial water bodies consist mainly of ponds and small gravel pit lakes with a surface area of less than 10 ha (Cyrus et al., 2020).

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

Managed lakes were identified through a survey of all organized angling clubs in the Angler Association of Lower Saxony. Lakes were selected according to the following criteria: the lake was owned by a fishing club, was of small size (1–20 ha), and had not been dredged in the last 10 years ('old age'). This approach yielded 16 managed lakes for use as study sites spread across Lower Saxony in 10 angling clubs (Figure 1; Table 1). The angler density (number of anglers per unit water area) for these clubs ranged from 8 to 43 anglers per ha (mean ± SE: 21 ± 3.6 anglers per ha). These angler densities correspond to averages known for German and Lower Saxonian angling clubs: 24 ± 2.5 and 22 ± 10.8 anglers per ha, respectively. All selected angler-managed lakes experienced regular angling activities and fisheries management actions, including the annual stocking of a range of fish species and regular shoreline development activities, such as mowing of angling sites and litter removal.

Gravel pits not managed by anglers were identified in close vicinity to the managed lakes, where possible (Figure 1). The number of unmanaged lakes in the state was much smaller than the number of managed lakes. Overall, 10 unmanaged lakes were identified, which were of similar age, size, and other environmental conditions to the managed lakes, but differed from the managed lakes in the absence of an angling club and any form of legal angling and fisheries management for at least 5 years before the onset of our study (Figure 1;

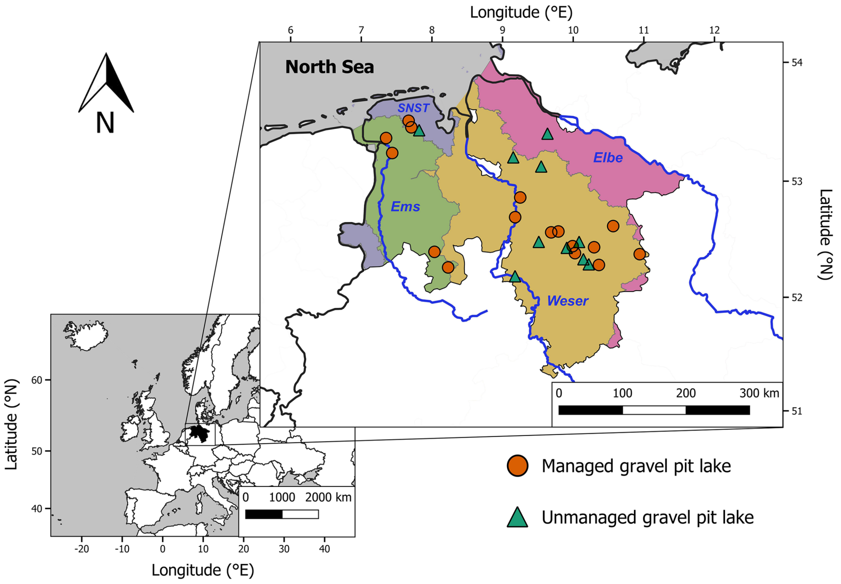

FIGURE 1 Map of study sites in Lower Saxony, Germany, together with the catchments (green, Ems; orange, Weser; magenta, Elbe; blue, small North Sea tributaries, SNST) and main rivers (dark blue: Ems, Weser, and Elbe)

TABLE 1 Descriptors of the gravel pits sampled in Lower Saxony

No.	Lake name	Lake type	Catchment	End of mining	Trophic state	Maximum depth (m)	Lake area (ha)	pH value	Conductivity (µS cm^{-1})	Main recreational visitors and activities identified during on-site visits
01	Chodhemster Kolk	Managed	Ems	1971	Mesotrophic	10.1	3.2	6.7	208	Anglers, dog walkers
02	Collrunge	Managed	SNST[a]	1982	Mesotrophic	8.6	4.3	7.9	200	Anglers, dog walkers
03	Donner Kiesgrube 3	Managed	Weser	2000	Eutrophic	5.2	1.0	7.8	632	Anglers, cyclists
04	Kiesteich Brelingen	Managed	Weser	1999	Mesotrophic	8.7	8.5	7.5	299	Anglers, dog walkers
05	Kolshorner Teich	Managed	Weser	1980	Mesotrophic	16.1	4.3	7.6	547	Anglers, horse riders
06	Linner See	Managed	Ems	2000	Mesotrophic	11.2	17.7	8.5	301	Anglers
07	Meitzer See	Managed	Weser	2006	Oligotrophic	23.5	19.5	7.9	618	Anglers, dog walkers, swimmers
08	Neumanns Kuhle	Managed	Ems	1970	Polytrophic	6.2	6.9	8.6	585	Anglers, dog walkers
09	Plockhorst	Managed	Weser	1998	Eutrophic	8.2	14.3	8.0	338	Anglers, dog walkers, horse riders
10	Saalsdorf	Managed	Weser	1995	Mesotrophic	9.2	9.0	9.0	566	Anglers, dog walkers
11	Schleptruper See	Managed	Ems	1965	Mesotrophic	10.1	4.0	8.2	502	Anglers, dog walkers
12	Stedorfer Baggersee	Managed	Weser	1983	Eutrophic	2.8	1.9	7.5	352	Anglers, dog walkers
13	Steinwedeler Teich	Managed	Weser	1978	Mesotrophic	9.1	10.4	7.5	742	Anglers, dog walkers, cyclists
14	Wahle	Managed	Weser	1990	Mesotrophic	12.1	8.1	7.6	728	Anglers, dog walkers, cyclists, horse riders
15	Weidekampsee	Managed	Weser	1994	Oligotrophic	4.3	2.9	8.0	461	Anglers, dog walkers
16	Wiesedermeer	Managed	SNST[a]	1990	Mesotrophic	9.2	2.9	8.0	136	Anglers, dog walkers
17	Bülstedt	Unmanaged	Weser	1991	Polytrophic	1.1	2.4	7.6	285	Birdwatchers
18	Goldbeck	Unmanaged	Elbe	1992	Eutrophic	5.0	2.3	7.9	293	Owner/friends, horse riders, swimmers
19	Handorf	Unmanaged	Weser	2004	Eutrophic	23.0	13.6	9.2	666	Horse riders, dog walkers
20	Hänigsen	Unmanaged	Weser	2011	Mesotrophic	12.3	6.2	8.6	437	Swimmers, dog walkers, anglers, campfires
21	Heeßel	Unmanaged	Weser	1963	Eutrophic	7.4	0.9	8.2	537	None
22	Hopels	Unmanaged	SNST[a]	1998	Mesotrophic	14.5	5.5	7.7	215	Swimmers, dog walkers
23	Lohmoor	Unmanaged	Weser	1991	Eutrophic	7.4	4.1	8.2	159	Birdwatchers
24	Pfütze	Unmanaged	Weser	2000	Mesotrophic	7.3	10.6	7.7	342	Dog walkers, canoeists, swimmers, cyclists
25	Schwicheldt	Unmanaged	Weser	2007	Mesotrophic	10.0	1.7	8.4	895	Owner/hunter, dog walkers
26	Xella	Unmanaged	Weser	1975	Mesotrophic	7.3	2.1	7.5	957	None (restricted access)

The locations of the catchments (fourth column) are shown in Figure 1. Trophic state was determined using Riedmüller, Hoehn, and Mischke (2013). The pH values and conductivities are annual means.

[a] Small North Sea tributaries.

Table 1). Both lake types were accessible to non-angling recreation, as they were not fenced (with the exception of Linner See).

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

Despite the attempt to select lakes with similar environments (e.g. age, surface area, and trophic state), a set of environmental variables was assessed and integrated within the statistical analyses to isolate the possible impact of recreational fisheries management on biodiversity, while controlling for other key environmental differences among lakes that might also affect the community composition of specific taxa (e.g. morphometry, land use, and habitat structure).

2.2 | Land use

Several indicators of land use and spatial arrangement across catchments in Lower Saxony were assessed. Shortest-path distances of lakes to nearby cities, villages, lakes, canals, and rivers were calculated in GOOGLE MAPS 2017. Subsequently, a share of different land-use categories within 100 m around each lake (buffer zone) was calculated in QGIS 3.4.1 with GRASS 7.4.2 using ATKIS® land-use data with a 10 m × 10 m grid scale (©GeoBasis-DE/BKG 2013; AdV - Working Committee of the Surveying Authorities of the States of the Federal Republic of Germany, 2006). The ATKIS® object categories were merged into seven land-use classes: (i) urban (including all anthropogenic infrastructures, such as buildings, streets, railroad tracks, etc.); (ii) agriculture (all arable land, such as fields and orchards, but not meadows or pastures); (iii) forest; (iv) wetland (e.g. swamps, fens, and peatlands); (v) excavation (e.g. open pit mines); (vi) water (e.g. lakes, rivers, and canals); and (vii) other (not fitting elsewhere, such as succession areas, grassland, boulder sites, etc.).

2.3 | Recreational use intensity

The lake-specific recreational use intensity was assessed by counting the type and number of recreational visitors during each site visit (with between six and nine visits per lake, see description of biodiversity sampling below). Metrics for the intensity of indirect use encompassed measures of accessibility and litter, which were assessed as follows: the length of all trails and pathways around each lake were measured with a measuring wheel (2 m circumference, 0.1% accuracy; Cross-country measuring wheel, model 12015001; NESTLE, Dornstetten, Germany). These variables were summed and normalized to shoreline length. Angling sites and other open spaces accessible to other recreational visitors (e.g. swimmers) along the shoreline were counted, and all litter encountered along paths and sites were counted and assigned to: (i) angling related (e.g. lead weight, nylon line, artificial bait remains); or (ii) other litter not directly related to angling (e.g. plastic packaging, beer bottles, cigarette butts). More intensively used lakes were expected to receive larger volumes of litter and be more easily accessible through paths and trampled sites, which could damage biodiversity.

2.4 | Age and morphology

The age of each lake was assessed through records in the angling clubs and by interviewing owners of lakes and regional administrations or municipalities. Bathymetry and the size of each lake was mapped with a SIMRAD NSS7 evo2 echo sounder paired with a Lawrence TotalScan transducer mounted on a boat driven at 3–4 km h^{-1} along transects spaced at 25–45 m, depending on lake size and depth. The data were processed using BioBase (Navico, Minneapolis, MN), and the post-processed data (depth and Global Positioning System (GPS) position per ping) were used to calculate depth contour maps using ordinary kriging with the GSTAT package in R 3.5.1 (Gräler, Pebesma, & Heuvelink, 2016; R Core Team, 2013). Maximum depth and relative depth ratio (Damnjanović et al., 2018) were extracted from the contour maps. Shoreline length and lake area were estimated in QGIS 3.4.1 and used to calculate the shoreline development factor (*SDF*), which is the ratio of the lake shoreline length (*L*) to the circumference of a circle with the same area (*A*): $SDF = \frac{L}{2\sqrt{\pi A}}$.

2.5 | Water chemistry and nutrient levels

During the spring overturn, epilimnic water samples were taken to analyse total phosphorus concentrations (TP), total organic carbon (TOC), ammonium and nitrate concentrations (NH_4, NO_3), and chlorophyll *a* (chl *a*; with three samples per lake) as a measure of algal biomass. TP was determined using the ammonium molybdate spectrophotometric method (EN ISO 6878, 2004; Murphy & Riley, 1962), TOC was determined with a non-dispersive infrared detector (NDIR) after combustion (DIN EN 1484, 1997), ammonium and nitrate were assessed using the spectrometric continuous flow analysis (DIN EN ISO 13395, 1996; EN ISO 11732, 2005), and chl *a* was quantified using high-performance liquid chromatography (HPLC), where the phaeopigments (degradation products) were separated from intact chl *a* and only the concentration of intact chl *a* was measured (Mantoura & Llewellyn, 1983; Wright, 1991). For chl *a* the mean of three samples per lake was determined for each sampling. Also, during the spring overturn the conductivity and pH of each lake were measured in epilimnic water with a WTW Multi 350i sensor probe (WTW GmbH, Weilheim, Germany), and turbidity was assessed using a standard Secchi disc. For all variables, the mean values for 2 years (i.e. two samplings) were used in the analyses.

2.6 | Littoral and riparian habitat assessment

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

2.7 | Riparian plant species

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

2.8 | Submerged macrophytes

All lakes were sampled for submerged macrophytes between late June and late August, following the sampling protocol of Schaumburg, Schranz, Stelzer, and Vogel (2014). Every lake was scuba-dived and snorkelled along transects set perpendicular to the shoreline from the bank (depth = 0 m) to the middle of the lake until the deepest point of macrophyte growth was reached. The position of the first transect was randomly chosen and all other transects were spaced evenly along the shoreline at 80–150 m distances, depending on lake size, resulting in between four and 20 transects sampled per lake. Along each transect, the dominance of submerged macrophyte species in every depth stratum (0–1, >1–2, >2–4, >4–6 m) was visually estimated following the Kohler scale (Kohler, 1978). No macrophytes were found below a depth of 6 m. Macrophytes were identified directly under water, or if this was not possible samples were taken and identified under a stereomicroscope following Van de Weyer and Schmitt (2011). Stonewort species were identified only to genus level (*Chara* and *Nitella*), and thus exact species numbers might be underestimated. Macrophyte dominance was transformed to percentage cover for each transect (Van der Maarel, 1979). The average cover per stratum was extrapolated to the total lake using the contour maps. The total macrophyte cover in the littoral zone was calculated using the extrapolated cover from strata between 0 and 3 m in depth. The regional species pool was estimated from the Red Lists of Lower Saxony, which include full species inventories, in combination with the expected species for gravel pit lakes following the list of plant species associations in Lower Saxony (Garve, 2004; Korsch, Doege, Raabe, & van de Weyer, 2013; Preising et al., 1990).

2.9 | Amphibians

Amphibians were sampled during the mating seasons (from March to May). Every lake was sampled twice: (i) during the day, with an inflatable boat driving slowly along the shore searching for adults, egg balls (frogs), and egg lines (toads); and (ii) after sunset, by foot around the lake searching for calling adults. Each observation (adult or eggs) was marked with a GPS (Oregon 600; Garmin, Olathe KS) and identified in the field or photographed for later identification, following Schlüpmann (2005). Numbers were recorded (adults) or estimated (eggs), assuming 700 to 1,500 eggs per egg ball (frogs) or 10,000 eggs per (100% covered) m^2 of egg-line assemblages (toads). The egg numbers were calculated from pictures taken in the field and verified following Trochet et al. (2014). The regional species pool was estimated from the Red List of Lower Saxony, which includes a full species inventory, in combination with expected distributions (Podloucky & Fischer, 2013).

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

2.11 | Waterfowl and songbirds

Waterfowl were identified following Dierschke (2016) and counted at every visit (with between six and nine visits per lake). Songbirds were sampled once per lake between early- and mid-summer using point-count sampling combined with a bioacoustics approach, which has also been used in other studies (Rempel, Hobson, Holborn, Van Wilgenburg, & Elliott, 2005; Wilson, Barr, & Zagorski, 2017). Two-minute audio recordings (Handy Recorder H2, Surround 4-Channel setting, 44.1-kHz sampling frequency, 16-bit quantification; Zoom, Tokyo, Japan) were taken at sampling points placed 200 m apart around the whole lake, assuming that each sampling point covers a radius of 100 m. Sampling points were marked with GPS. At each point all birds seen (or heard while not recording) were also noted when identified following Dierschke (2016). The audio recordings were analysed in the laboratory, and singing species were identified using reference audio samples (www.deutsche-vogelstimmen.de; www.vogelstimmen-wehr.de) and birdsong-identifying software (BIRDUP 2018 automatic birdsong recognition, developed by Jonathan Burn, https://play.google.com/store/apps/details?id=com.jb.birdlistener.birdup%26hl=en_GB%26gl=US). The regional species pools for waterfowl and songbirds were estimated from the Red List of Lower Saxony (Krüger & Nipkow, 2015), which includes a full species inventory, in combination with their expected occurrence according to habitat type and preferences (Dierschke, 2016).

2.12 | Diversity metrics

The analysis focused on species presence–absence data to arrive at measures of taxonomic species richness, an aggregate index of species diversity. In addition, the Simpson diversity index (Pielou, 1969) was computed using relative abundance data by species to consider the dominance of certain species within each taxon-specific community. There was no consideration of whether a particular species detected actually recruits in a given gravel pit lake, only noting that the species was present, and assuming that the estimates represented a minimal estimate of local richness as rare species probably remained undetected. To weight rare and threatened species more heavily, the richness of threatened species was computed and an index of taxon-specific conservation value for the study region was estimated following Oertli et al. (2002). To that end, each species was ranked according to its threat status on the Red Lists of Lower Saxony (Altmüller & Clausnitzer, 2010; Garve, 2004; Korsch et al., 2013; Krüger & Nipkow, 2015; Podloucky & Fischer, 2013). Species of Least Concern were ranked lowest: $c(0) = 2^0 = 1$. All species classified with an increasing threat status category r according to the regional Red List were weighted exponentially more strongly, as $c(r) = 2^r$ (Table 2), following Oertli et al. (2002). For each lake, the final taxon-specific conservation value (CV) was calculated as the sum of all values for the observed species s_i ($s_1, s_2, s_3, \ldots, s_n$) divided by the total number of species (n) for a given taxon:

TABLE 2 Ranking of Red List categories used for the calculation of conservation values

Red List categories of Lower Saxony	Rank r	Weight c
1 – Critically Endangered	4	16
2 – Endangered or R – Rare	3	8
3 – Vulnerable or G – Indeterminate	2	4
V – Near Threatened	1	2
* – Least Concern or – Data Deficient	0	1

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

The conservation index value increases with more species of a given taxon being threatened or rare. A range of different allocations of threat status were tested to estimate the conservation value, also using national and European Red Lists. The results remained robust, however.

To test for differences in species composition across all lakes, the pooled species inventory by lake type (managed and unmanaged) was used, and the Sørensen index (Sørensen, 1948) as a measure of community similarity was calculated. The Sørensen index ranges from 0 (no species in common between the two lakes types) to 1 (all species the same), and is calculated as $2a/(2a + b + c)$, with a being the number of shared species and b and c being the numbers of unique species to each lake type, respectively. As an indicator for whether species compositions are substantially (i.e. biologically meaningfully) different or not, so called 'faunal breaks' as well as 'floral breaks' were searched for. Following Matthews (1986), faunal or floral breaks among lake types were assumed to occur when the Sørensen index was <0.5.

2.13 | Statistical analysis

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

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

TABLE 3 Univariate comparison of environmental variables between managed and unmanaged gravel pit lakes

		Mean ± SD (minimum–maximum)		Comparison		
Class	**Environmental variable (abbreviation)**	**Managed (n = 16)**	**Unmanaged (n = 10)**	**Test[a]**	**Statistic**	***P***
Morphology	Maximum depth (m) (MaxDep)	9.7 ± 4.9 (2.8–23.5)	9.5 ± 6.0 (1.1–23.0)	U	W = 89	0.986
	Lake area (ha) (LArea)	7.4 ± 5.6 (1.0–19.5)	4.9 ± 4.2 (0.9–13.6)	U	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	$t = -1.0$	0.824
	Relative depth ratio (RelDepR)	0.04 ± 0.01 (0.02–0.07)	0.04 ± 0.02 (0.01–0.07)	t	$t = -1.1$	0.754
Trophic state	Total phosphorus (µg l^{-1}) (TP)	25.7 ± 36.5 (8–160)	27.2 ± 20.9 (12–72)	U	W = 63.5	0.983
	Total organic carbon (mg l^{-1}) (TOC)	6.6 ± 2.8 (2.5–13)	6.0 ± 2.5(2.9–12.4)	U	W = 93	0.997
	Mean chlorophyll *a* (µg l^{-1}) (chl *a*)	11.6 ± 15.9 (2.05–65.3)	21.2 ± 26.1 (2.6–90.6)	U	W = 53	0.765
	Secchi depth (m) (Secchi)	2.6 ± 1.5 (0.5–5.5)	2.0 ± 1.1 (0.5–4.5)	t	$t = 0.9$	0.972
	Ammonium (µg l^{-1}) (NH_4)	56.9 ± 71.2 (15.0–240.0)	84.0 ± 164.8 (15.0–550.0)	U	W = 75	1.000
	Nitrate (µg l^{-1}) (NO_3)	283.8 ± 380.4 (5.0–1040.0)	733.0 ± 984.1 (5.0–2940.0)	U	W = 50	0.604
	Conductivity (µS cm^{-1}) (Con)	450.9 ± 192.3 (136–742)	478.6 ± 279.8 (159–957)	t	$t = -0.3$	1.000
	pH Value (pH)	7.9 ± 0.5 (6.7–9)	8.1 ± 0.5 (7.5–9.2)	t	$t = -1$	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	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	W = 86.5	1.000
	Mean riparian tree cover on an ordinal scale from 0 to 4 (Rip_Trees)	1.0 ± 0.2 (0.4–1.5)	0.9 ± 0.3 (0.4–1.2)	t	$t = 0.9$	0.942
	Mean litoral reed cover on an ordinal scale from 0 to 4 (Reed)	1.3 ± 0.9 (0–2.5)	0.8 ± 0.7 (0–1.7)	t	$t = 1.25$	0.779
	Mean riparian vascular plant cover on an ordinal scale from 0 to 4 (Rip_Herbs)	1.7 ± 0.4 (1.1–3.0)	1.0 ± 0.7 (0.1–1.9)	U	W = 118	0.225
	Submerged macrophyte cover in the littoral zone in % (MP_Cov)	*39.3 ± 19.9 (12.5–82.3)*	*21.1 ± 27.5 (0–85.2)*	U	*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	$t = 1.05$	0.303

P values are Sidak corrected to account for multiple comparisons within classes of related environmental variables. Statistical tendencies ($P < 0.1$) are set in italics.

[a] t, Student's *t*-test; U, Mann–Whitney *U*-test.

Second, the among-lake variation in species richness was modelled as a function of lake type and a set of lake-specific environmental descriptors. These analyses aimed to further isolate the impact of fisheries management and type of recreational use on species inventories across all taxa and lakes, in a joint model that included other predictor variables of the lake environment. To reduce the dimensionality of the environmental variables, principal component analyses (PCAs) without rotations were conducted on related classes of environmental variables (groups of environmental variables were structured into variables related to morphology, productivity, habitat structure, land use, and recreational use). Environmental variables forming principal components (PCs) were considered to be correlated, and their loadings were identified, axes interpreted, and the PC scores used as indicator variables. A multivariate redundancy analysis (RDA) was then conducted to examine whether recreational fisheries management explained variation in environmental variables or in species richness across multiple taxa in the multivariate space. In addition to lake type, all relevant environmental variables (e.g. trophic state, surface area/steepness, land use, riparian/littoral habitat structure, water chemistry), intensity of recreational use, gravel pit age, and catchment were included in the multivariate analysis of species richness. With the RDA, a forward selection process (Blanchet, Legendre, & Borcard, 2008) was used to identify the environmental predictors that explained the most variance in species richness across different taxa and lakes, including management as a key variable of interest in this study. Using the variance inflation factor (VIF; Neter, Kutner, Nachtsheim, & Wasserman, 1996), correlated environmental variables were removed before model building. All data were scaled and centred (transformed to z-values) before analysis. The degree of explanation was expressed using the adjusted coefficient of multiple determinations (R^2_{adj}). Variables significantly explaining variation in richness across lakes were also assessed using analysis of variance (ANOVA) at a significance level of $P < 0.05$. All calculations and analyses were carried out in R 3.5.1 using the VEGAN package (Oksanen et al., 2018; R Core Team, 2013).

3 | RESULTS

3.1 | Description of lake types in relation to the environment

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

3.2 | Environmental characteristics of managed and unmanaged gravel pit lakes

Both lake types did not differ statistically in age, size, trophic state, and land use (Table 3). A similar result was obtained in a multivariate RDA, which confirmed the absence of significant differences between managed and unmanaged lakes in 'classes of environmental variables' (i.e. PC scores, for details see Tables S5 and S6) representing morphology (an index of steepness and water body size; $R^2_{adj} = -0.005$, $F = 0.86$, $P = 0.470$), trophic state ($R^2_{adj} = -0.006$, $F = 0.86$, $P = 0.544$), proximity to other water bodies ($R^2_{adj} = -0.023$, $F = 0.45$, $P = 0.867$), proximity to human presence ($R^2_{adj} = 0.035$, $F = 1.90$, $P = 0.143$), and land-use variables ($R^2_{adj} = 0.033$, $F = 1.85$, $P = 0.135$). However, in multivariate space the habitat structure differed significantly among managed and unmanaged lakes along the first PC axis (Dim 1), which represented a vegetation gradient below and above water (Figure 2).

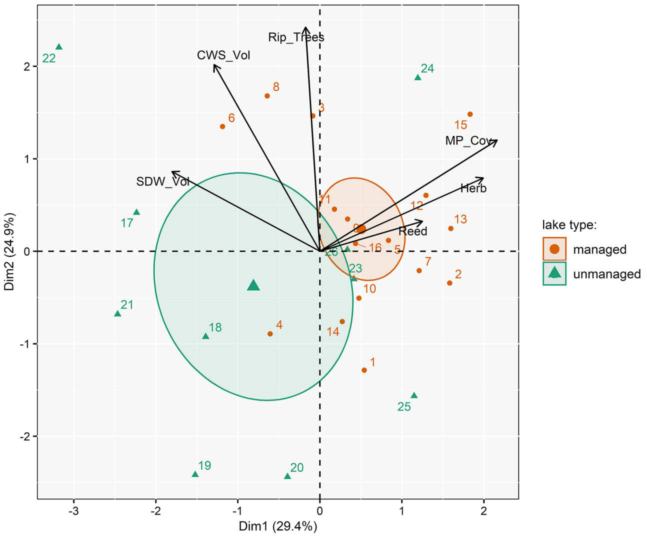

FIGURE 2 Principal component analysis (PCA) by classes of related environmental variables visualized for habitat structure (SDW_Vol, volume % of simple dead wood; CWS_Vol, volume % of coarse woody structure; Rip_Trees, mean riparian tree cover; Herb, mean riparian vascular plants cover; Reed, mean litoral reed cover; MP_Cov, submerged macrophyte cover in the littoral zone; Table 3). Percentages in brackets show the proportional variance explained by each axis, respectively. Numbers reflect the different lakes (Table 1). The centroids of lake types are plotted as supplementary variables that did not influence the ordination. The 95% confidence levels around centroids are plotted to visualize differences between lake types

TABLE 4 Univariate comparison of environmental variables between managed and unmanaged gravel pit lakes

		Mean ± SD (minimum–maximum)		Comparison		
Class	**Environmental variable (abbreviation)**	**Managed (n = 16)**	**Unmanaged (n = 10)**	**Test[a]**	**Statistic**	***P***
Land use	Excavation within 100-m buffer (%) (Excav)	4.8 ± 7.2 (0–21.3)	9.4 ± 14.6 (0–39.0)	U	W = 63	0.718
	Agriculture within 100-m buffer (%) (Agric)	22.8 ± 19.9 (2.4–55.9)	33.8 ± 25.4 (3.5–79.0)	U	W = 58	0.598
	Forest within 100-m buffer (%) (Forest)	22.0 ± 25.1 (0–72.6)	5.6 ± 6.0 (0–15.5)	U	W = 118	0.132
	Urban area within 100-m buffer (%) (Urban)	27.8 ± 29.2 (0–87.5)	17.4 ± 24.5 (0–59.5)	U	W = 99	0.767
Water	Wetland within 100-m buffer (%) (Wetland)	0.9 ± 3.6 (0–14.4)	5.1 ± 14.1 (0–45.1)	U	W = 61.5	0.504
	Water surface within 100-m buffer (%) (Water)	9.7 ± 12.5 (0.9–50.4)	8.7 ± 8.8 (0.5–30.1)	U	W = 80	1.000
	Distance to next lake (m) (DistLake)	164.1 ± 236.4 (5–850)	264.1 ± 440.6 (1–1,280)	U	W = 87	0.999
	Distance to next river (m) (DistRiver)	5,226.1 ± 9,805.2 (25–29,900)	3,999.5 ± 9,841.6 (220–31,920)	U	W = 92	0.980
	Distance to next canal (m) (DistCanal)	312.4 ± 462.3 (1–1,630)	224.5 ± 367.9 (5–1,180)	U	W = 84	1.000
Human presence	Distance to next road (m) (DistRoad)	265.3 ± 314.4 (15–1,010)	558.0 ± 510.1 (30–1,530)	U	W = 50.5	0.416
	Distance to next settlement (m) (DistVille)	504.1 ± 407.8 (20–1,400)	801.0 ± 673.0 (60–1,810)	t	$t = -1.4$	0.530
	Distance to next city (m) (DistCity)	7,135.0 ± 4,087.6 (170–13,130)	5,859.0 ± 4,488.3 (1,070–15,110)	t	$t = 0.8$	0.917
Recreational use	**Litter related to angling (pieces per m shoreline) (A_Lit)**	**0.05 ± 0.05 (0–0.20)**	**0.002 ± 0.007 (0–0.021)**	**U**	**W = 140.5**	**0.007**
	Litter unrelated to angling (pieces per m shoreline) (NonA_Lit)	0.70 ± 0.50 (0.02–1.48)	0.34 ± 0.71 (0–2.29)	U	W = 126	0.124
	Angling sites and open spaces (% of shoreline) (open_sites)	**18.5 ± 19.8 (3.6–87.7)**	**8.4 ± 14.4 (0–48.6)**	**U**	**W = 133**	**0.044**
	Trails and paths per shoreline ($m\ m^{-1}$) (Trails)	**0.9 ± 0.1 (0.6–1.1)**	**0.4 ± 0.5 (0–1.4)**	**U**	**W = 138**	**0.019**
	Anglers per lake per visit (Anglers)	**1.6 ± 1.6 (0–5.1)**	**0.1 ± 0.2 (0–0.8)**	**U**	**W = 143**	**0.006**
	Dog walkers per lake per visit (Dogs)	1.7 ± 1.9 (0–6)	0.5 ± 1.0 (0–3.3)	U	W = 123.5	0.154
	Swimmers per lake per visit (Swimmers)	*2.9 ± 2.6 (0–10)*	*0.7 ± 1.0 (0–3.1)*	*U*	*W = 129.5*	*0.075*
	Other recreational visitors per lake per visit (other_people)	*2.9 ± 3.2 (0.3–11.9)*	*0.9 ± 1.4 (0–3.8)*	*U*	*W = 128.5*	*0.087*

P values are Sidak corrected to account for multiple comparisons within classes of related environmental variables. Statistically significant results ($P < 0.05$) are shown in bold; statistical tendencies ($P < 0.1$) are set in italics.

[a] t, Student's *t*-test; U, Mann–Whitney *U*-test.

Along this axis, managed lakes were found to be more vegetated than unmanaged lakes in both the riparian and the littoral zones ($R^2_{adj} = 0.056$, $F = 2.48$, $P = 0.022$).

3.3 | Recreational uses of managed and unmanaged lakes

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

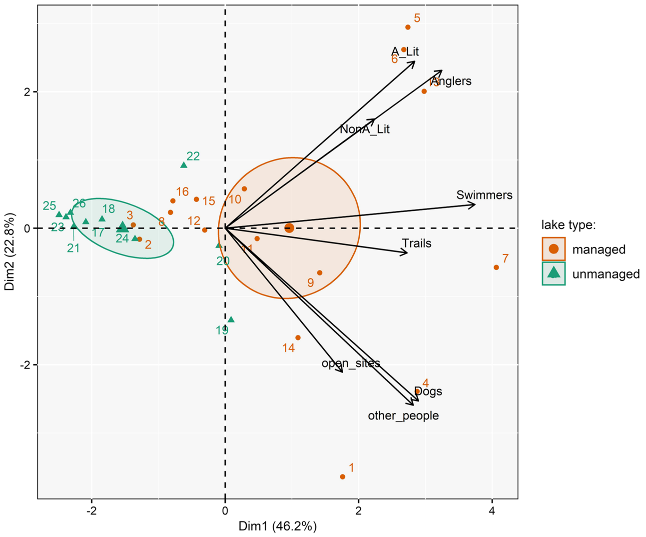

FIGURE 3 Principal component analysis (PCA) by classes of related environmental variables visualized for recreational use intensity (A_Lit, litter related to angling; NonA_Lit, litter unrelated to angling; open_sites, angling sites and open spaces; Trails, trails and paths per shoreline; Anglers, number per visit; Dogs, dog walkers per visit; Swimmers, number per visit; other_people, other recreational visitors per visit; Table 4). Percentages in brackets show the proportional variance explained by each axis, respectively. Numbers reflect the different lakes (Table 1). The centroids of lake types are plotted as supplementary variables that did not influence the ordination. The 95% confidence levels around centroids are plotted to visualize differences between lake types

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

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

Based on the pooled species inventories (gamma diversity), unique species (i.e. species present in only one lake or only one lake type) were found in all taxonomic groups except for amphibians (Table 5). Managed lakes hosted more unique species within most taxonomic groups than unmanaged lakes, whereas unmanaged lakes had more unique Odonata. No faunal or floral breaks were detected between managed and unmanaged lakes using the Sørensen index (all indices ≥0.5; Table 5). The average taxon-specific species richness (alpha-diversity), the Simpson diversity index, the average number of threatened species, and the average taxon-specific conservation value were statistically similar in managed and unmanaged lakes across all taxonomic groups when analysed using univariate statistics (Table 6).

TABLE 5 Overview about unique species of different taxa found at managed and unmanaged gravel pits in Lower Saxony, Germany

	Species number found only in:		
Taxon	managed lakes	unmanaged lakes	Sørensen index (similarity)
Submerged macrophytes	15 (13)	10 (9)	0.58
Riparian vascular plants	55 (35)	31 (23)	0.73
Riparian trees	6 (4)	5 (4)	0.86
Amphibians	0 (0)	0 (0)	1.00
Odonata	5 (3)	8 (4)	0.76
Songbirds	9 (7)	6 (5)	0.74
Waterfowl	10 (3)	6 (3)	0.69

The numbers in brackets refer to single-lake observations, i.e. the number of species found at only one lake each.

TABLE 6 Univariate comparison of species richness, Simpson index, threatened species, and taxon-specific conservation values in managed and unmanaged gravel pit lakes

		Mean ± SD (minimum–maximum)		Comparison		
Diversity measure	**Taxa**	**Managed (n = 16)**	**Unmanaged (n = 10)**	**Test[a]**	**Statistic**	***P***
Species richness	Submerged macrophytes	6.4 ± 3.2 (2–14)	5.2 ± 3.6 (0–11)	t	t = 0.91	0.962
	Riparian vascular plants	42.3 ± 12.6 (15–57)	49.2 ± 11.2 (30–64)	t	*t* = −1.43	0.718
	Riparian trees	12.8 ± 2.1 (9–17)	12.6 ± 5.3 (3–24)	F	*t* = 0.08	1.000
	Amphibians	1.6 ± 0.5 (1–2)	2.2 ± 0.8 (1–3)	U	W = 43	0.220
	Amphibians with reproduction	1 ± 0.6 (0–2)	1.4 ± 0.8 (0–3)	U	W = 59	0.832
	Odonata	7.9 ± 2.8 (2–12)	9 ± 4.3 (4–18)	t	*t* = −0.77	0.985
	Damselflies	4.3 ± 1.3 (2–6)	4.4 ± 1.3 (3–7)	t	*t* = −0.29	1.000
	Dragonflies	3.7 ± 2.1 (0–7)	4.6 ± 3.4 (1–12)	t	*t* = −0.84	0.975
	Songbirds	9.2 ± 2.8 (5–14)	11.3 ± 3 (7–17)	t	*t* = −1.81	0.452
	Waterfowl	9.5 ± 2.8 (3–13)	9.1 ± 3.5 (2–13)	t	t = 0.32	1.000
Simpson index	Submerged macrophytes	0.6 ± 0.2 (0.1–0.9)	0.5 ± 0.3 (0–1)	t	*t* = 0.32	1.000
	Riparian vascular plants	0.9 ± 0.1 (0.8–0.9)	0.9 ± 0.0 (0.8–0.9)	U	W = 79	1.000
	Riparian trees	0.7 ± 0.2 (0.2–0.8)	0.7 ± 0.1 (0.4–0.9)	U	W = 94	0.990
	Amphibians	0.1 ± 0.1 (0–0.4)	0.3 ± 0.2 (0–0.6)	U	W = 46	0.382
	Amphibians with reproduction	0.2 ± 0.4 (0–1)	0.2 ± 0.3 (0–1)	U	W = 69.5	0.997
	Damselflies	0.5 ± 0.1 (0.3–0.6)	0.6 ± 0.1 (0.4–0.8)	t	*t* = −2	0.339
	Dragonflies	0.6 ± 0.3 (0–1)	0.5 ± 0.4 (0–0.9)	U	W = 87	1.000
	Songbirds	0.8 ± 0.0 (0.7–0.9)	0.9 ± 0.0 (0.8–0.9)	t	*t* = −2.41	0.156
	Waterfowl	0.7 ± 0.1 (0.3–0.8)	0.7 ± 0.1 (0.4–0.9)	U	W = 81	1.000
Threatened species	Submerged macrophytes	1.3 ± 1.1 (0–4)	0.6 ± 1.0 (0–3)	U	W = 109	0.565
	Riparian vascular plants	0.6 ± 0.7 (0–2)	0.5 ± 0.7 (0–2)	U	W = 88	0.999
	Riparian trees	0 ± 0 (0–0)	0.1 ± 0.3 (0–1)	U	W = 72	0.848
	Amphibians	0.4 ± 0.5 (0–1)	0.8 ± 0.4 (0–1)	U	W = 51	0.440
	Odonata	0.8 ± 0.8 (0–2)	1.3 ± 1.2 (0–4)	U	W = 61.5	0.929
	Damselflies	0.3 ± 0.4 (0–1)	0.1 ± 0.3 (0–1)	U	W = 92	0.963
	Dragonflies	0.6 ± 0.7 (0–2)	1.2 ± 1.2 (0–4)	U	W = 54.5	0.692
	Songbirds	0.3 ± 0.5 (0–1)	0.5 ± 0.5 (0–1)	U	W = 65	0.958
	Waterfowl	1.1 ± 1.0 (0–3)	0.9 ± 1.0 (0–3)	U	W = 88	1.000
Conservation value	Submerged macrophytes	2.0 ± 0.8 (1–3.5)	1.6 ± 1.2 (1–4.6)	U	W = 99.5	0.571
	Riparian vascular plants	1.1 ± 0.2 (1–1.9)	1.0 ± 0.0 (1–1.1)	U	W = 94.5	0.978
	Riparian trees	1.0 ± 0.0 (1–1)	1.0 ± 0.1 (1–1.3)	U	W = 72	0.848
	Amphibians	1.7 ± 0.8 (1–2.5)	2.2 ± 0.9 (1–4)	U	W = 61.5	0.924
	Odonata	1.5 ± 0.5 (1–2.3)	1.7 ± 0.5 (1–2.6)	U	W = 59.5	0.901
	Damselflies	1.2 ± 0.4 (1–2.2)	1.1 ± 0.2 (1–1.8)	U	W = 91.5	0.972
	Dragonflies	1.7 ± 0.9 (1–3.3)	2.2 ± 1.0 (1–3.8)	U	W = 55.5	0.889
	Songbirds	1.2 ± 0.2 (1–1.6)	1.2 ± 0.1 (1–1.3)	U	W = 72.5	1.000
	Waterfowl	2.2 ± 1.0 (1.1–3.9)	2.2 ± 0.8 (1.2–3.2)	U	W = 79	1.000

[a] F, Welch's *F*-test; t, Student's *t*-test; U, Mann–Whitney *U*-test.

3.5 | Environmental correlates of among-lake variation in species richness

Across lakes, the species richness of amphibians, Odonata, songbirds, and riparian vascular plants covaried along the first axis (Figure 4), collectively representing riparian diversity (for full PCA results, see Table S8). The second PCA axis mainly represented submerged macrophytes (Figure 4). The third axis was related to the diversity of riparian tree species and the fourth axis was mainly related to waterfowl diversity (Figure 5). Therefore, lakes offering high riparian species richness were not necessarily rich in the biodiversity of submerged macrophytes, waterfowl, or trees. The RDA

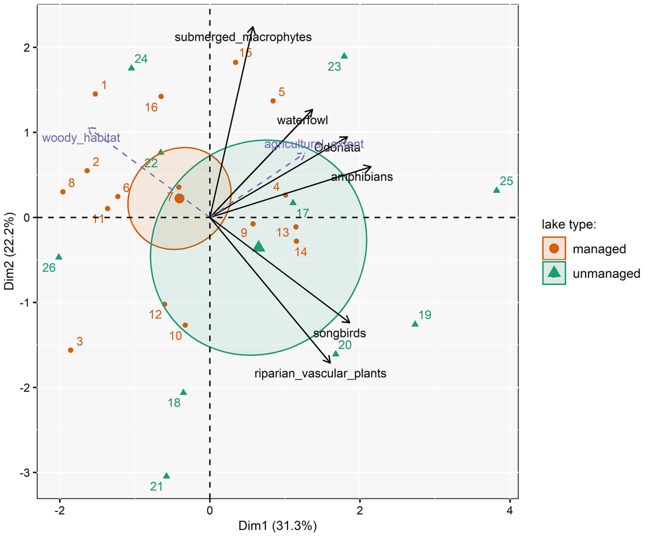

FIGURE 4 Principal component analysis (PCA) of species richness plotted for the first two axes (only relevant, i.e. highly contributing, variables are shown). Percentages in brackets show the proportional variance explained by each axis, respectively. Numbers reflect the different lakes (Table 1). The centroids of lake types and the explanatory variables from redundancy analysis (RDA, dashed purple lines, with only the important ones for Dim 1 and Dim 2 shown) are plotted as supplementary variables so as not to influence the ordination. The 95% confidence levels around centroids are plotted to visualize differences between lake types

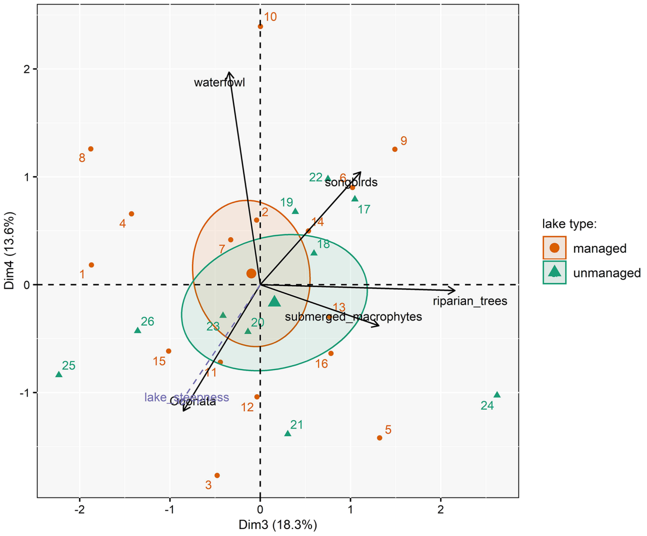

FIGURE 5 Principal component analysis (PCA) of species richness plotted for the third and fourth axis (only relevant, i.e. highly contributing, variables are shown). Percentages in brackets show the proportional variance explained by each axis, respectively. Numbers reflect the different lakes (Table 1). The centroids of lake types and the explanatory variables from redundancy analysis (RDA, dashed purple lines, with only the important ones for Dim 3 and Dim 4 shown) are plotted as supplementary variables so as not to influence the ordination. The 95% confidence levels around centroids are plotted to visualize differences between lake types

analysis used to explain the among-lake variation in species richness as a function of lake type alone revealed no influence of this factor on among-lake richness across several taxa (RDA, $R^2_{adj} = 0.028$, $F = 1.73$, $P = 0.114$).

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

4 | DISCUSSION

In line with initial expectations, no differences in species richness, Simpson diversity, and conservation value were found across all examined taxa between managed and unmanaged gravel pit lakes, and a similar species pool was found to be present in both lake types. Collectively, this study did not reveal that recreational fisheries management (through impacts on fish communities) or the presence of anglers (through disturbance effects on shoreline habitat and wildlife or lethal impacts through lost fishing gear) significantly constrains the development of diverse communities of amphibians, birds, submerged macrophytes, terrestrial plants, and Odonata, relative to those expected at lakes that are not managed for recreational fisheries. Instead, the best predictors of the variation in species richness among lakes were found to be related to land-use variables, the extent of woody habitat on the lake shores, and the lake morphology (surface area and steepness). Therefore, this study suggests that for the taxonomic groups and lake types that were examined, broader environmental factors and land use, and not the presence of recreational fisheries, and its management of fish stocks and littoral zones, shape the taxonomic diversity of plants, birds, amphibians, and dragonflies.

TABLE 7 Analysis of variance (ANOVA) results of forward selection of redundancy analysis models explaining species richness across taxa

Modelling step	Variable	Variance explained	R^2_{adj}[a]	F	P
Full model	**Woody_habitat**	**14.7%**	**0.112**	**6.63**	**<0.001**
	Catchment	**14.8%**	**0.080**	**2.22**	**0.028**
	Acidity	**6.9%**	**0.063**	**3.12**	**0.019**
	Agricultural_extent	**9.1%**	**0.060**	**4.10**	**0.003**
	Age	3.6%	0.050	1.63	0.165
	Lake_steepness	**6.9%**	**0.043**	**3.12**	**0.015**
	Lake type	2.3%	0.028	1.04	0.424
	Vegetated_habitat	3.8%	0.024	1.73	0.145
	Conductivity	4.2%	0.015	1.91	0.116
	Nitrogen	3.7%	0.012	1.65	0.160
	Wetland	2.3%	0.009	1.04	0.406
	Lake_shallowness	3.5%	0.009	1.57	0.186
	Inaccessibility	2.2%	0.000	1.00	0.431
	Trophic_state	1.1%	−0.004	0.48	0.825
	Rural	3.7%	−0.007	1.66	0.163
	General_recreational_use_intensity	2.1%	−0.011	0.96	0.466
	Forest_extent	2.4%	−0.015	1.10	0.379
	Distance_to_next_river	1.4%	−0.016	0.65	0.694
Best model	**Woody_habitat**	**14.7%**	**0.271**	**5.05**	**<0.001**
	Agricultural_extent	**11.8%**		**4.06**	**0.001**
	Lake_steepness	**9.3%**		**3.20**	**0.004**

Variables are ordered by their R^2_{adj} value. Statistically significant results ($P < 0.05$) are shown in bold.

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

4.1 | Biodiversity potential of gravel pit lakes

Gravel pit lakes in Lower Saxony, Germany, were found to host substantial species diversity and a high proportion of the regional species pools of aquatic and riparian taxa, especially trees, Odonata, and waterfowl. This finding supports related work in other areas of Europe (Damnjanović et al., 2018; Holtmann, Juchem, Brüggeshemke, Möhlmeyer, & Fartmann, 2018; Oertli, 2018; Spyra & Strzelec, 2019), yet only small proportions of the regional species pools were detected for vascular plant species, submerged macrophytes, songbirds, and amphibians. In particular, amphibians are considered very sensitive to predation from fish (Hecnar & M'Closkey, 1997), and none of the study lakes were free of fish (Matern et al., 2019). Many amphibian species depend on shallow water and develop best in small, temporary water bodies (Shulse, Semlitsch, Trauth, & Williams, 2010). The gravel pits in this study also had relatively steep slopes, with small areas of littoral zone, were disconnected from rivers, were located in agricultural landscapes, and were close to anthropogenic infrastructure. All of these factors are unfavourable for amphibian diversity and can explain the low species richness detected for this taxonomic group (Shulse et al., 2010). Importantly, the results of this study indicate that management by recreational fisheries and the substantially different fish communities in managed and unmanaged lakes can be excluded as an additional stressor.

4.2 | Environmental differences between managed and unmanaged lakes

The gravel pit lakes studied were similar in the majority of the environmental factors examined (including age), except for the cover of submerged macrophytes, which was more prevalent in managed gravel pit lakes compared with unmanaged lakes. Submerged macrophytes have been reported to be strongly affected by stocking benthivorous fishes, such as the common carp (Bajer et al., 2016; Miller & Crowl, 2006). In a subset of the same gravel pit lakes presented here, however, Matern et al. (2019) found a similar biomass of fishes in managed and unmanaged lakes, with carp and bream (*Abramis brama*) being present in both lake types. Owing to the sampling gear used by Matern et al. (2019), the authors are likely to have underestimated the abundance and biomass of the common carp and other large benthivorous fish (Ravn et al., 2019). Although no data are available on the absolute biomass of carp or other species in the study lakes, the fact that submerged macrophytes were more diverse and more developed in the angler-managed lakes suggests that the co-existence of carp and other game fish with a species-rich submerged macrophyte community, including threatened stonewort species (*Chara* sp. and *Nitella* sp.), is possible. This is contrary to expectations expressed elsewhere that managing lakes with benthivorous fish necessarily harms submerged macrophytes (Van de Weyer, Meis, &

Krautkrämer, 2015). Instead, the more developed submerged macrophytes in the managed lakes studied here suggests that critical biomass thresholds for benthivorous fish, after which macrophytes often vanish or strongly decline (approx. 100 kg ha^{-1}; Vilizzi, Tarkan, & Copp, 2015), might not have been reached. Alternatively, the transferability of the typical mesocosm studies that have reported substantial impacts of carp on macrophytes to occur after reaching approximately 100 kg ha^{-1} may not hold under conditions found in the wild (Arlinghaus, Hühn, et al., 2017).

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

4.3 | Differences in recreational use of managed and unmanaged lakes

Managed lakes were found to have more developed tracks, paths, parking places, and other facilities that attract anglers and other recreational visitors. Thus, angler-managed lakes were generally more accessible to water-based recreational visitors, although these differences were not always statistically significant between the two lake types for recreational uses other than angling. Importantly, despite managed lakes receiving regular fisheries management activities, such as stocking and angler use, both lake type and the index of general recreational use intensity were not related to species richness across multiple taxa and lakes. Thus, for the diversity metrics and the taxa examined (amphibians, birds, Odonata, vegetation), this study does not suggest that the use of gravel pits by recreational fisheries significantly constrains the development of aquatic and riparian biodiversity across a range of taxa. Clearly, species-specific effects on disturbance-sensitive species may still occur (e.g. selected bird species; Knight, Anderson, & Marr, 1991), which the combined metrics of taxonomic richness or the Simpson diversity index might have been too insensitive to detect. Further work on community differences between managed and unmanaged lakes is warranted.

4.4 | Differences in biodiversity among managed and unmanaged lakes

Across all taxa examined, no statistical differences were found in species richness, number of threatened species, conservation value, and Simpson diversity index between managed and unmanaged lakes. This result was unexpected. The management of recreational fisheries can affect aquatic and riparian biodiversity through various pathways: (i) through supporting and enhancing fish stocks that exert predation pressure (e.g. on tadpoles and Odonata larvae; Hecnar & M'Closkey, 1997; Knorp & Dorn, 2016); (ii) through indirect fish-based effects (e.g. uprooting macrophytes through benthivorous feeding; Bajer et al., 2016); (iii) through the direct removal or damage of submerged and terrestrial plants during angling activities (O'Toole et al., 2009), which may have knock-on effects on dragonflies (Müller et al., 2003); and (iv) through activity-based disturbance effects or lethal impacts through lost fishing sinkers, in particular for birds (Cryer et al., 1987; Sears, 1988). This study design was not tailored towards directly measuring disturbance effects on particular species; instead, it was designed to examine a range of taxonomic richness indices in aggregate for communities present at gravel pit lakes used by recreational fisheries compared with ecologically similar lakes that are not used by recreational fisheries. When judged against these aggregate biodiversity metrics, the study presented here does not support the idea that recreational fisheries management and angler presence have major impacts that modify species inventories to such a degree that they strongly depart from the biodiversity expected at unmanaged lakes without anglers. Previous work has reported relevant reductions in bird biodiversity from lakes exposed to human disturbances caused by recreation, including angling (Bell et al., 1997); however, similar species richness and conservation value, both of waterfowl and riparian songbirds, in managed and unmanaged lakes were found in the present work. This does not exclude the possibility, for example, that the breeding success of specific disturbance-sensitive taxa might have been impaired in angler-managed lakes (Park, Park, Sung, & Park, 2006; Reichholf, 1988), but if such effects were present they were not strong enough to alter species richness (not to be confused with species identity) substantially. Overall, against the metrics chosen, the findings supported the initial hypothesis of no impacts from recreational fishing on non-targeted taxa in gravel pits situated in agricultural landscapes.

4.5 | Environmental determinants of aquatic and riparian biodiversity in gravel pit lakes

The species richness of different taxa did not vary uniformly among lakes, in contrast to the findings from a study of managed shallow ponds conducted by Lemmens et al. (2013). While examining strictly aquatic taxa (zooplankton, submerged and emergent aquatic macrophytes, benthic invertebrates), Lemmens et al. (2013) recorded uniform responses in species richness across taxa and ponds in their study. The much broader trophic and habitat requirements of aquatic and riparian taxa examined here resulted in significantly more variable biotic responses. For example, lakes rich in riparian biodiversity were not necessarily rich in submerged macrophytes and waterfowl biodiversity. The reason was that the aquatic and riparian biodiversity responded to many variables beyond those measured within the lake. The multivariate analyses showed that variation in species richness across multiple taxa was driven by structural variables such as habitat quality, lake morphometry (surface area and steepness) and land use in a buffer zone around the lake, but not by recreational use intensity or the presence of recreational fisheries management activities. Thus, environmental factors unrelated to recreational fishing seem to overwhelm any specific impacts of angling, at least for the taxonomic diversity metrics and the taxa examined here.

Mosaics of different habitats (reeds, overhanging trees, etc.) along the shoreline support species richness and diversity for most taxa (Kaufmann, Hughes, Whittier, Bryce, & Paulsen, 2014), and the presence of endangered biota increase the recreational value of gravel pit lakes as perceived by anglers (Meyerhoff et al., 2019). Extended woody habitat both in water and particularly in the riparian zone was correlated with increased tree diversity, but reduced riparian species richness of vascular plants, amphibians, Odonata, and songbirds. This might be explained by the shading effect of trees on non-woody vegetation (Monk & Gabrielson, 1985). Odonata, songbirds, and amphibian species benefited from more vegetated littoral habitats, in agreement with previous work (Paracuellos, 2006; Remsburg & Turner, 2009; Shulse et al., 2010). The species richness of waterfowl was strongly governed by lake surface area and steepness of the littoral zone, with larger and shallower lakes having a higher waterfowl species richness, confirming earlier findings reported by Paszkowski and Tonn (2000). The three dominant waterfowl species (occurring on 85% or more of the sampled lakes) were either omnivorous (mallard, *Anas platyrhynchos*) or herbivorous–invertivorous (common coot, *Fulica atra*; tufted duck, *Aythya fuligula*). In addition, 77% of the lakes were used by the grey goose (*Anser anser*), which feeds on terrestrial plants. Thus, it can be concluded that the dominant waterfowl detected at the lakes studied benefit from submerged macrophytes or riparian plants, which are both found to be more abundant at managed lakes.

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

4.6 | Limitations

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

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

A further limitation is that the design did not include entirely unused lakes where recreation is totally prohibited. The present data must be interpreted against the possibility that gravel pits situated in reserves with strictly no human access might show higher species diversity than that found in the lakes sampled. All the lakes were situated in agricultural environments and all were exposed to a certain level of recreational use. Background disturbance might have affected the observed species pool, affecting the detectability of species in the study region. The conclusions of the present work are also confined to the environmental gradients that could be observed. For example, higher intensities of angler use than found in the present work might reveal different results.

The intensity of recreational use was mainly recorded during weekdays when the field visits took place. Thus, potentially high-intensity phases at weekends might be unrepresented. This would actually strengthen our conclusions, however, if the real recreational use of managed lakes was well beyond that considered in this analysis.

4.7 | Conclusions

This study shows that the co-existence of recreational fisheries and aquatic and riparian biodiversity of high conservation value and richness is possible, at least under the specific ecological conditions of gravel pit lakes in agricultural landscapes. From a conservation perspective, it is suggested that recreational fishing clubs should increasingly use habitat enhancement activities to support fish and other taxa present at gravel pit lakes. The development of diverse shorelines as well as the creation of more gently sloping littoral areas is recommended as actions to be completed during the creation of gravel pit lakes. If these actions are taken, prohibiting recreational fishing is unlikely to produce further conservation benefits if the aim is to create high species diversity, independent of a specific-species identity.

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ORCID

Robert Nikolaus https://orcid.org/0000-0002-6639-2743
Malwina Schafft https://orcid.org/0000-0003-0633-4063
Andreas Maday https://orcid.org/0000-0002-0092-8744
Thomas Klefoth https://orcid.org/0000-0003-3659-5336
Christian Wolter https://orcid.org/0000-0002-2819-2900
Robert Arlinghaus https://orcid.org/0000-0003-2861-527X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Influence of protected riparian areas on habitat structure and biodiversity in and at small lakes managed by recreational fisheries

Robert Nikolaus[a], Sven Matern[a,b], Malwina Schafft[a,b], Andreas Maday[a], Christian Wolter[a], Thomas Klefoth[c], Robert Arlinghaus[a,b]

[a] *Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, Berlin 12587, Germany*

[b] *Division for Integrative Fisheries Management, Thaer-Institute for Agricultural and Horticultural Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, Berlin 10155, Germany*

[c] *Ecology and Conservation, Faculty 5 - School of Nature and Engineering, Hochschule Bremen, City University of Applied Sciences, Neustadtswall 30, Bremen 28199, Germany*

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ABSTRACT

Protected areas are a common management tool to conserve habitats and species by controlling access and disturbances by humans. Whenever protected areas result in restricting access to riparian zones in lakes, they may have positive effects on habitats and taxa beyond fish by lowering influences of trampling or boating on plants, by reducing the degree of human-induced disturbances to sensitive taxa such as birds, and by reducing fishing effort. However, especially in small freshwater systems knowledge about the functioning of protected areas that cover only parts of the lake shorelines is limited. We studied small gravel pit lakes in Germany where recreational fishing clubs have voluntarily assigned no-access riparian protected areas on parts of the lake shorelines and examined outcomes for habitat quality, plants, fish and bird populations. A total of 15 lakes were sampled, and we assessed habitat structure and abundance of plants, and fish within and outside protected areas and bird abundance at the lake scale, relying on standardized sampling methods. After controlling for confounding environmental factors related to lake morphology, age, nutrients, and land use, we detected positive contributions of small-scale riparian protected areas on habitat structure, riparian vegetation, local fish abundance and abundance of sensitive songbirds at the lake-scale, but we found no effects on aquatic vegetation and on disturbance-sensitive waterfowl species. Scale-restricted riparian protected areas voluntarily assigned by recreational fishing clubs can have positive outcomes for habitat quality and biodiversity, particularly by reducing trampling and access to anglers and other recreationists. Moreover, through provision of key habitat for young fish, small-scale riparian protected areas can also benefit fish abundance and in turn recreational fisheries.

1. Introduction

Conservation management shares similarities with the objectives of fisheries management related to protecting and enhancing biodiversity and habitats (Sandbrook et al., 2019). For example, one key goal of fisheries management is to maintain and enhance exploited populations towards biomass levels that produce acceptable services to humans (Ahrens et al., 2020; FAO, 2012; Hilborn, 2010). Achieving such aims may involve protection of water and shoreline areas and where needed restoration of habitats to maintain productive fisheries (Arlinghaus et al., 2016; Roni et al., 2008; Sass et al., 2017). Habitat-oriented actions can affect taxa beyond fish and thereby benefit biodiversity more generally (Friberg et al., 1998; Iversen et al., 1993). The management tools available to conservation range from habitat protection or restoration, to captive breeding (e.g. for species restoration), to (international) trade and hunting/fishing regulations (Chandra and Idrisova, 2011). Fisheries management is similarly concerned with a range of tools that involve protecting or enhancing habitats, stocking fish, or implementing harvest regulations that regulate access or removal rates by fishers and anglers (Arlinghaus et al., 2016). The difference between conservation and fisheries management is often the scope of the targeted taxa. Where conservation typically targets species of concern (e.g. threatened species) or protection of vulnerable habitats, fisheries management typically aims at exploited fish species, sometimes also

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E-mail address: robert.nikolaus@igb-berlin.de (R. Nikolaus).

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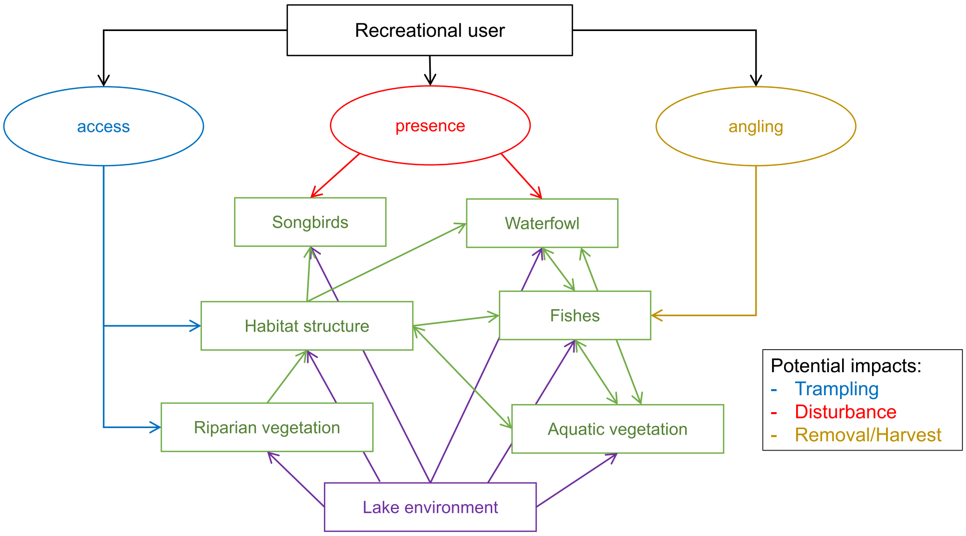
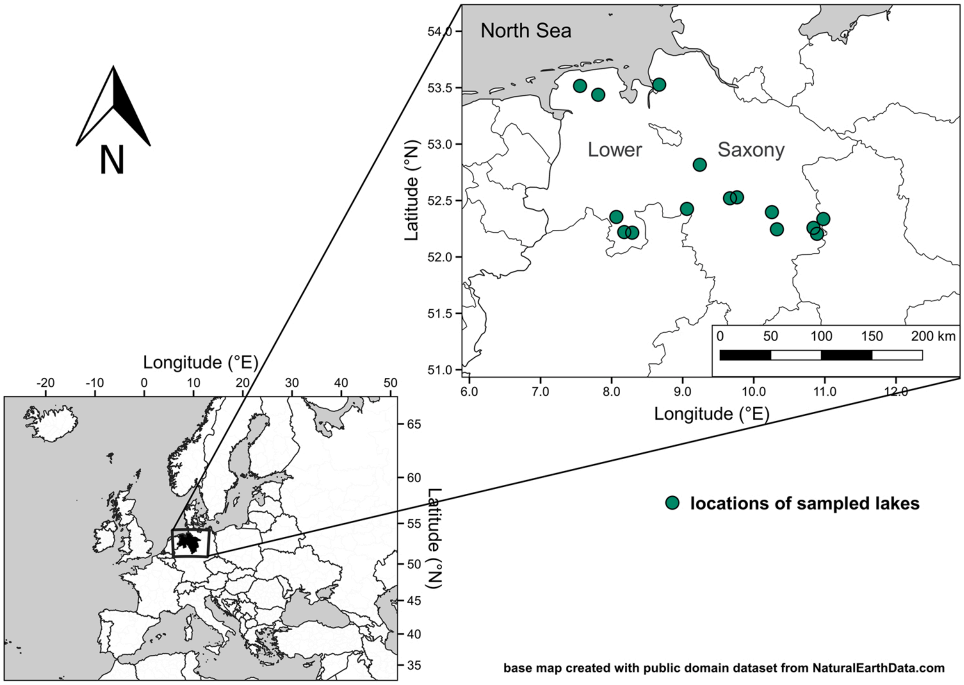


Fig. 1. Conceptual representation of how humans interact with freshwater ecosystems over three pathways related to trampling, disturbance, and removal/harvest of fish.



base map created with public domain dataset from NaturalEarthData.com

Fig. 2. Map of Lower Saxony, Germany, with positions of sampled gravel pit lakes for studying the influence of protected areas.

including “non-game” fishes (Arlinghaus et al., 2015) but rarely directs specific attention towards other taxa than those that are exploited or support the exploited species (e.g., prey fish for targeted predators). Therefore, fisheries management can be seen as specialized part of conservation management, preoccupied with fish and fisheries conservation (Arlinghaus et al., 2017). Support for conservation by fisheries stakeholders is typically high as long as the chosen conservation actions involve the continued use of the species or population of interests. More conflicts exist when fisheries management actions constrain access to the resource (Dorow et al., 2010; Hilborn et al., 2021, 2005).

Although seemingly related, conservation and fisheries stakeholders tend to intensively debate the proper tools to achieve their goals. Specifically, assigning protected areas with partial or full removal of capture fisheries from certain zones are a continuous source of conflict among conservation and fisheries (Hilborn et al., 2021). This is because a net benefit to fisheries stemming from no-take protected areas can only be expected if the catch of fish is increased outside the boundaries of protected areas relative to the situation before the implementation of the measure (Hilborn et al., 2004; Moland et al., 2013). There is abundant evidence that lasting spill-over effects of protected areas are either not present or difficult to detect because the fishing effort saved from protected areas is typically displayed beyond the protected area boundaries or because of ecological constraints preventing significant spill-over by species of relevance to fisheries (Fletcher et al., 2015; Hilborn and Sinclair, 2021; Ovando et al., 2021). The implementation of protected areas, especially marine protected areas, and their effectiveness continues to be controversial, specifically in commercial marine fisheries where often a central authority is the decision-maker (Edgar et al., 2007; Jameson et al., 2002; Sale et al., 2005).

In other fishing rights systems, such as small-scale inland fisheries in

Table 1
General information about the studied gravel pit lakes.

Lake Name	Primary recreational use	Lake size [ha]	Islands present [yes/no]	Year when excavation ended (lake age at 1st sampling)	Year when recreational fishing started	Protection established [year]	Length of Protected area [m]	Share of shoreline for protection
Kiesteich Brelingen	angling, walking	8.48	yes	1999 (17)	1997	2007	527	23.2%
Linner See	angling	17.68	no	2000 (16)	1975	2010	272	9.9%
Meitzer See	angling, swimming	19.49	no	2006 (10)	1982	2012	386	19.0%
Plockhorst	angling	14.33	yes	1998 (18)	1999	(unknown)	789	35.2%
Saalsdorf	angling	9.04	no	1995 (21)	1973	2000	360	25.5%
Schleptruper See	angling	3.97	yes	1965 (51)	1966	1995	197	20.6%
Stedorfer Baggersee	angling	1.89	no	1983 (33)	1983	1985	181	30.6%
Wahle	angling	8.10	yes	1990 (26)	1991	(unknown)	270	18.5%
Wiesedermeer	angling	2.93	yes	1990 (26)	1998	2001	242	22.9%
Buschmühlenteich[*]	angling	2.96	yes	1978 (41)	1978	1978	551	39.0%
Mergelgrube[*]	angling	0.74	yes	1982 (37)	1982	1982	325	58.2%
Röhrsteich[*]	angling	6.15	no	1969 (50)	1971	2000	631	41.2%
Stockumer See[*]	angling	10.35	yes	1986 (33)	1999	2010	1342	54.9%
Tannenhausen[*]	angling, swimming, water skiing, boating	19.72	no	1978 (41)	1963	1995	419	13.5%
Spadener See[*]	angling, swimming, camping, boating	19.85	no	1972 (47)	1971	(unknown)	344	14.7%
Mean (± SD)	–	9.71 (6.9)	–	31 (13) years old	–	–	456 (288)	28.5% (14.6)

[*] Lake with only one electrofishing survey in 2019

central Europe, protected areas are regularly installed and enforced by fisher communities who have the sovereignty to devise their own rules and regulations (Alcala et al., 2005; Galal et al., 2002; Gilchrist et al., 2020; Hamilton et al., 2012). These self-imposed, often small-scale protection zones typically cover part of a fishery ecosystem or are aligned in a network of small protected patches (Koning et al., 2020; Hannah et al., 2019). These areas are typically installed to serve specific fisheries objectives, such as regaining catch rates in spear fished areas where fish have become timid (Feary et al., 2011; Januchowski-Hartley et al., 2013), or protect spawning sites of fish with a hope to increase recruitment (Suski et al., 2002; Zolderdo et al., 2019). Properly planned and executed, protected areas can serve conservation and fisheries goals by either excluding all human use or allowing for regulated exploitation within a confined spatial boundary (sometimes called partial protected areas, Smallhorn-West et al., 2022; Suski and Cooke, 2007). Beyond protection offered to fish, small-scale protected areas assigned to serve fisheries may have unintended effects on nontarget habitats and taxa of lower interest to fisheries and thereby indirectly contribute to conservation more generally (Cucherousset et al., 2007; Langlois and Ballantine, 2005).

The key influence of protected areas, especially of no-take protected areas, is excluding fishing as a source of fish mortality as well as reducing disturbances of habitats from fishing gear and boating (Cambray, 2002; Hilborn, 2016; Hilborn and Sinclair, 2021; Sanyanga et al., 1995; Schram et al., 1995). Therefore, it can be expected that the fish biomass and the length of fish increase in protected areas relative to open areas if the size of the protected area is large enough relative to the movements of the fish beyond the protection borders (Lester and Halpern, 2008; Ohayon et al., 2021). Indeed, major international syntheses of protected-area effectiveness have documented strong increases in fish biomass and size of fish within reserves (e.g. Edgar et al., 2014; Lester et al., 2009), where five key features seem to determine the performance of marine protected areas: reserve age, reserve size, degree of enforcement, isolation of the protected area from adjacent fished areas and degree of protection from fishing (e.g. no-take relative to partial use; Edgar et al., 2014; Lester et al., 2009; Lester and Halpern, 2008). Similar features also seem important for the functioning of freshwater protected areas (Acreman et al., 2020), but research on protected areas is far less developed in freshwater compared to marine environments (Hermoso et al., 2016; Suski and Cooke, 2007). Yet, reserve size relative to ecosystem size must be of relevance and too small-scaled reserves will constrain the effectiveness of protected areas (Chu et al., 2018), especially in small freshwater lakes where moving fish may use the entire ecosystem (Nakayama et al., 2018; Vanovac et al., 2021) and thus use the unprotected areas over the course of a season and might then get captured despite the presence of scale-restricted protected areas (Cooke et al., 2017; Suski and Cooke, 2007; Zolderdo et al., 2019). However, in riverine systems spatially confined freshwater protected areas arranged as a network have shown positive effects for fish biomass (Koning et al., 2020; Koning and McIntyre, 2021), such that small reserve sizes may still have positive effects for fisheries conservation.

Effectiveness of protected areas requires regular enforcement of the regulations with adequate penalties, because in their absence human tend to not comply (Cripps and Gardner, 2016; Guidetti et al., 2008). In small-scale fisheries, enforcement by local stakeholders tends to be strong, especially if the protected areas are self-devised and self-enforced by local communities (Gilchrist et al., 2020). This situation is typical in many recreational fishing clubs of European countries (e.g., UK, Switzerland, Austria, Germany) where angling communities are not only users, but also fishing rights holders and fisheries managers who can self-determine to close off certain fractions of local fisheries and prohibit access to their membership (Daedlow et al., 2011). Here we use no-access riparian protected areas at small gravel pit lakes voluntarily implemented by recreational angling clubs to study their potential effects on freshwater fishes and non-target biodiversity and habitats within the aquatic and the adjacent terrestrial environment.

There are several levels by which human recreational use of lake shorelines can affect habitats and wildlife (Francis and Schindler, 2009; Gaeta et al., 2011; Radomski and Goeman, 2001; Scheuerell and Schindler, 2004) but we focused on the following three (Fig. 1): trampling, disturbance and removal of organisms. The meta-analysis of Schafft et al. (2021) showed a consistently negative effect of shore-based recreation (angling and non-angling) on habitat structure and quality, which mainly relates to trampling-effects of shoreline vegetation (Fig. 1). In addition, angling clubs regularly cut riparian structures to prepare or maintain access to angling sites, which may also reduce habitat quality (Dustin and Vondracek, 2017; O'Toole et al., 2009). Also, if walked regularly, shoreline vegetation has been found to increasingly

Table 2
Lake characteristics and environmental descriptors of the gravel pit lakes.

Group	Variable	Meaning	Scale level	Range of values	Mean (± SD)	Unit	Determination
Morphology	lake area	Surface area of lake	lake	0.7 – 19.9	9.7 (6.9)	ha	QGIS 3.4
	shoreline development factor (SDF)	Length of shoreline relative to lake area	lake	1.2 – 2.3	1.7 (0.4)		$\frac{shoreline\ length * 100}{2\sqrt{\pi * area}}$
	maximum depth	Maximum depth	lake	1.1 – 23.5	10.2 (6.6)	m	echo sounding
	bottom slope	Slope of the lake bottom on average	lake	1 – 5	3 (1)	%	$\frac{maximum\ depth * \sqrt{\pi}}{2\sqrt{area}}$
Nutrients	chlorophyll a	Proxy for biomass of phytoplankton	lake	1.3 – 138.1	14.2 (21.2)	µg/l	HPLC of spring samples
	total phosphorus	Proxy for nutrient loading	lake	3 – 235	23.5 (32.1)	µg/l	chemical analysis of spring samples; see Nikolaus et al. (2021) for methods
	ammonium	Proxies for nitrogen concentrations	lake	0.02 – 0.3	0.1 (0.1)	mg/l	
	nitrate		lake	0.01 – 3.3	0.4 (0.6)	mg/l	
Habitat quality	Lakeshore Anthropogenic Disturbance	Index of human activities	lake	0.1 – 0.9	0.4 (0.3)	Index	standardized sampling (Kaufmann et al., 2014a)
	Riparian Vegetation Cover Complexity	Index for terrestrial part of plots	lake	0.2 – 0.7	0.3 (0.2)	Index	
	Littoral Cover Complexity	Index for aquatic part of plots	lake	0.3 – 0.8	0.5 (0.2)	Index	
	Littoral-Riparian Habitat Complexity	Combined index for all structures	lake	0.2 – 0.8	0.4 (0.2)	Index	
	Lakeshore Physical Habitat Quality	Combined index for structures and disturbances	lake	0.3 – 0.7	0.5 (0.1)	Index	
Mesoscale structures	riparian wood	Share of woody structures	transect	0 – 100	38 (33)	%	field sampling (Matern et al., 2021)
	riparian vegetation	Share of plant structures	transect	0 – 100	35 (34)	%	
	lack of riparian structure	Share of structureless parts	transect	0 – 100	27 (29)	%	
	riparian structure heterogeneity	Diversity of riparian structures	transect	0 – 1.4	0.6 (0.3)		Simpson index of riparian structures
	littoral wood	Share of woody structures	transect	0 – 100	30 (29)	%	field sampling (Matern et al., 2021)
	littoral vegetation	Share of plant structures	transect	0 – 100	35 (33)	%	
	lack of littoral structure	Share of structureless parts	transect	0 – 100	34 (29)	%	
	littoral structure heterogeneity	Diversity of littoral structures	transect	0 – 1.6	0.7 (0.4)		Simpson index of littoral structures
Recreational use	extent of angling sites	Share of angling spots	transect	0 – 100	17 (24)	%	field sampling (Nikolaus et al., 2021)
	angling garbage	Number of litter items related to angling or not	lake	0 – 0.2	0.1 (0.1)	m^{-1}	
	other garbage		lake	0.2 – 3.4	1.1 (1)	m^{-1}	
	angling use	Observed recreational activities during field samplings	lake	0.2 – 5.8	1.8 (1.6)	day^{-1}	visitor counts
	other use		lake	0 – 74.7	9.2 (21.5)	day^{-1}	
Land use	forest in 1 km-buffer	Proportion of different land use categories in a buffer around the lake	lake	1 – 50	17 (13)	%	QGIS 3.4 using ATKIS® land use data with a 10 × 10 m grid scale (© GeoBasis-DE/ BKG 2013)
	agriculture in 1 km-buffer		lake	40 – 84	65 (14)	%	
	urbanization in 1 km-buffer		lake	3 – 23	13 (6)	%	
	distance to next road	Shortest-path distances of lakes to nearby roads, streets, cities, villages, lakes, canals and rivers	lake	15 – 1010	195 (298.2)	m	
	distance to next settlement		lake	20 – 1160	337 (355.2)	m	
	distance to next waterbody		lake	1 – 250	62.5 (82.1)	m	

consist of more trampling-resistant species (Fig. 1; Andrés-Abellán et al., 2005). Studies of recreational activities affecting aquatic macrophytes are rare (Meyer et al., 2021), but boating and wading of vegetated shorelines can have strong negative influences (Ostendorp et al., 2009; O'Toole et al., 2009; Schafft et al., 2021; Willby and Eaton, 1996). Fishes are the main target of recreational angling and directly affected by harvest, which can reduce biomass, size structure, or both (Fig. 1; Ahrens et al., 2020; Lewin et al., 2006). Noise and human disturbances emerging from the visitation of shorelines in the process of angling or other recreational activities may also negatively affect bird breeding success (Fig. 1; Fernández and Azkona, 1993; Flemming et al., 1988; Guillemain et al., 2007; Yalden, 1992). Negative influences are especially true for disturbance-sensitive taxa with high flight initiation distances (FIDs; Blumstein et al., 2003; Braimoh et al., 2018; Krüger, 2016). Thus, small-scale protected areas designed to reduce access by recreationists can have a range of (largely unintended) ecological effects from changes in habitat quality and reductions in vegetation to positive effects on fish and bird abundance. The objective of our study was to test whether such effects could be detected in gravel pit lakes managed by recreational fishing clubs in north-western Germany.

We hypothesized that the lower use level of humans in no-access protected areas that cover part of the lake will locally lead to (H_1) higher structural diversity and habitat quality, (H_2) less trampling resistant species in terrestrial vegetation, and (H_3) changes in cover of submerged and emergent aquatic macrophytes, because increased riparian vegetation provides increased shading, particularly in lakes such

Table 3
PC-Axes from environmental variables (Table 2) used in the analysis (see Appendix Tables A1 & A2 for details).

Group	PC-Axis	Main contributor
Morphology	Lake depth (1st dimension)	maximum depth, slope
	Lake size (2nd dimension)	lake area, SDF
Nutrients	Chlorophyll a & total phosphorus (1st dimension)	chlorophyll a, total phosphorus
	Nitrogen concentrations (2nd dimension)	ammonium, nitrate
Habitat quality	Habitat complexity (1st dimension)	Complexity indices of Riparian Vegetation Cover, Littoral Cover, and Littoral-Riparian Habitat
	Habitat disturbance (2nd dimension)	Lakeshore Anthropogenic Disturbance index, [negatively] Lakeshore Physical Habitat Quality
Mesoscale structures	Vegetated structure (1st dimension)	riparian and littoral vegetation
	No structure (2nd dimension)	Lack of riparian and littoral structure, [negatively] riparian and littoral wood
	Structure heterogeneity (3rd dimension)	riparian and littoral structure heterogeneity
Recreational use	Angling use (1st dimension)	angling use, angling garbage
	Other recreation (2nd dimension)	other use, other garbage
	Angling sites (3rd dimension)	extent of angling sites, angling use
Land use	Rural area (1st dimension)	agriculture, [negatively] urbanization, distance to next road, distance to next settlement
	Forest land use (2nd dimension)	forest in 1 km-buffer
	Connectedness (3rd dimension)	[negatively] distance to next road, [negatively] distance to next waterbody

as the one we sampled where boating is prohibited (only shoreline angling use). In terms of fish, we expected (H_4) higher (relative) abundance within protected areas of small and larger fish as smaller fish benefit from the potentially higher structural diversity within protected areas or from assigning protected areas at known breeding grounds, whereas larger fish find refuge from fishing pressure in protected areas. For birds, we hypothesized that (H_5) the average flight initiation distance (FID) of the community, as a measure of their sensitivity, would be positively related to the size of the protected area at the lake level. Such effects would indicate a spill-over of the impact of protected areas on community levels at the scale of the entire lakes.

2. Material and methods

2.1. Study site and lake selection

The study was carried out in Lower Saxony, north-western Germany (Fig. 2). Data from 15 gravel pit lakes (also known as quarry lakes) managed for recreational fisheries were collected and analyzed. All lakes were created through mining of mineral resources and were owned or fishing rights leased by recreational angling clubs, as it is typical in Western Germany (Daedlow et al., 2011). The lakes were identified through a survey of all angling clubs organized in the Angler Association of Lower Saxony and selected according to the following criteria: First, the lake should be small (1–20 ha) without any dredging or excavation in the last ten years (“old age”) (see also Nikolaus et al., 2021). Second, the lake had to have a no-fishing zone assigned by the angling club with signs indicating the fishing ban and, in some cases, also a trespassing ban. The fishing clubs had to have voluntarily assigned parts of riparian zones at their lakes that are not allowed to be accessed from the bank or by boat to fish in or from outside the area. The protected areas were typically placed at known or suspected fish breeding grounds or were otherwise largely inaccessible to the public. The access restrictions typically also applied to other recreational users, which was indicated by signposts at the lake shoreline. Angling was predominantly conducted from shoreline in the lakes that we studied. The protected areas we studied have no legal protection status, though many recreationists might not have been able to distinguish voluntary and legal protected

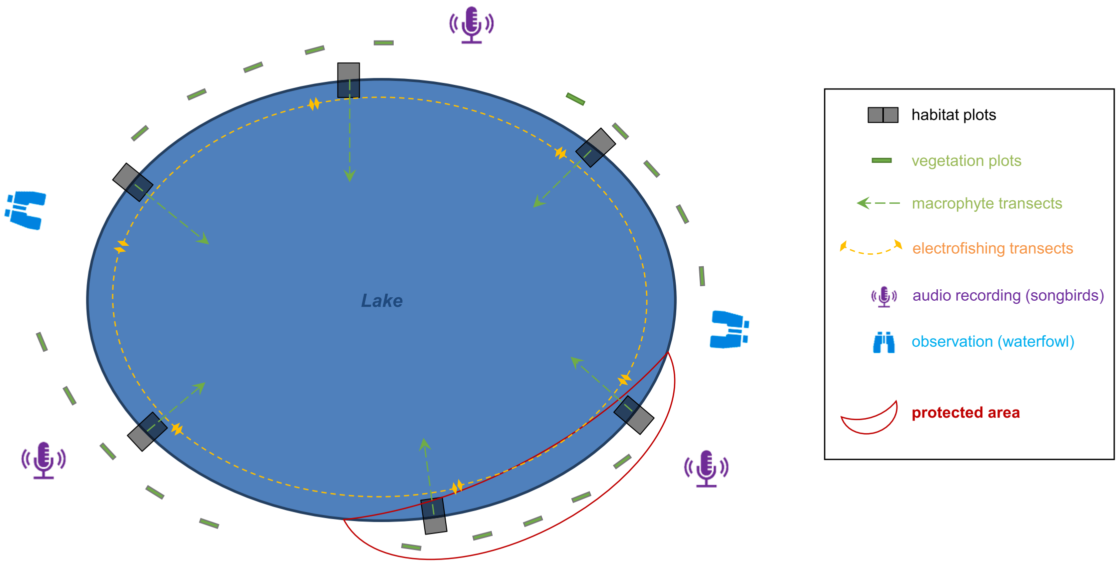


Fig. 3. Schematic outline of the survey methods used in our study on the influence of protected areas. Plots for assessment of habitat quality following Kaufmann and Whittier (1997) and transects for assessment of aquatic macrophytes were placed at almost every 100 m along the shoreline. Five 1-m^2 Plots for assessment of riparian vegetation were placed at 25-m distances from each other along the shore in each cardinal direction. Littoral electrofishing took place along the whole shoreline, divided into transects along continuous compositions of mesoscale structures. The position of plots and transects was random in relation to the position of the protected area. Positions for audio recording of songbirds were randomly but 200 m apart from each other distributed along the shoreline. Observations of waterfowl took place during all other sampling events. Further explanations of sampling details in the text and in Nikolaus et al. (2021).

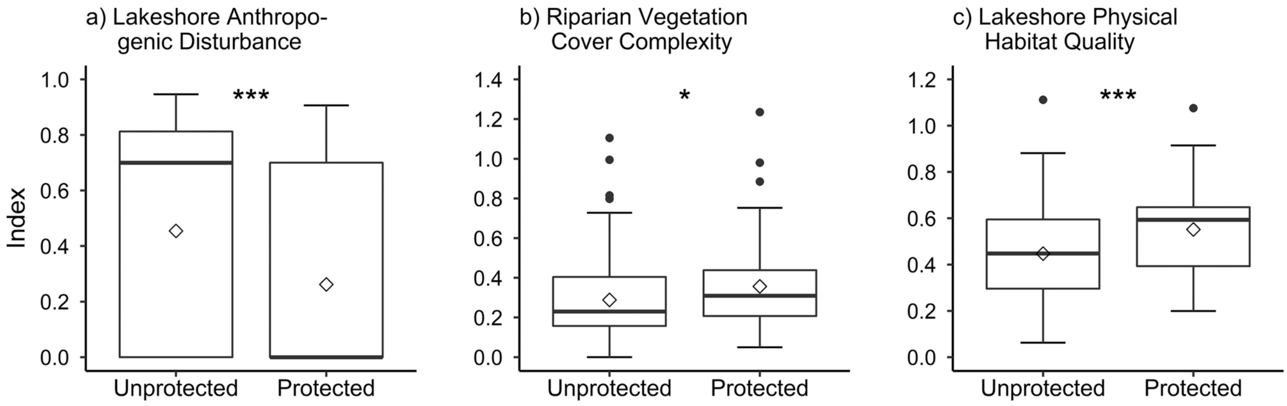


Fig. 4. Comparison of habitat quality indices for plots inside (“Protected”, N = 55) and outside (“Unprotected”, N = 146) protected areas at small gravel pit lakes in Lower Saxony, Germany. ⋄= Mean, —= Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers, *** = very high significance (P < 0.001) and * = significant (P < 0.05).

Table 4
Estimated coefficients (with standard error) for modeled response variables of habitat structure as related to the presence of protected areas and other environmental predictors. Parameter estimates in italics indicate strong trends (• = P < 0.1). Parameter estimates in bold are significantly different from 0. Asterisks reflect the significance level: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Predictor variables (PC = scores from Principal Components)	Lakeshore Anthropogenic Disturbance Index	Riparian Vegetation Cover Complexity Index	Lakeshore Physical Habitat Quality Index
(Intercept)	**0.454 *** (0.044)**	**0.311 *** (0.017)**	**0.462 *** (0.015)**
Protected area	**-0.232 *** (0.054)**	**0.071 * (0.031)**	**0.107 *** (0.027)**
Lake age	0.005 (0.005)	**0.004 * (0.002)**	-0.002 (0.001)
Lake depth (PC)	-0.041 (0.043)	-0.019 (0.015)	-0.011 (0.013)
Lake size (PC)	-0.051 (0.077)	0.020 (0.027)	0.001 (0.023)
Angling use (PC)	-0.044 (0.039)	*-0.022• (0.013)*	0.003 (0.012)
Other recreation (PC)	*0.105 • (0.056)*	**-0.061 *** (0.018)**	**-0.043 ** (0.016)**
Angling sites (PC)	-0.026 (0.061)	**-0.074 *** (0.021)**	**-0.040 * (0.019)**
Rural area (PC)	-0.059 (0.039)	0.0003 (0.013)	0.007 (0.012)
Connectedness (PC)	0.083 (0.065)	**0.142 *** (0.022)**	**0.070 *** (0.019)**

areas because the signs are often comparable. The protected areas were specified in the club’s internal regulations and are not to be confused with officially designated nature conservation areas like Natura 2000 sites or nature reserves; they thus have a status of being local rules decided within the fishing rights of the local fishing clubs. Although the fishing ban could be enforced by the regular patrols of the club’s own fisheries wardens, the full control of a trespassing ban by non-anglers was not considered possible for legal reasons, but many local recreationists still abide by the rules. Eight of the lakes also had islands that cannot be entered due to prohibition of boating in these study lakes. We also considered shorelines on these islands protected from access to humans. Most lakes (N = 13) were mainly used by anglers with some other recreational use (local walkers, dog owners, swimmers etc.), two lakes additionally had intensive other recreational uses (boating, diving, water skiing facilities, camping sites, public bathing including large-scale parking facilities and tourist infrastructure) (Table 1). The degree of recreational use by anglers and non-anglers was quantified and controlled in subsequent analyses (Nikolaus et al., 2021).

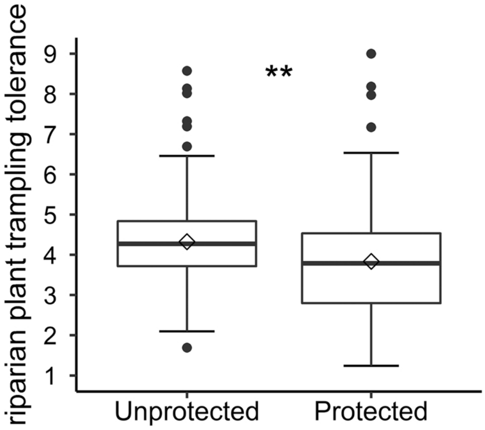


Fig. 5. Comparison of trampling tolerance of terrestrial riparian vegetation communities inside (“Protected”, N = 92) and outside (“Unprotected”, N = 182) protected areas at small gravel pit lakes in Lower Saxony, Germany. ⋄ = Mean, — = Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers, ** = high significance (P < 0.01).

2.2. Lake characteristics and environmental variables

In addition to the gravel pit lake age, we collected data of 32 environmental variables which can be grouped into morphology, nutrients, habitat quality, mesoscale habitat structures, recreational use, and land use. We assessed lake age through records in the angling clubs and by asking land owners. Bathymetry was mapped with an echo sounder, and the post-processed data was used to extract maximum depth, from which we calculated the lake bottom slope (Table 2). We estimated lake area and shoreline length in QGIS 3.4.1 and used them to calculate the shoreline development factor (Table 2). We collected epilimnic water samples during the full circulation in spring for lake nutrients analysis. Total phosphorus was determined using the ammonium molybdate spectrophotometric method, ammonium and nitrate were assessed using the spectrometric continuous flow analysis and chlorophyll a was quantified using high performance liquid chromatography (HPLC). We assessed habitat quality using the plot design and protocol of Kaufmann and Whittier (1997) and calculated the indices following Kaufmann et al. (2014a) for each plot (see also Section 2.3.1 below). The extent of different shoreline structures was visually determined for each electrofishing transect. We differentiated the extent (in percentage of transect length) of woody (e.g. branches, trees, roots, deadwood) and plant (reeds, submerged or floating aquatic macrophytes, shoreline herbal

Table 5
Estimated coefficients (with standard error) for modeled response variables of riparian and aquatic vegetation as related to the presence of protected areas and other environmental predictors. Parameter estimates in bold are significantly different from 0. Asterisks reflect the significance level: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Predictor variables (PC = scores from Principal Components)	Riparian plant trampling tolerance	Submerged macrophytes cover	Emergent macrophytes cover
(Intercept)	**4.302** *** **(0.097)**	**0.332** *** **(0.036)**	**0.233** *** **(0.054)**
Protected area	**-0.503** ** **(0.164)**	-0.025 (0.029)	0.005 (0.038)
Mean depth in transect	*Not tested*	-0.002 (0.014)	-0.015 (0.022)
Degree of shading: no	*Not tested*	-0.020 (0.028)	-0.0003 (0.037)
Degree of shading: full	*Not tested*	**-0.078** * **(0.033)**	**-0.100** * **(0.043)**
Lake age	0.008 (0.011)	**-0.011** *** **(0.002)**	**0.006** * **(0.003)**
Lake depth (PC)	**0.200** * **(0.086)**	**-0.207** *** **(0.017)**	-0.003 (0.025)
Lake size (PC)	0.100 (0.127)	**0.075** * ** **(0.021)**	**-0.085** * **(0.037)**
Chlorophyll a & total phosphorus (PC)	*Not tested*	**-0.047** *** **(0.014)**	**-0.059** ** **(0.022)**
Nitrogen concentrations (PC)	*Not tested*	**-0.185** *** **(0.018)**	-0.019 (0.027)
Habitat complexity (PC)	0.025 (0.049)	*Not tested*	*Not tested*
Habitat disturbance (PC)	0.094 (0.098)	*Not tested*	*Not tested*
Angling use (PC)	-0.028 (0.067)	**-0.113** *** **(0.017)**	0.033 (0.027)
Angling sites (PC)	0.026 (0.164)	**0.103** *** **(0.025)**	**-0.117** ** **(0.038)**
Rural area (PC)	**0.168** * **(0.075)**	**0.060** *** **(0.014)**	-0.002 (0.024)
Forest land use (PC)	-0.066 (0.106)	*Not tested*	*Not tested*
Connectedness (PC)	*Not tested*	0.016 (0.021)	**0.110** *** **(0.032)**

vegetation) structures in the littoral and the riparian part of the shoreline (see also Matern et al., 2021). The lake-specific recreational use intensity was assessed by counting the type and number of recreationists during each site visit. We also measured the extent of angling spots and collected garbage at each site (Table 2; Nikolaus et al., 2021). We calculated the share of different land use categories within 1 km around each lake (buffer zone) in QGIS 3.4.1 with GRASS 7.4.2 using ATKIS® land use data with a 10 × 10 m grid scale (© GeoBasis-DE/BKG 2013; AdV, 2006), and we estimated the shortest-path distances of lakes to nearby roads, villages, lakes, canals and rivers in Google Maps (© 2017). The lakes were generally small (< 20 ha), on average 31 ± 13 years old and mesotrophic, embedded in an agricultural landscape and had a high proportion of natural, undisturbed shoreline (> 80% on average). The colonization with macrophytes was natural, but the lakes were initially and thereafter regularly stocked with different native fish species desired by anglers (Matern et al., 2019; Arlinghaus et al., 2022; Appendix species list). For each group of environmental variables (morphology, nutrients, habitat quality, mesoscale habitat structures of each transect, recreational use, and land use) a principal component analysis without rotations was carried out on a matrix of z-transformed indicator variables to reduce the dimensions (Mardia et al., 1979). The axes in Table 3 were identified and their values (PC-scores) used in further analyses to control for environmental variability among lakes (see also Appendix Tables A1, A2). To prevent covariance among the final set of environmental variables in the models, before each analysis the variance inflation factors (VIF) for all variables was calculated. If one or more variables had a VIF > 5, variables were removed stepwise according to the following criteria: i) to retain most important PC axes following expected impacts on biodiversity variables, the 3rd or 2nd dimensions were removed first, ii) of the dimensions under consideration, the variable with the highest variance inflation factor was removed, followed by a recalculation (Zuur et al., 2010). This was repeated until all environmental variables had VIFs < 5 (Appendix Tables A3-A8).

2.3. Biodiversity and habitat sampling

We used a stratified random sampling design to test for differences in habitat structure and selected biodiversity variables between protected areas and unprotected reference sites using a transect-based approach. Sampling points or transects for habitat structure, vegetation and fishes were randomly allocated either within or outside of riparian protected areas (Fig. 3). For birds, the extent of protection (share of the shoreline, Table 1) was used as explanatory variable, because the bird community data was assessed at the lake level (Fig. 3). The individual survey methods are explained below and in more detail in Nikolaus et al. (2021).

2.3.1. Habitat Quality

In each lake, sampling sites (following the protocol of Kaufmann and Whittier, 1997) were randomly located along the shoreline with a

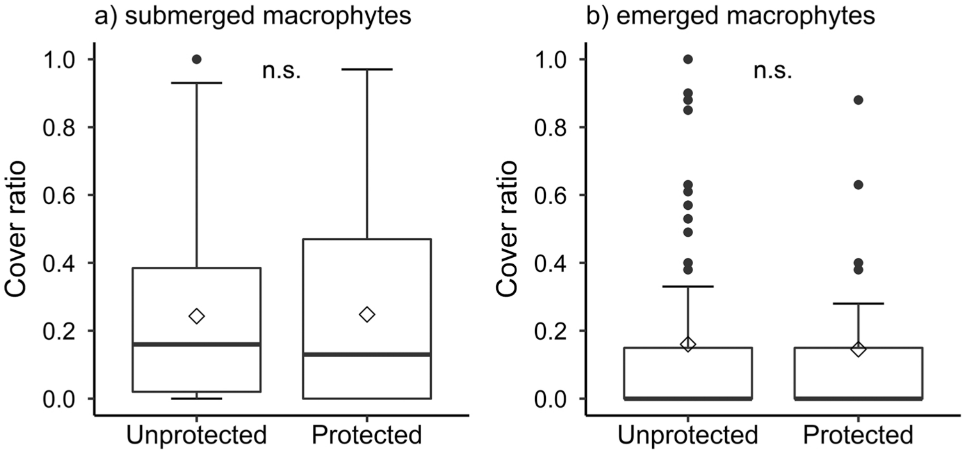


Fig. 6. Comparison of aquatic vegetation metrics for transects inside (“Protected”, N = 65) and outside (“Unprotected”, N = 171) protected areas at small gravel pit lakes in Lower Saxony, Germany. ◇ = Mean, — = Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers. n.s. = not significant (P ≥ 0.05).

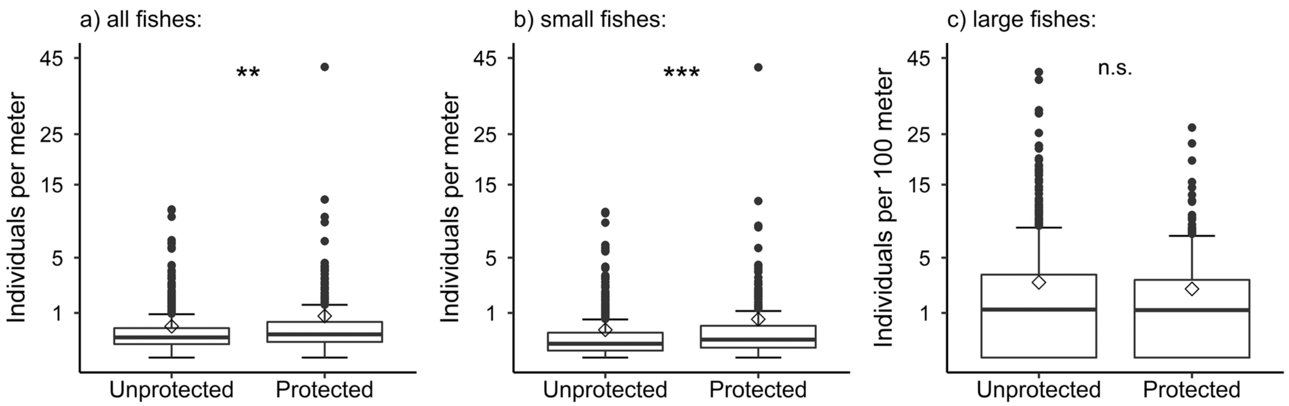


Fig. 7. Comparison of observed relative fish abundance for transects inside (“Protected”, N = 283) and outside (“Unprotected”, N = 651) protected areas for all fishes (a), small fishes (<10 cm, b) and large fishes (>20 cm, c) in small gravel pit lakes in Lower Saxony, Germany. ⋄ = Mean, — = Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers. Circles represent the model mode for predicted unconditional counts (i.e., lake effect = 0) and error bars represent the 95% confidence interval. n.s. = not significant ($P > 0.1$), * * = high significance ($P < 0.01$), * ** = very high significance ($P < 0.001$).

Table 6

Estimated coefficients (with standard error) for modeled response variables of fishes as related to the presence of protected areas and other environmental predictors. Parameter estimates in italics indicate strong trends (• = $P < 0.1$). Parameter estimates in bold are significantly different from 0. Asterisks reflect the significance level: *= $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Predictor variables (PC = scores from Principal Components)	general fish abundance (per meter)	small (< 10 cm) fish abundance (per meter)	large (> 20 cm) fish abundance (per meter)
(Intercept)	**0.293** *** **(0.050)**	**0.154** *** **(0.040)**	**0.017** *** **(0.004)**
Protected area	**0.089** ** **(0.034)**	**0.078** *** **(0.027)**	-0.001 (0.002)
Lake age	-0.003 (0.005)	0.0004 (0.004)	-0.0004 (0.0004)
Chlorophyll a and Total Phosphorus (PC)	**0.095** * **(0.048)**	**0.085** * **(0.046)**	0.003 (0.002)
Nitrogen concentrations (PC)	0.011 (0.041)	0.023 (0.037)	-0.001 (0.002)
Vegetated Structure (PC)	**0.047** *** **(0.009)**	**0.032** *** **(0.006)**	**0.002** *** **(0.001)**
No Structure (PC)	**-0.048** *** **(0.007)**	**-0.025** *** **(0.005)**	**-0.003** *** **(0.0005)**
Structure Heterogeneity (PC)	**0.057** *** **(0.010)**	**0.027** *** **(0.007)**	**0.003** *** **(0.001)**
Angling use (PC)	-0.060 (0.037)	*-0.050* *(0.027)* •	-0.0004 (0.003)
Other recreation (PC)	-0.050 (0.032)	-0.026 (0.027)	**-0.004** * **(0.002)**
Angling sites (PC)	-0.005 (0.018)	-0.003 (0.013)	-0.001 (0.001)
Rural area (PC)	*0.049* *(0.031)* •	0.032 (0.026)	-0.002 (0.002)
Forest land use (PC)	0.005 (0.036)	*0.053* *(0.038)* •	**-0.007** ** **(0.002)**
Connectedness (PC)	-0.060 (0.040)	-0.028 (0.035)	-0.002 (0.004)

minimum distance of 100 m between two sites. Some sampling sites were located in protected areas, others outside (i.e. unprotected). Each plot consisted of two subplots: a riparian plot with 15 × 4 m and a littoral plot with 10 × 4 m extent (Fig. 3). The Lakeshore Physical Habitat Quality Index was calculated, which is composed of several individual indices (Kaufmann et al., 2014b): the Lakeshore Anthropogenic Disturbance Index (based on 8 metrics representing human impacts), the Riparian Vegetation Cover Complexity Index (based on 5 metrics representing terrestrial habitat structures) and the Littoral Cover Complexity Index (based on 10 metrics representing aquatic habitat structures). To control for the lake environment in other analyses of our study, we calculated all indices including the Lakeshore Physical Habitat Quality Index on the lake level (Table 2). For the analysis of the impact of protected areas on habitat quality we focused on the Lakeshore Anthropogenic Disturbance Index, the Riparian Vegetation Cover Complexity Index, and the Lakeshore Physical Habitat Quality Index, which were then calculated separately for each plot. We expected the main impacts on terrestrial habitats emerging from recreational activities. The extent of submerged and emergent aquatic macrophytes was analyzed separately (see below), thus we did not analyze the aquatic components of the habitat quality index.

All three indices were analyzed in linear mixed-effects models by using the package “glmmTMB” in R with lake identity as random effect (Brooks et al., 2017; R Core Team, 2021). We tested whether the indices were different between plots within protected areas and outside them, while controlling for the other lake environment using the PC-scores of following dimensions: lake age, lake size, angling use, other recreational use, angling sites, rural area, forest land use and connectedness. We chose these variables as the habitat quality could be affected by the age of the lake, the complexity of the shoreline (SDF), recreational intensity and land use around the lake.

2.3.2. Riparian vegetation

For each lake, 20 plots randomly placed along the shoreline were surveyed for terrestrial vegetation. Each plot had an area of one square meter and was at least 25 m away from neighboring plots. Some plots were located within protected areas, others outside (i.e. unprotected). Within each plot, the cover of each identified plant species was determined. Based on species-specific trampling tolerance (Briemle et al., 2002; Ellenberg, 1952) ranging from 1 (intolerant to trampling) to 9 (very tolerant to trampling), an abundance-weighted (i.e. coverage-weighted) sensitivity value (S_{veg}) of the community was determined for each plot by multiplying the trampling tolerance (t) of a species (s) by its share of the total cover in the plot (c), summed over the number of species (n) in the plot:

$$S_{veg} = \sum_{s_{i=1}}^{s_n} t_{s_i} * c_{s_i}.$$

The sensitivity value per plot was analyzed in a linear mixed-effects model using the package “glmmTMB” in R with lake identity as random effect (Brooks et al., 2017; R Core Team, 2021). We tested whether the indices were different between plots within and outside protected areas, while controlling for the environment using lake age and the PC-scores of following dimensions: lake depth, lake size, habitat complexity, habitat disturbance, angling use, angling sites, rural area, and forest land

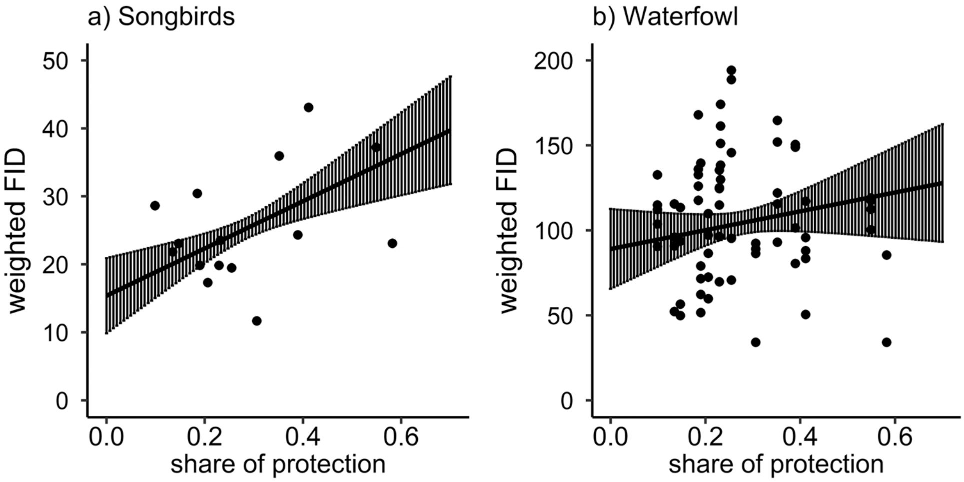


Fig. 8. Correlations of extent of protected areas with bird sensitivity at small gravel pit lakes in Lower Saxony, Germany. The dots are weighted mean FIDs per lake for songbirds (a) and per lake and season for waterfowl (b) communities.

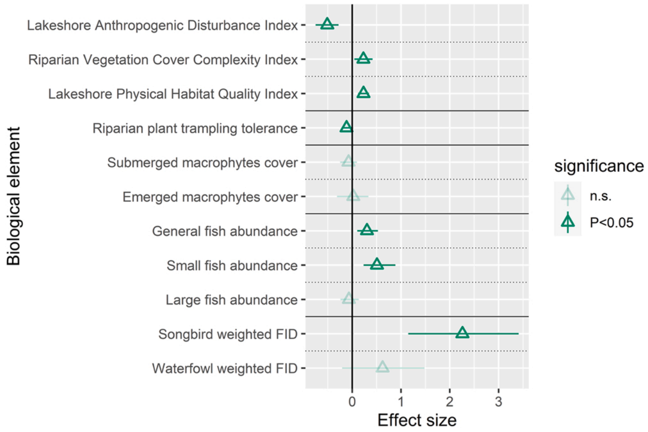


Fig. 9. Comparison of effects of protected area on different biological elements at small gravel pit lakes in Lower Saxony, Germany. The estimated coefficients from Tables 4 to 7 are standardized by intercepts.

use. We chose these variables as the plant community could be affected by the age of the lake, the morphology of the lake, habitat quality, recreational intensity and land use around the lake.

2.3.3. Aquatic vegetation

For each lake, several transects with a minimum distance of 100 m distributed along the shore were examined by snorkeling for aquatic macrophytes (for details, see Nikolaus et al., 2021). The transects pointed to the lake center (Fig. 3), ranged from the shoreline (depth = 0 m) to the maximum depth of vegetation growth, and had a width of 4 m. Some transects were within protected areas, others outside. Macrophyte coverage was determined for each species. From the data, two values were calculated based on the ecological potential and according to Pottgiesser et al. (2008): cover of submerged macrophytes and cover of the reed zone (i.e. emergent macrophytes).

Table 7

Estimated coefficients (with standard error) for modeled response variables of bird communities as related to the share of protection and other environmental predictors. Parameter estimates in italics indicate strong trends (• = $P < 0.1$). Parameter estimates in bold are significantly different from 0. Asterisks reflect the significance level: * * = $P < 0.01$, * ** = $P < 0.001$.

Predictor variables (PC = scores from Principal Components)	Songbird weighted FID	Waterfowl weighted FID
(Intercept)	**15.390 ***** **(2.823)**	**89.063 ***** **(11.982)**
Share of protection	**34.757 ***** **(9.543)**	55.416 (41.192)
Lake age	0.043 (0.102)	**-1.567 ***** **(0.442)**
Lake size (PC)	**3.930 **** **(1.417)**	5.148 (6.336)
Habitat complexity (PC)	**-4.499 ***** **(0.829)**	**-14.649 ***** **(3.621)**
Angling use (PC)	1.386 (0.936)	-5.467 (4.043)
Other recreation (PC)	**-3.526 ***** **(1.014)**	**-14.609 **** **(4.541)**
Angling sites (PC)	*-3.113 •* *(1.675)*	**-24.731 ***** **(7.310)**
Rural area (PC)	-0.883 (0.852)	-4.467 (3.555)
Forest land use (PC)	**-2.537 **** **(0.941)**	**-10.597 **** **(3.974)**
Connectedness (PC)	**6.240 ***** **(1.659)**	**21.606 **** **(6.885)**

We analyzed the effect of the transect protection status (protected or unprotected) on the two ecological potential values using linear mixed-effects models from the R package “glmmTMB” (Brooks et al., 2017; R Core Team, 2021). We further integrated the mean depth of the transects vegetated part and the degree of shading in the transect (tree-covered bank on the south shore -> fully shaded, tree-covered bank on the east or west shore -> half-shaded, north side shore or shore without trees -> no shade) as fixed effects in the model, and lake identity as random effect. We again controlled for the environment using lake age and the PC-scores of following dimensions: lake depth, lake size, chlorophyll a & total phosphorus, nitrogen concentrations, angling use, angling sites, rural area, and connectedness. We chose these variables as the cover of macrophytes could be affected by the age of the lake, lake morphology, nutrients, recreational intensity and land use around the lake.

2.3.4. Fishes

From 2016–2020, 9 lakes were sampled for fish annually by direct-current (DC) boat electrofishing (FEG 8000 electrofishing device; 8 kW; 150–300 V/300–600 V; EFKO Fischfanggeräte GmbH; www.efko-gmbh.de) with one anodic hand net of near-shore transects in the littoral zone (Matern et al., 2021). For 6 lakes, the transect-wise electrofishing was done only once in 2019 (Table 1). Some transects were within protected areas, others outside (i.e. unprotected). In each transect, all fish caught were identified and their length was measured. The transect length varied according to habitat structures along the shoreline.

Dividing the shoreline in transects of continuous habitat compositions allowed for the estimation of relative compositions of certain habitat types, e.g. the relative fraction of reed vs. woody habitat for a given transect. On average, each transect was 100 m long (unprotected: 96.19 m ± 25.56 m; protected: 106.99 m ± 36.65 m).

We analyzed the effects of transect protection status (protected or unprotected), on the relative abundance (number of individuals per meter transect) of all fish, small fish (length < 10 cm), and large fish using generalized linear mixed-effects models from the package "glmmTMB" in R (Brooks et al., 2017; R Core Team, 2021). For large fish we used data on fish with length > 20 cm except European eel (*Anguilla anguilla*, length > 35 cm), northern pike (*Esox lucius*, length > 40 cm), common carp (*Cyprinus carpio*, length > 35 cm), pikeperch (*Sander lucioperca*, length > 35 cm) and wels catfish (*Silurus glanis*, length > 50 cm). These thresholds were based on minimum-length regulations in Lower Saxony (Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten, 1989) or those in effect within the angling clubs. For small fish the threshold of 10 cm was supposed to reflect juvenile fishes. Lake identity and sampling year were integrated as (nested) random effects. We modeled a negative binomial distribution of the response variables (count data of fish abundance) to account for overdispersion and zero-inflation (revealed by preliminary tests using the DHARMa package; Harting, 2021). The length of each transect was considered as offset in the models to account for different fishing effort (i.e., relative abundance) and we again controlled for the environment using lake age and the PC-scores of following dimensions: chlorophyll a & total phosphorus, nitrogen concentrations, vegetated structure, no structure, structure heterogeneity, angling use, other recreation, angling sites, rural area, forest land use, and connectedness. We chose these variables as the abundance of fishes could be affected by the age of the lake, nutrients, mesohabitat structures, recreational intensity and land use around the lake. Lake morphology was highly correlated with other variables and could therefore not be considered (Appendix Table A6).

2.3.5. Birds

For the songbird survey, audio recordings (each two minutes long) were made once per lake at several points along the shore (200 m distance to each other). The audio files were analyzed and the abundance per species was noted for all identified songbirds and averaged per lake by dividing the total number per species and lake by the number of recording points per lake. For the waterfowl survey, the abundance per species was recorded for all observed waterfowl (birds associated with the aquatic environment as feeding or reproduction habitat) during several surveys in different seasons and years (5–6 surveys per lake). Using the species-specific flight initiation distances (FIDs, extracted from Garniel and Mierwald, 2010; and from Krüger, 2016), an abundance-weighted FID value was calculated for each lake and for each lake season combination for the community of songbirds and waterfowl, respectively.

We analyzed the effect of the protected zone extension (as proportion of total shoreline, Table 1) on FID values using linear models from the R package "glmmTMB" (Brooks et al., 2017; R Core Team, 2021), while controlling for the environment using lake age and the PC-scores of following dimensions: lake size, habitat complexity, angling use, other recreation, angling sites, rural area, forest land use, and connectedness. We chose these variables as the communities of birds could be affected by the age of the lake, lake morphology, habitat quality, recreational intensity and land use around the lake. For waterfowl we included a random effect of season and lake in the model.

3. Results

3.1. Habitat quality

Data from 201 sampling sites across 15 lakes having protected areas were analyzed, of which 55 sites were within protected areas and 146 were unprotected. There was significantly less habitat disturbance (indexed by a lower Lakeshore Anthropogenic Disturbance Index value) suggesting less human influence within the protected areas ($P < 0.001$, Fig. 4a, Table 4). Also, the Riparian Vegetation Cover Complexity Index was significantly higher in protected areas compared to unprotected sites ($P = 0.021$, Fig. 4b, Table 4). Thus, driven by the anthropogenic disturbance on the shore and the riparian habitat quality, the Lakeshore Physical Habitat Quality Index showed significantly higher values inside protected areas compared to sites outside ($P < 0.001$, Fig. 4c, Table 4). Note that the protected area effect was significant, while controlling for a range of environmental variables that also correlated with the habitat quality indices, specifically lake age (positive relationship with riparian structure complexity), recreational use intensity at the lake-level (negative relationships), extent of angling sites at the lake-level (negative relationships), and connectedness (positive relationships; Table 4, Appendix Fig. A1 & A2).

3.2. Riparian vegetation

Data from 274 plots across 15 lakes were analyzed, of which 92 plots were within protected areas and 182 were unprotected. After controlling for the environment, the terrestrial vegetation communities inside protected areas showed significantly lower riparian plant trampling tolerance compared to the riparian community outside ($P = 0.002$, Fig. 5, Table 5), while lake age had no effect ($P = 0.471$). Lake depth and rural area were positively correlated with trampling tolerance (Table 5, Appendix Fig. A3).

3.3. Aquatic vegetation

Data from 263 sampling sites across 15 lakes were analyzed, of which 65 plots were within protected areas and 171 were unprotected. After controlling for the environment, the cover of submerged macrophytes was not statistically different inside and outside protected areas ($P = 0.380$, Fig. 6a, Table 5). Also, the cover of emergent macrophytes (e.g. reed) was not statistically different inside and outside protected areas ($P = 0.310$, Fig. 6b, Table 5). The mean depth of the transect was not correlated with submerged or emergent macrophyte cover, but full shading of the transect correlated with a significantly lower cover of submerged and emergent macrophytes (Table 5, Appendix Fig. A4 & A5) compared to intermediate shading (half-shaded) conditions. Lake age was positively correlated with cover of emergent macrophytes, but negatively correlated with cover of submerged macrophytes (Table 5, Appendix Fig. A6 & A7). Lake size and extent of angling sites were positively correlated with submerged macrophyte cover, but negatively with emergent macrophyte cover (Table 5, Appendix Fig. A6 & A7). The trophic state (chlorophyll a and total phosphorus) was negatively correlated with submerged and emergent macrophyte cover (Table 5, Appendix Fig. A6 & A7). Lake depth, nitrogen concentrations and angling use were only negatively correlated with submerged macrophyte cover (Table 5, Appendix Fig. A6 & A7). Rural area and connectedness were positively correlated with cover of submerged macrophytes and cover of emergent macrophytes, respectively (Table 5, Appendix Fig. A6 & A7).

3.4. Fishes

Data from 934 transects across 15 lakes and 5 survey years (with 6 lakes fished only once in 2019) were analyzed, of which 283 transects were within protected areas and 651 were unprotected.

After controlling for the environmental variation among transects, the relative abundance of all fishes was significantly greater in transects within protected areas compared to those outside (Fig. 7a, Table 6, $P = 0.002$). Specifically, the relative abundance of small fishes ($<$ 10 cm) was significantly greater in transects within protected areas compared to those outside (Fig. 7b, Table 6, $P < 0.001$). Larger fishes were not more abundant in protected areas compared to areas outside (Fig. 7c, Table 6, $P = 0.503$). Chlorophyll a and total phosphorus were positively correlated with relative abundance of fish (Table 6, Appendix Fig. A8 & A9). All transect structure variables were significantly correlated (woody structures and vegetation positively, lack of structure negatively) with the relative abundance of small and large fish (Table 6, Appendix Figs. A8 – A10). Non-angling recreation and forest land use were negatively correlated with relative abundances of large fishes (Table 6, Appendix Fig. A10). Angling intensity as well as extent of angling sites were not correlated with relative fish abundance.

3.5. Birds

The proportion of the protected area was positively correlated with the weighted FID of songbird communities in a model including all environmental variables (Fig. 8a, $P < 0.001$). This was the highest observed effect size relative to all other analyzed response variables (Fig. 9). By contrast, the proportion of the protected area was not correlated with the weighted FID of waterfowl communities (Fig. 8b, $P = 0.179$). The mean extent of protected areas at the 15 lakes was 28.5% of the lake shoreline with a standard deviation of 14.6% (Table 1). Lake age was negatively correlated with waterfowl FID, while lake size was positively correlated with songbird FID (Table 7, Appendix Fig. A11 & A12). Habitat complexity, angling sites, non-angling related recreational activity (but not angling intensity), and forest land use were all negatively correlated with FID of songbird and waterfowl communities, while connectedness was positively correlated with both of them (Table 7, Appendix Fig. A11 & A12).

4. Discussion

The voluntary establishment of protected areas at angler-managed gravel pit lakes correlated positively with habitat quality and the presence of disturbance-sensitive biota. Importantly, the overall habitat quality was found improved at shorelines that were protected from access to anglers, supporting H_1. The data suggest that protected areas reduced trampling and other disturbances, to which plant species sensitive to trampling responded by higher abundance, and generally habitat complexity and quality improved in the riparian zone (Fig. 1). This finding supported our second hypothesis (H_2) of a generally higher trampling resistance of the plant community found outside protected areas. The negative effect of frequent recreational use on riparian plant trampling tolerance agreed with previous research (Andrés-Abellán et al., 2005; O'Toole et al., 2009). We found that the habitat quality indices responded positively and in expected ways to protected areas. Moreover, the riparian vegetation complexity was positively related to lake age, indicating that terrestrial vegetation responds positively to successional time (Margóczi, 1993; Pickett et al., 2013), in addition to benefiting from reduced anthropogenic disturbances through protected areas.

We did not detect any effect of small-scale protected areas on the coverage of submerged or emergent macrophytes. However, in accordance with other studies we found a negative correlation of angling intensity and the coverage of aquatic macrophytes (Andrés-Abellán et al., 2005; O'Toole et al., 2009; Schafft et al., 2021), perhaps because anglers clear the shorelines to facilitate angling. Although submerged macrophyte cover also benefited from clearance of the riparian zone for angling sites (as revealed by the positive effect of "angling sites"; see also Nikolaus et al., 2021), increased access to the lakes was negatively correlated with reed cover. Other environmental factors were also important for the extension of submerged and emergent macrophytes in our models. For example, lake bottom slope (i.e. lake depth) was negatively correlated with submerged macrophyte cover (due to the reduction of the photic zone), and nutrient content was strongly negatively correlated with submerged and emergent macrophytes, in agreement with previous research (Duarte and Kalff, 1986; Hilt et al., 2018; Phillips et al., 2016). In addition, the rather broad classification into three shading regimes enabled capturing the significant correlations between full shading and less macrophyte cover. In our study, completely shaded transects had significantly less plant cover, as expected. Thus, our hypotheses that protected areas would change the plant cover of submerged and emergent vegetation (H_3) in protected zones was not supported, likely because of the benefits of reduced access were counteracted by increased shading effects (also shown by Willby and Eaton, 1996) from terrestrial vegetation.

In line with other research in this field (Koning et al., 2020; Koning and McIntyre, 2021), we showed that protected areas established primarily for fish have indeed higher relative abundance of fish within protected zones relative to sites outside, after controlling for environmental effects. This supported our fourth hypothesis (H_4). In particular, smaller fish (< 10 cm) were significantly more abundant inside the protected areas than outside. Therefore, the protected areas fulfilled the roles sought by the fishing clubs who often design protected areas to serve as spawning habitats where fish can recruit without disturbances by anglers. As protected areas were not randomly allocated across the shorelines, it is possible that the angling clubs positioned the sites in areas known to be good breeding or nursery sites. Our research is correlational and does not imply that the reduced access per se was mechanistically responsible for enhanced recruitment.

We found no difference in relative abundance of larger fish (> 20 cm) in protected areas, suggesting that the small-scale areas were not sufficient to protect the relative abundance of large fish from harvest or refuge effects were nullified through movement of fish beyond protected area boundaries across the year. However, we cannot rule out methodological issues because the electrofishing gear might have undersampled the presence of large fish in the study area, as it is confined to the shallow littoral and large bodied individuals may show fleeing reactions to the approaching boat (Chick et al., 1999; Erős et al., 2009; Matern et al., 2021). In addition to the level of protection, for all fish as well as for small and large fish separately, the mesohabitat structure significantly predicted relative fish abundance. Vegetated habitats were positively, no structure negatively associated with relative abundance, indicating the function of structured habitats as refuge and food source for fish, also shown by previous research in small lakes and gravel pit lakes (e.g. Lewin et al., 2004; Matern et al., 2021). Therefore, if protected areas also increase or maintain vegetation under water, indirect effects on fish abundance can result from protected areas. However, in our work, the cover of submerged macrophytes was not altered by the protected areas.

The results on songbirds and waterfowl were not consistent. Therefore, our last hypothesis (H_5) only received partial support. In the case of songbirds, a higher proportion of shore with protected areas from angling was associated with the presence of a significantly more disturbance-sensitive (in terms of flight initiation distances) species community at the lake-level. This finding suggested the songbird community responded to reduced disturbance (e.g. noise) by higher abundances of disturbance sensitive taxa (indicated by their FID), which is also shown in other research (Bötsch et al., 2018, 2017). Also the size of the lake was strongly positively associated with the sensitivity of the songbird community, which could be the result of larger distances between birds and recreational visitors at larger lakes compared to smaller lakes. By contrast, for waterfowl the share of protected area or the lake size was not correlated with the community's sensitivity to disturbances. We did not measure flight initiation distances in our study but used values from the literature with high between-study variability in FID (Tablado and Jenni, 2017; Weston et al., 2012). Therefore, the actual bird community at the lakes might have different sensitivities than our analyses implied. Perhaps the lakes in our study were also too small (< 20 ha) to allow for differences in the influence of disturbance at the community level for waterfowl. Most important for waterfowl sensitivity was the proportion of open shoreline, the non-angling recreational intensity and the distance to other waterbodies (and/or roads), which could be interpreted as refuge availability for sensitive taxa. Such findings were also reported by other studies (Cryer et al., 1987; Tuite et al., 1984, 1983). Schafft et al. (2021) revealed that influences of angling use on bird populations were on average not significant, while influences of other recreationists were more consistent and significantly negative in the published records. Similarly, in our research it was the non-angling recreational intensity, but not the angling intensity, that correlated negatively with presence of disturbance-sensitive songbird and waterfowl species, perhaps as a result of walkers with dogs or other noisy recreation. Overall, the impact of angling on waterfowl specifically was not supported by our research. Other studies at gravel pit lakes similarly failed to identify negative influences of angling-based recreation on waterfowl communities and species richness (e.g. Bell et al., 1997; Nikolaus et al., 2021), suggesting context-dependent effects and a greater influence of general environmental factors than those related to protected areas and angling use (Schafft et al., 2021).

Our research broadly supported the study concept (Fig. 1) in terms of showcasing influences of trampling on shoreline habitat quality and terrestrial vegetation, a correlation of protected area presence and relative abundance of small fish and influences of disturbances (reduced in intensity by protected areas) on shorebird communities. However, a refuge effect on large fish suggestive of reduced exploitation was not supported, most likely due to the small-scale nature of the protected areas relative to the movement of the fish targeted by anglers (Kramer and Chapman, 1999; Vanovac et al., 2021; Zolderdo et al., 2019). We conclude that implementation of “no-access” protection can strongly affect local habitat quality, terrestrial vegetation and may benefit small fish and some bird populations.

There are several limitations to our study. Most importantly, we analyzed observational data of already established systems. The conclusions drawn are based on a paired control-impact design, which is not as robust as a before-after-control-impact-paired-series design (BACIPS: Osenberg et al., 2006; Stewart-Oaten et al., 1986). Especially the higher relative abundance of fish inside protected areas could be either a recruitment effect or an attraction effect, which can only be clarified through a rigorous before-after-impact design.

Fish stocking has a long tradition in recreational-fisheries management (Arlinghaus et al., 2016). Relatedly, also the lakes we examined were subjected to stocking in the past (Matern et al., 2019). Although we cannot rule out that stocking affected the results of our study, we do not think the effect is ecologically relevant. Introductory fish stocking has been documented to facilitate the establishment of species in gravel pit lakes (Zhao et al., 2016), and the lakes we studied are no exception (Matern et al., 2019). However, once the fish community is developed and naturally reproducing, further fish stocking with native species already present in the lake has not been found to increase the abundance of the stocked fish, suggesting that most enhancement stocking activities with naturally reproducing fish in gravel pit and other lakes fail (Arlinghaus et al., 2015, Hühn et al., 2014, Li et al., 1996, Guillerault et al., 2018; Daupagne et al., 2021, Cyrus et al., 2022). Therefore, we find it implausible that stocking differentially affected the ecological outcomes of our work, but we lack detailed stocking records and our conclusion thus remains speculative.

We had different sample sizes per year (some lakes sampled only once) which was partially controlled for by including year as random effect in the models. But there might still be year effects influencing the results. We also had different sample sizes from protected areas and reference sites because at most lakes, the proportion of protected shoreline was less than the rest of the shoreline (i.e., the references; Table 1). We still used all data per lake to capture all variability and all environmental influences within our models. This might have increased uncertainty in the estimated coefficients (larger confidence intervals for protected areas than for unprotected areas) but should not affect the conclusions drawn from significant differences. We controlled for the most obvious environmental variables, but there might still be variables that remained uncontrolled, such as differences in microclimate, behavioral differences of recreational users, or geological differences. Further research experimentally allocating sites to either protection or controls and long-term monitoring is needed to better understand the remaining uncertainties. We also recommend the use of statistical matching tools such as propensity scores for observational data (Chessman, 2013; Rosenbaum and Rubin, 1983).

4.1. Conclusion

We conclude that protected areas, voluntarily established by fishing clubs at gravel pit lakes, can achieve positive effects on habitat and biodiversity, some of which are not intended by design of the measure. Importantly, for the target organisms, our study showed higher relative abundance of fish within protected areas, in line with other small-scale freshwater protection studies from rivers (Koning et al., 2020). Moreover, we found these areas also positively affected habitat quality and riparian vegetation. To let protected areas generate additional benefits for other taxa, we recommend developing specific management plans, which should assess the possible benefits of protection zone in light of other environmental factors at a given lake. Any non-access rule should be strictly enforced and include anglers and non-anglers to achieve positive effects on sensitive bird species as we found non-recreational influences to be perhaps even more consequential than angling-related shoreline use, specifically on birds (in line with Schafft et al., 2021). Overall, the design and implementation of protected areas of riparian zones by angling clubs can contribute to conservation beyond the intended target organisms. Building on the potential of angling clubs to benefit conservation more broadly through fisheries-management actions is therefore recommended, and even small-scale protection can generate relevant conservation outcomes.

CRediT authorship contribution statement

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

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Co-author previously employed by the Angling Association of Lower Saxony - T. K. / co-author currently employed by the Angling Association of Lower Saxony - A. M.

Data Availability

Data will be made available on request.

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Appendix

See Tables A1–A8 and Figs. A1–A12 here.

Table A1

PCA-axes and their interpretation for groups of environmental variables. Only the first four axes are shown. Other axes had eigenvalues < 1. For negative [-] interpreted axes, the negated (inverse) PC-scores were used in further analyses.

Group	*Variable*	Dim 1	Dim 2	Dim 3	Dim 4
Morphology	*Eigenvalue*	2.45	1.05	0.48	0.02
	Proportion of explained variance in %	61	26	12	1
	Maximum depth	0.62	0.19	-0.04	-0.76
	Lake area	0.50	0.52	0.46	0.52
	SDF	-0.30	0.78	-0.55	-0.02
	slope	0.53	-0.28	-0.70	0.40
	Interpretation of axes	Lake deepness	Lake size	*(not used)*	*(not used)*
Nutrients	*Eigenvalue*	1.99	1.66	0.30	0.04
	Proportion of explained variance in %	50	42	7	1
	Chlorophyll a (Chl a)	0.63	-0.20	0.27	-0.06
	Total phosphorus (TP)	0.66	-0.20	0.13	0.33
	Ammonium	-0.02	-0.75	-0.29	-0.24
	Nitrate	-0.40	-0.60	-0.01	-0.40
	Interpretation of axes	Chlorophyll a & total phosphorus	[-] Nitrogen concentrations	*(not used)*	*(not used)*
Habitat quality	*Eigenvalue*	3.15	1.53	0.33	< 0.01
	Proportion of explained variance in %	63	31	6	< 0.01
	Lakeshore Anthropogenic Disturbance	-0.14	0.78	0.02	-0.60
	Riparian Vegetation Cover Complexity	-0.51	0.08	-0.72	0.18
	Littoral Cover Complexity	-0.52	0.06	0.69	0.19
	Littoral-Riparian Habitat Complexity	-0.56	0.08	0.02	0.28
	Lakeshore Physical Habitat Quality	-0.37	-0.61	0.002	-0.70
	Interpretation of axes	[-] Habitat complexity	Habitat disturbance	*(not used)*	*(not used)*

Table A2

PCA-axes and their interpretation for groups of environmental variables. Only the first four axes are shown. Other axes had eigenvalues < 1. For negative [-] interpreted axes, the negated (inverse) PC-scores were used in further analyses.

Characteristic	*Variable*	Dim 1	Dim 2	Dim 3	Dim 4
Mesoscale structures	*Eigenvalue*	3.30	2.23	1.32	0.69
	Proportion of explained variance in %	41	28	16	9
	riparian wood	-0.36	-0.47	-0.03	0.31
	riparian vegetation	0.52	0.14	0.01	-0.11
	no riparian structure	-0.33	0.44	0.03	-0.26
	riparian structure heterogeneity	0.18	-0.35	0.55	0.43
	littoral wood	-0.33	-0.44	-0.29	-0.31
	littoral vegetation	0.51	-0.06	-0.23	0.03
	no littoral structure	-0.29	0.40	0.48	0.21
	littoral structure heterogeneity	0.09	-0.30	0.57	0.66
	Interpretation of axes	Vegetated structure	No structure	Structure heterogeneity	*(not used)*
Recreational use	*Eigenvalue*	2.01	1.61	0.81	0.49
	Proportion of explained variance in %	40	32	16	10
	extent of angling sites	0.46	-0.10	-0.77	0.10
	angling garbage	-0.57	-0.31	-0.11	-0.46
	other garbage	-0.18	-0.74	0.11	-0.23
	angling use	-0.51	0.05	-0.61	-0.69
	other use	0.42	-0.58	0.001	0.19
	Interpretation of axes	[-] Angling use	[-] Other recreation	[-] Angling sites	*(not used)*
Land use	*Eigenvalue*	2.24	2.09	0.87	0.60
	Proportion of explained variance in %	37	35	15	10

(*continued on next page*)

Table A2 (*continued*)

Characteristic	*Variable*	Dim 1	Dim 2	Dim 3	Dim 4
	forest in 1 km-buffer	-0.18	0.63	-0.15	-0.08
	agriculture in 1 km-buffer	0.49	-0.43	-0.01	-0.61
	urbanization in 1 km-buffer	-0.56	-0.21	0.32	-0.46
	distance to next road	0.47	-0.02	0.51	-0.65
	distance to next settlement	0.43	0.44	-0.30	-0.46
	distance to next waterbody	0.07	0.41	0.73	-0.65
	Interpretation of axes	Rural area	Forest land use	[-] Connectedness	*(not used)*

Table A3
Variance inflation factors of variables for analyzing Habitat Quality Indices.

Initial variables	1st calculation	final set
Protected area	1.16	1.15
Lake age	3.25	3.25
Lake deepness (PC)	6.95	*removed*
Lake size (PC)	3.82	3.76
Angling (PC)	3.46	2.04
Other recreation (PC)	5.91	2.70
Angling sites (PC)	5.64	2.93
Rural area (PC)	3.48	3.13
Forest land use (PC)	6.79	2.91
Connectedness (PC)	2.60	2.31

Table A4
Variance inflation factors of variables for analyzing riparian plant trampling tolerance.

Initial variables	1st calculation	2nd calculation	final set
Protected area	1.08	1.08	1.07
Lake age	3.82	3.52	3.47
Lake deepness (PC)	6.52	3.49	2.92
Lake size (PC)	4.45	2.74	2.56
Habitat complexity (PC)	4.23	1.94	1.26
Habitat disturbance (PC)	3.48	3.25	1.94
Angling (PC)	4.12	3.09	1.46
Other recreation (PC)	6.35	5.89	*removed*
Angling sites (PC)	4.40	3.70	3.62
Rural area (PC)	2.17	2.01	1.83
Forest land use (PC)	5.70	5.26	4.31
Connectedness (PC)	7.06	*removed*	*removed*

Table A5
Variance inflation factors of variables for analyzing aquatic vegetation.

Initial variables	1st calculation	2nd calculation	final set
Protected area	1.16	1.16	1.16
Degree of shading	1.19	1.18	1.15
Mean depth in transect	1.65	1.64	1.52
Lake age	5.24	5.24	3.65
Lake deepness (PC)	12.26	5.86	4.31
Lake size (PC)	5.48	4.06	2.61
Chlorophyll a & total phosphorus (PC)	5.59	3.03	2.76
Nitrogen concentrations (PC)	3.41	3.31	3.31
Angling (PC)	5.70	5.69	4.86
Other recreation (PC)	10.63	*removed*	*removed*
Angling sites (PC)	7.04	6.63	2.92
Rural area (PC)	4.72	4.60	3.29
Forest land use (PC)	8.36	6.71	*removed*
Connectedness (PC)	3.15	3.00	2.98

Table A6
Variance inflation factors of variables for analyzing fish densities.

Initial variables	1st calculation	2nd calculation	final set
Protected area	1.49	1.47	1.47
Lake age	5.42	2.67	2.67
Lake deepness (PC)	6.52	5.45	*removed*
Lake size (PC)	6.79	*removed*	*removed*
Chlorophyll a & total phosphorus (PC)	2.71	2.69	2.03
Nitrogen concentrations (PC)	1.69	1.68	1.67
Vegetated structure (PC)	1.51	1.50	1.49
No structure (PC)	1.65	1.62	1.62
Structure heterogeneity (PC)	1.13	1.13	1.12
Angling (PC)	3.14	2.86	2.70
Other recreation (PC)	3.83	1.93	1.60
Angling sites (PC)	1.70	1.70	1.70
Rural area (PC)	2.19	1.55	1.44
Forest land use (PC)	3.75	3.70	3.13
Connectedness (PC)	5.89	4.89	2.46

Table A7
Variance inflation factors of variables for analyzing songbird community FID.

Initial variables	1st calculation	2nd calculation	final set
Share of protection	7.42	3.53	3.04
Lake age	4.35	2.84	2.83
Lake deepness (PC)	10.13	7.73	*removed*
Lake size (PC)	8.04	4.55	3.29
Habitat complexity (PC)	4.65	3.96	3.39
Habitat disturbance (PC)	8.94	*removed*	*removed*
Angling (PC)	4.83	3.03	2.76
Other recreation (PC)	5.70	4.51	2.60
Angling sites (PC)	4.86	3.85	3.55
Rural area (PC)	3.71	2.60	2.54
Forest land use (PC)	5.10	5.01	2.90
Connectedness (PC)	6.66	5.48[*]	3.77

[*] when removed next, lake deepness was the only variable left with VIF > 5.

Table A8
Variance inflation factors of variables for analyzing waterfowl community FID.

Initial variables	1st calculation	2nd calculation	final set
Share of protection	5.98	3.11	3.04
Lake age	5.51	2.99	2.83
Lake deepness (PC)	9.56	8.34	*removed*
Lake size (PC)	9.09	4.73	3.29
Habitat complexity (PC)	3.77	3.57	3.39
Habitat disturbance (PC)	9.31	*removed*	*removed*
Angling (PC)	4.72	2.76	2.76
Other recreation (PC)	5.70	4.30	2.60
Angling sites (PC)	5.80	3.83	3.55
Rural area (PC)	4.01	2.57	2.54
Forest land use (PC)	6.48	5.91	2.90
Connectedness (PC)	6.83	5.99[*]	3.77

[*] when removed next, lake deepness was still the variable with highest VIF (5.23; Forest land use 5.17). When connectedness and forest land use both were removed, the resulting model had lower AIC and BIC than the presented one. Therefor we stayed with removing lake deepness, although it was not according to the criteria mentioned.

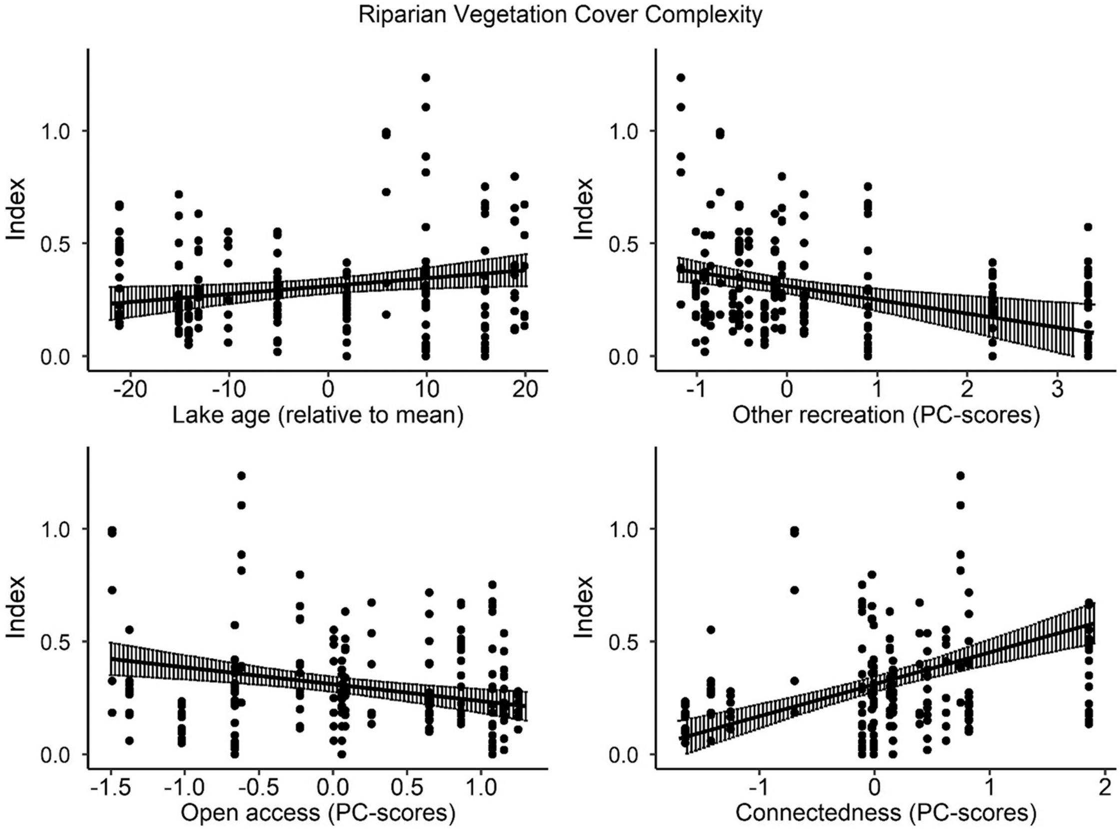

Fig. A1. Significant correlations between the Riparian Vegetation Cover Complexity Index and environmental predictors. Dots are observations, solid lines are the predicted model fit, and vertical bars are the 95% confidence intervals.

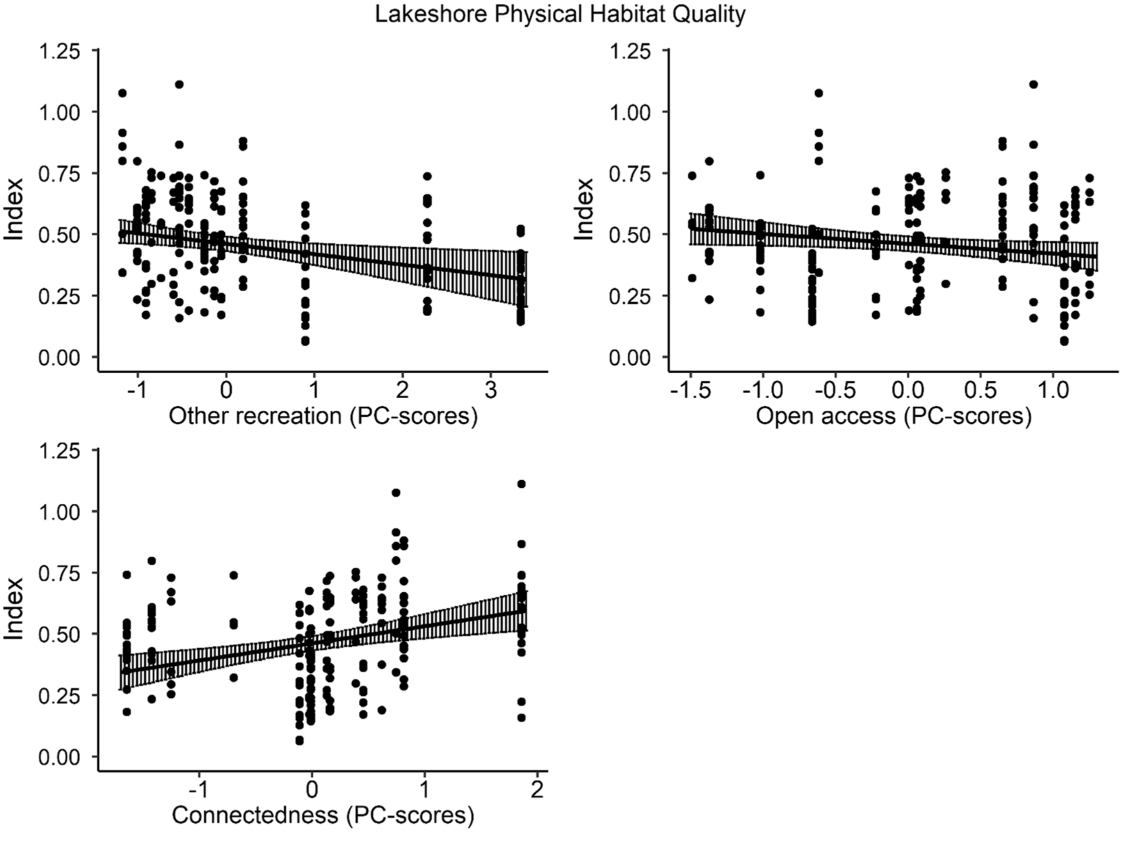

Fig. A2. Significant correlations between the Lakeshore Physical Habitat Quality Index and environmental predictors. Dots are observations, solid lines are the predicted model fit, and vertical bars are the 95% confidence intervals.

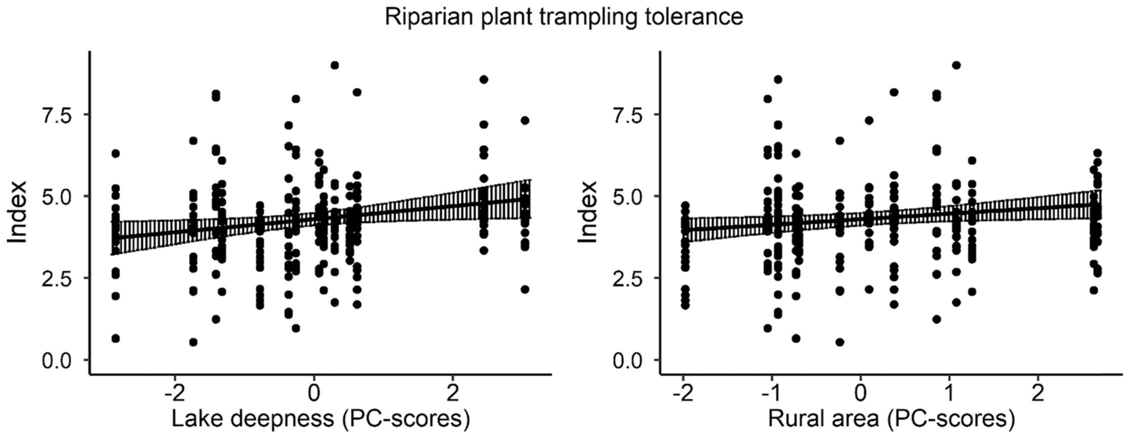

Fig. A3. Selected significant correlations between the Lakeshore Physical Habitat Quality Index and environmental predictors. Dots are observations, solid lines are the predicted model fit, and vertical bars are the 95% confidence intervals.

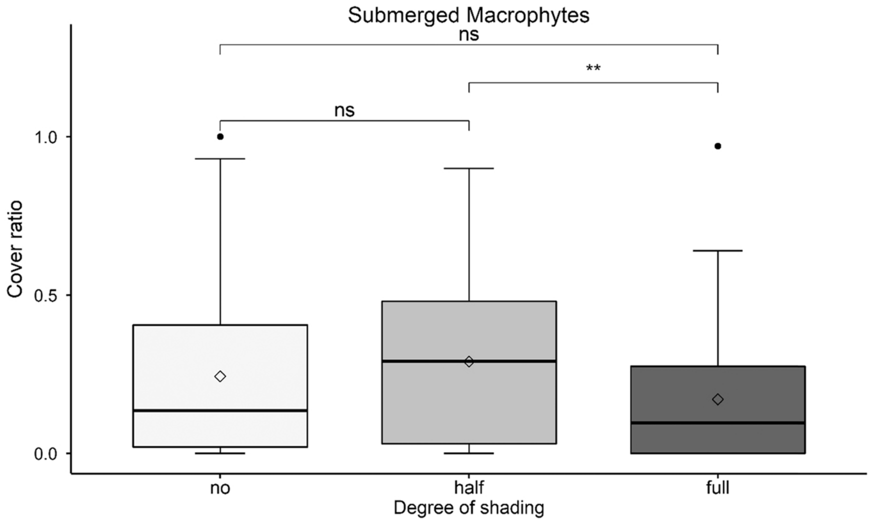

Fig. A4. Comparison of submerged macrophytes cover for transects with different shading by trees. Fully shaded transects (N = 54) are significantly (Wilcoxon test, P = 0.003) less covered by submerged macrophytes than half shaded transects (N = 90). Transects with no shade (N = 92) are statistically not different from the other transects. ◇ = Mean, — = Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers. n.s. = not significant ($P \geq 0.05$), * * = high significance ($P < 0.01$).

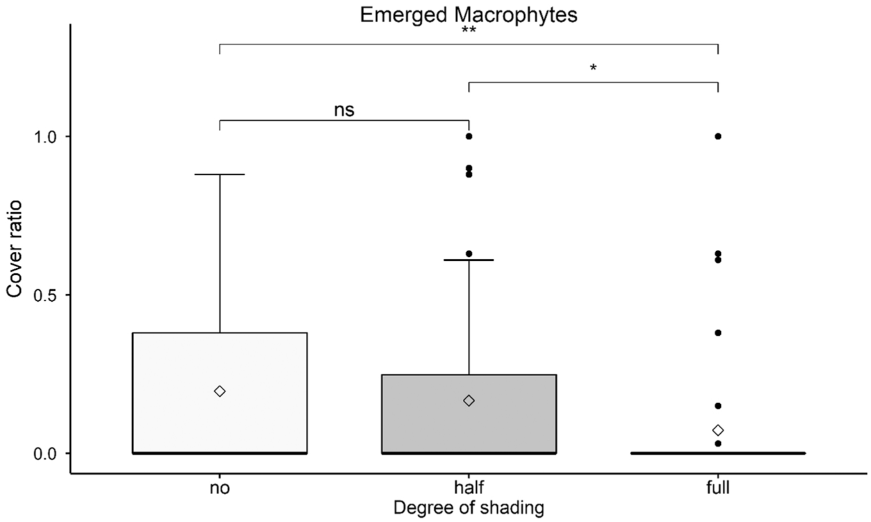

Fig. A5. Comparison of emerged macrophytes cover for transects with different shading by trees. Fully shaded transects (N = 54) are significantly (Wilcoxon test, P = 0.025) less covered by emerged macrophytes than half shaded transects (N = 90). Transects with no shade (N = 92) are statistically not different from half shaded transects but have significantly more emerged macrophytes than fully shaded transects (Wilcoxon test, P = 0.004). ◇ = Mean, — = Median, the upper and lower limits of the boxes represent the upper and lower quartile respectively, dots indicate statistical outliers. n.s. = not significant ($P \geq 0.05$), * = significant ($P < 0.05$), * * = high significance ($P < 0.01$).

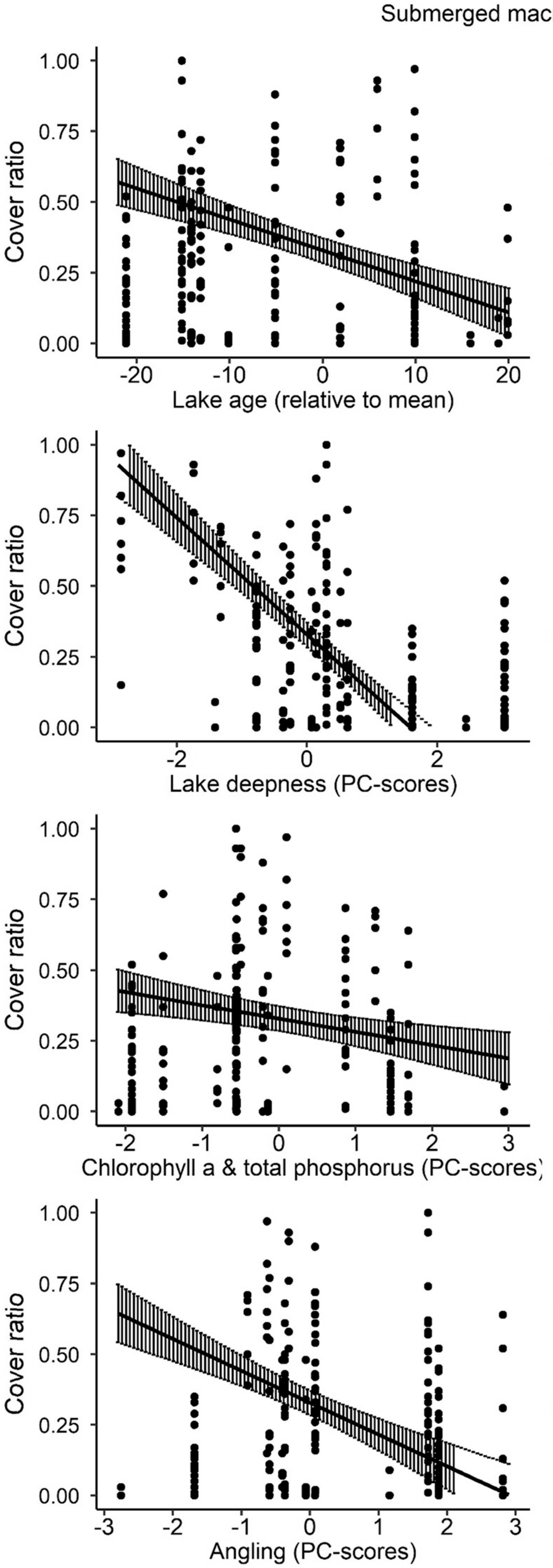

Fig. A6. Significant correlations between submerged macrophyte cover and environmental predictors. Dots are observations, solid lines are the predicted model fit, and vertical bars are the 95% confidence intervals.

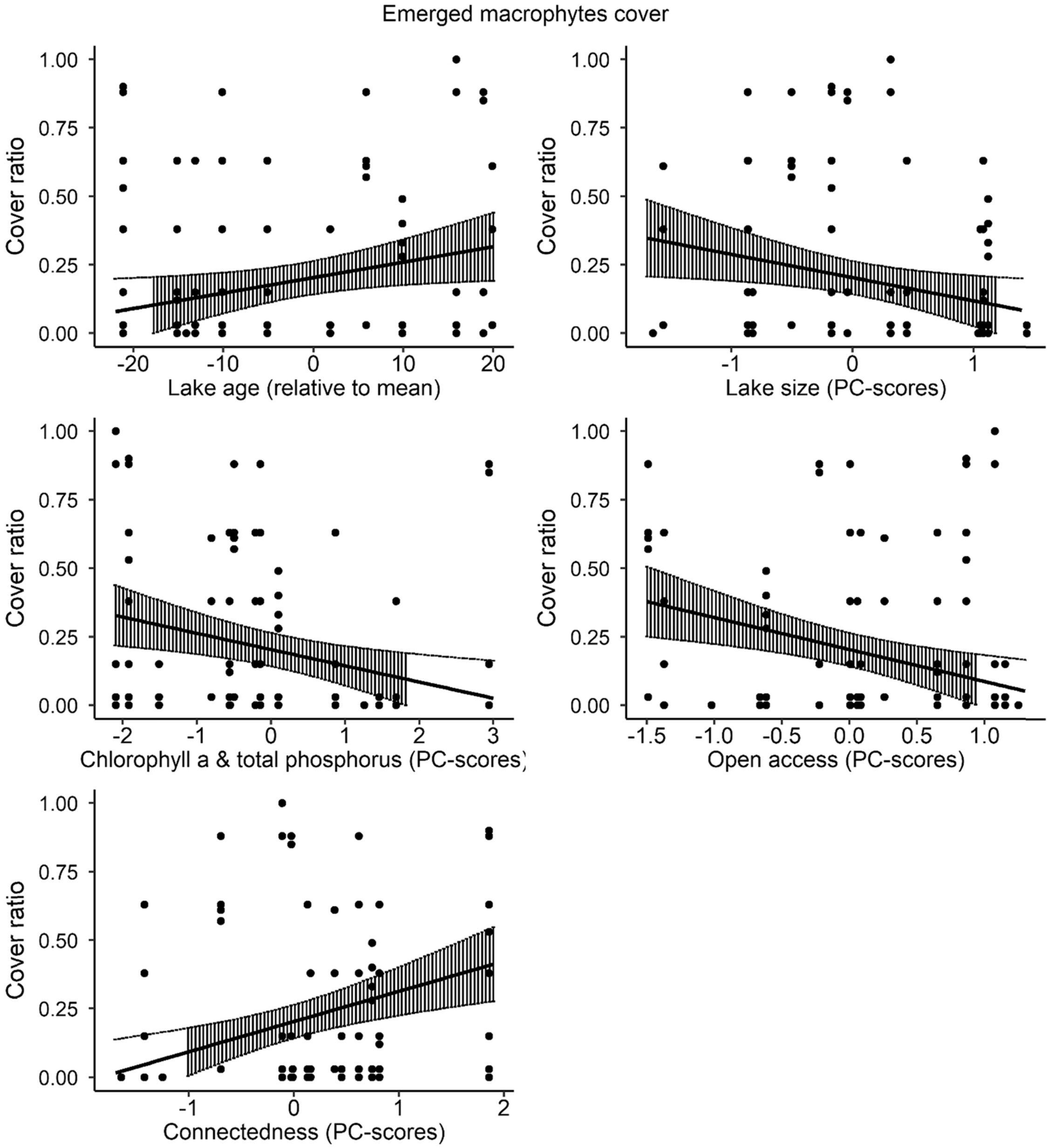

Fig. A7. Significant correlations between emerged macrophyte cover and environmental predictors. Dots are observations, solid lines are the predicted model fit, and vertical bars are the 95% confidence intervals.

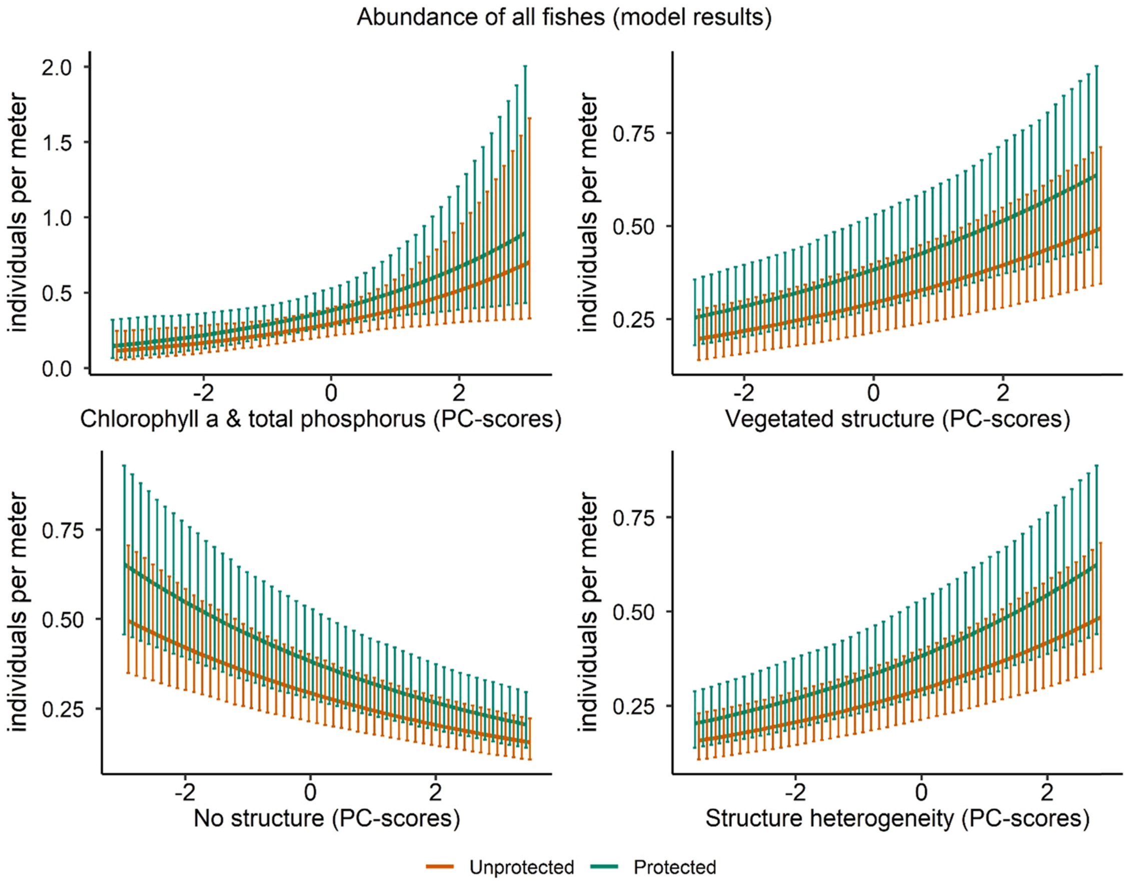

Fig. A8. Significant correlations between fish density and environmental predictors. Green and red lines are the predicted model fits for protected and unprotected areas, respectively. Vertical bars are the 95% confidence intervals.

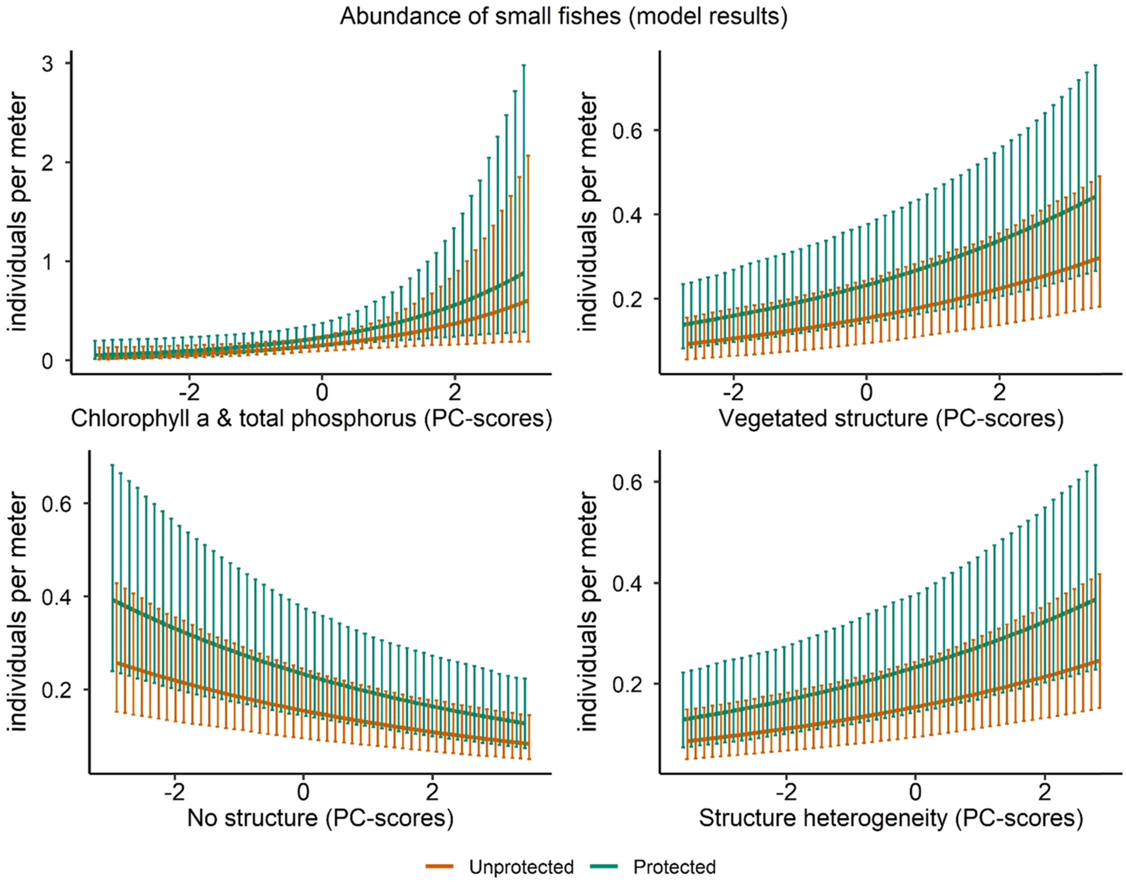

Fig. A9. Significant correlations between small fish (< 10 cm) density and environmental predictors. Green and red lines are the predicted model fits for protected and unprotected areas, respectively. Vertical bars are the 95% confidence intervals.

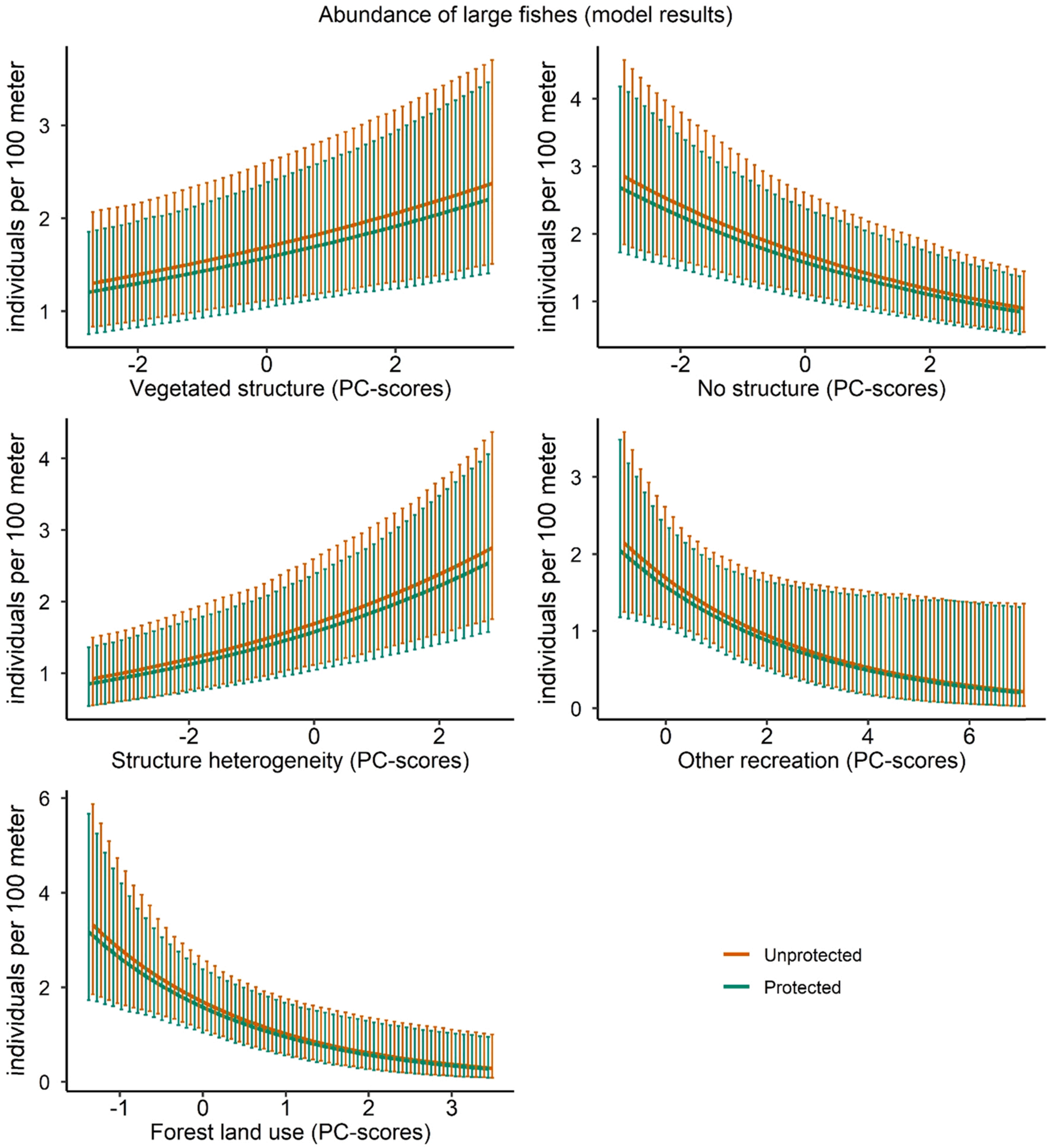

Fig. A10. Significant correlations between large fish (> 20 cm) density and environmental predictors. Green and red lines are the predicted model fits for protected and unprotected areas, respectively. Vertical bars are the 95% confidence intervals.

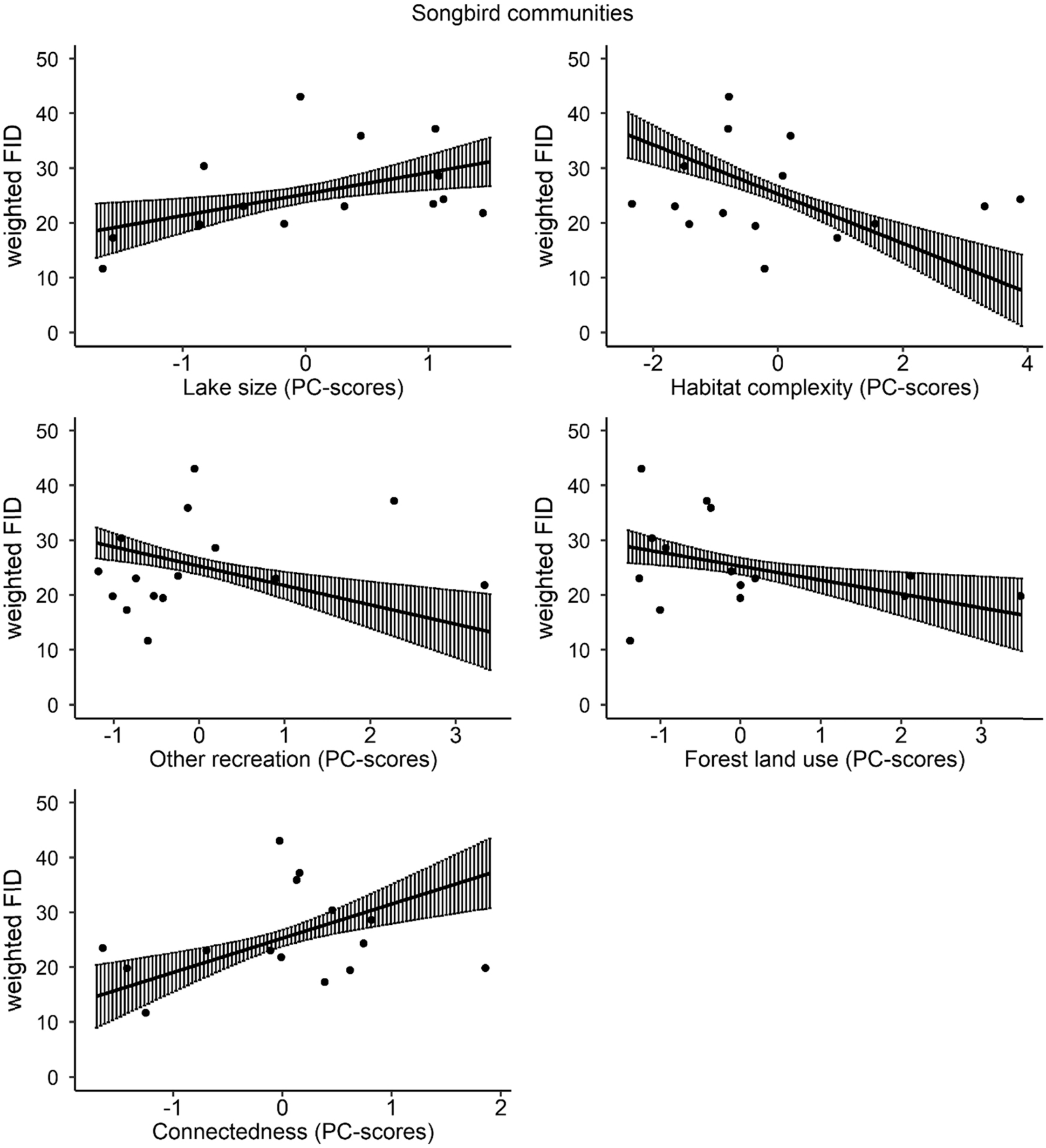

Fig. A11. Significant correlations between weighted FID of songbird communities and environmental predictors. Dots are observations, solid lines are the predicted model fit for lakes with 28.5% of shoreline protected, and vertical bars are the 95% confidence intervals.

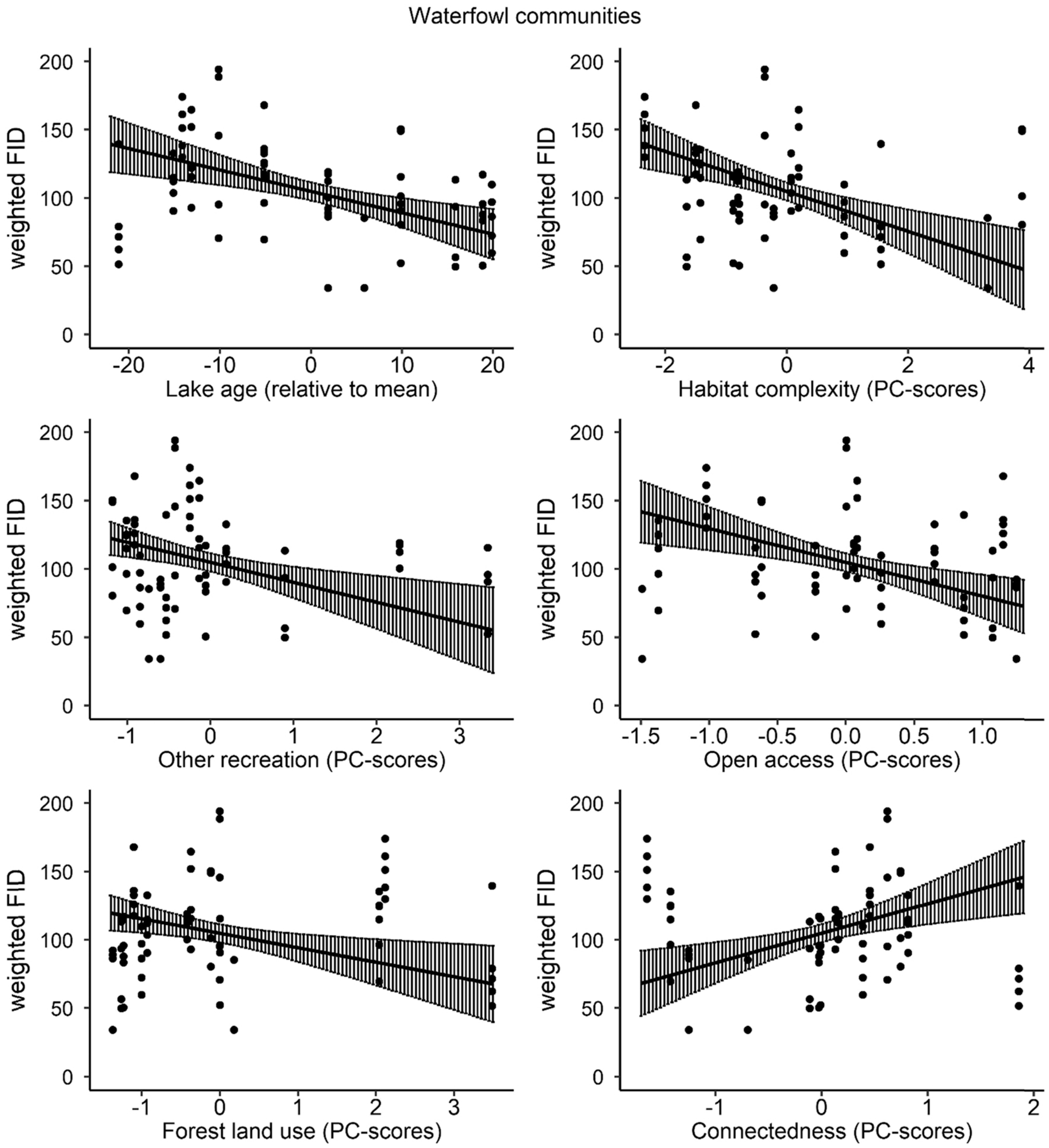

Fig. A12. Significant correlations between weighted FID of waterfowl communities and environmental predictors. Dots are observations, solid lines are the predicted model fit for lakes with 28.5% of shoreline protected, and vertical bars are the 95% confidence intervals.

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106476.

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