Technische Universität München
TUM School of Life Sciences

Determinants of diatom diversity in mountain lakes of the northern European Alps

Stefan Joachim Ossyssek

Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung eines

Doktors der Naturwissenschaften (Dr. rer. nat.)

genehmigten Dissertation.

Vorsitz: Prof. Dr. Johannes Kollmann

Prüfer*innen der Dissertation:

1. Prof. Dr. Jürgen Geist
2. apl. Prof. Dr. Tanja Gschlößl
3. Prof. Dr. Marco Cantonati

Die Dissertation wurde am 03.08.2022 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 20.11.2022 angenommen.

Die ganze Welt ist voll von Sachen, und es ist wirklich nötig, dass sie jemand findet.

Pippi Langstrumpf

Contents

Preface

The aim of this dissertation is to investigate the determinants of the diatom diversity in small, naturally oligotrophic mountain lakes in the northern European Alps. The thesis is structured in the three following parts.

The introduction presents the state of knowledge on the ecology and importance of mountain lakes in the European Alps. Then, the current ecological concepts in diatom research are explained in view of their historical development and advances of statistical methods and taxonomy. A focus is set on diatom diversity research in mountain lakes and practical consequences. Thereafter, a summary of the objectives and hypotheses of the work is presented, followed by an overview of the applied methods including lake sampling, sample processing and data analysis.

The main part consists of three chapters on different aspect of the diatom diversity in the studied lakes.

1. Chapter 3 describes the interaction of the frequent planktic diatom *Cyclotella comensis* and lake environmental conditions within a subset of the study lakes. The importance of lake mixing conditions and nutrient level is discussed in view of global change.
2. Chapter 4 identifies principal drivers of diatom α and β diversity in the assessed lakes. It describes the varying role of environmental and spatial constraints among the assessed assemblages and identifies the processes that led to the detected patterns.
3. Chapter 5 analyses the conservation value and human pressures impacting the lakes by studying the number, share and abundance of Red List diatom taxa among the lakes and assemblages. The comparison of the applied Red List indices and diversity metrics provides a framework for detecting lake conservation value and deterioration.

Chapter 6 is a general discussion which also consists of three parts. The first part embeds the results in view of global change with a focus on changing stratification and turbidity patterns on the within-lake processes and implications for regional diatom diversity. The second part identifies possible effects of historical legacies on diatom diversity and implications on biotic resilience under climate change. The final part of the general discussion pinpoints the implications of this thesis for mountain lake conservation in the study region.

List of Figures

List of Tables

Summary

This thesis explored the determinants of diatom diversity and composition in mountain lakes of the northern European Alps based on a field study that incorporated 43 lakes across an elevational gradient of c. 1,700 m and an area of 50 x 200 km (latitude x longitude). The results showed that the local aquatic environment had significant effects on assemblage structure of sedimentary, littoral and planktic assemblages with varying importance of different environmental variables and mechanisms. Variation purely explained by spatial variables was only observed for planktic diatoms, while shared effects of spatially structured environmental variables were relevant across all assemblages. Significant response variables in redundancy analysis and explained variation in variation partitioning and distance decay analysis were dependent on the investigated assemblages. The conservation value of the lake diatom assemblages was generally high with 64% of the 560 identified diatom species being on the Red List (RL) and 33% belonging to a category of endangerment (Hofmann et al., 2018). Ecological uniqueness of diatom assemblages and species richness contributed to the detection of high RL indices, i.e. those with high abundance or number of endangered species. The effects of catchment land use and fish stocking were mainly reflected within sedimentary and littoral diatom assemblages through lower share and abundance of RL diatom species, respectively. Accordingly, bottom-up and top-down control may affect the whole lake ecosystems due to the observed human pressures. In a subset of 20 deep and stratifying lakes, the most frequent planktic diatom from the data set *Cyclotella comensis* showed a strong response to lake surface temperature coupled with nitrogen availability and thermocline depth. In line with previous works in the study region, this indicates the sensitivity of mountain lakes towards ongoing climate change, probably leading to expanding dominance of *C. comensis* in the future.

Overall, the different assemblages showed varying values for alpha, spatial beta, and gamma diversity, unveiling processes that constrain within-lake and among-lake diatom diversity patterns and composition in temperate mountain lakes. This enables to place mountain lakes of the northern European Alps in a European and global context. It helps to understand the consequences of global change on mountain lake metacommunities and is a basis upon which mountain lake conservation strategies can be developed.

Zusammenfassung

In dieser Dissertation wurden die Einflussfaktoren auf die Diversität und Zusammensetzung von Diatomeengemeinschaften in Bergseen der nördlichen Europäischen Alpen basierend auf einer Geländestudie von 43 Seen entlang eines Höhengradienten von ca. 1.700 m in einem 50 x 200 km großen Gebiet untersucht. Die Ergebnisse zeigen einen signifikanten Einfluss der lokalen aquatischen Umwelt auf die Struktur der sedimentären, litoralen und planktischen Gemeinschaften und einen unterschiedlich starken Einfluss verschiedener Umweltvariablen und Mechanismen. Räumliche Faktoren erklärten die Varianz innerhalb der Artgemeinschaft nur bei planktischen Diatomeen, während räumlich strukturierte Umweltfaktoren auf alle Artgemeinschaften einen relevanten Einfluss hatten. Die Redundanzanalyse, Varianzpartitionierung und Distance Decay Analyse ergaben für die drei Artgemeinschaften unterschiedliche signifikante Variablen.

Von den 560 identifizierten Arten sind 64 % auf der Rote Liste (RL) Arten und 33 % werden eine Gefährdungskategorie zugeschrieben, was den hohen Naturschutzwert der Artgemeinschaften aufzeigt. Eine hohe ökologische Einzigartigkeit und Artenanzahl der Gemeinschaften spiegelt eine hohe Abundanz und Artenanzahl an RL Arten wider. Auswirkungen der Nutzung des Einzugsgebietes und von Fischbesatz waren insbesondere bei den Litoralen und Sedimentären Diatomeen erkennbar durch einen niedrigen Anteil und Häufigkeit an RL Arten. Bottom-up und top-down Effekte welche durch menschliche Eingriffe ausgelöst werden können dementsprechend die Seenökosysteme fundamental verändern.

In einem Teildatensatz aus 20 tiefen und geschichteten Seen war das Auftreten der häufigsten planktische Diatomee *Cyclotella comensis* durch die Kombination aus Oberflächenwassertemperatur, Nitratverfügbarkeit und die Tiefe der Sprungschicht bestimmt. Dies belegt die Sensitivität der Bergseen gegenüber Klimawandel Effekten, welche schon in früheren Arbeiten aufgezeigt wurde, und zu einer zukünftig noch häufigeren Dominanz von *C. comensis* führen wird.

Die unterschiedlich hohen Werte für α, räumliche β and γ Diversität der einzelnen Artgemeinschaften offenbarten unterschiedliche Prozesse, welche Diversitätsmuster innerhalb und zwischen den Seen bestimmen. Dies ermöglicht den Vergleich von Bergseen der nördlichen Kalkalpen im Europäischen und globalen Kontext. Es hilft die Auswirkungen von Klimaveränderungen und des globalen Wandels auf Bergseen Metagemeinschaften zu verstehen und ist eine Grundlage für die Entwicklung von Naturschutzstrategien für Bergseen.

1. Introduction

1.1 Mountain lakes in the European Alps

Mountain lakes are important to humans as they sustain a broad array of ecosystem services. In the eastern European Alps, maintenance of habitats, aesthetic value, outdoor recreation, representation, scientific value and entertainment were identified as important ecosystem services of mountain lakes (Ebner et al., 2022, Schirpke et al., 2021a). However, high recreational value can also lead to deterioration of lake ecosystems, for example through the construction of mountain huts (Hofmann et al., 2021, Sienkiewicz and Gasiorowski, 2014) and easy access of mountain lake shores via nearby trails (Senetra et al., 2020). Therefore, it is important to preserve the naturalness of remote lakes and not to improve their accessibility (Schirpke et al., 2021b).

Within the European Alps, three main groups of mountain lakes can be defined: Pre-alpine lakes (e.g. Lake Garda, Lake Chiemsee), which were formed by the glaciers of the alpine main valleys, large intra-alpine lakes, that often lie in the main valleys and were either formed by glaciers of these valleys (e.g. Lake Achensee, Lake Zeller See), tectonically (e.g. Lake Walchensee) or by a combination of both (e.g. Lake Königssee) and mountain lakes, that are located on mountains (e.g. within cirques) or within side valleys (Buckel et al., 2018) (mainly above 500 meters above sea level; hereafter called as "masl"; Figure 1). The latter group of lakes are the subject of this thesis. They often are in terrain shaped by cirque glaciers, dolines, rockslides and riverine peatlands, which accounts for all the assessed lakes in this study.

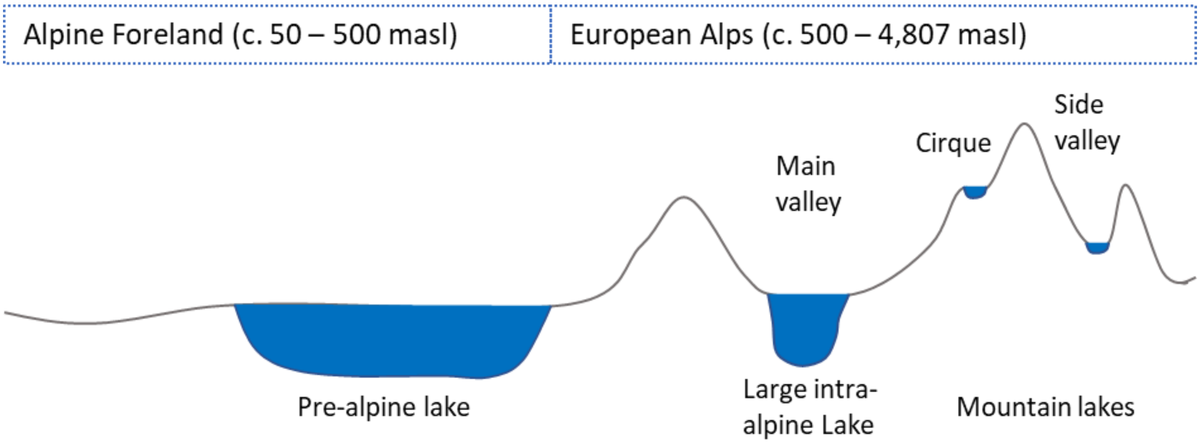

Figure 1: Schematic depiction of lakes in the European Alps.

Within the alpine environment, mountain lakes play an important role in various aspects:

(1) Mountain lakes often act as headwaters of alpine streams and rivers and as such directly influence biota and biogeochemical processes within downstream waters (Figure 2). Mountain lakes are known to cause both top-down and bottom-up control into downstream reaches: For example, fish presence

in mountain lakes strongly diminishes the downstream density of large zooplankton (Detmer et al., 2017), while downstream organic matter decomposition rate is up to 43% higher than upstream rate through a higher nitrogen to phosphorus ratio and elevated water temperatures (Goodman et al., 2010). Mountain lakes also act as sinks for sediment, leading to coarser sediment downstream of the lakes compared to the upstream reaches (Arp et al., 2007).

Figure 2: Outflow of the lake "Unterer Gaisalpsee", source of the “Gaisalpbach” that eventually drains in the river “Iller”, a tributary of the Danube.

(2) Mountain lakes have great biodiversity with many unique species and highly adopted taxa (Schmidt et al., 2004, Catalan et al., 2013). This is caused by highly variable environmental conditions with extreme values for ultraviolet radiation (UVR), water temperature and duration of snow and ice cover. The main driver for this variation is the long environmental gradient. High UVR at high altitudes selects adapted species among heterotrophic bacteria (Hugoni et al., 2017), diatoms (Cabrera et al., 1997), phytoplankton (Rodhe et al., 1966), zooplankton (Starkweather, 1990) and fish (Bullock and Coutts, 1985). UV stress can cause adaptions within algae such as mixotrophy, by using bacteria as a source of carbon and mineral nutrients in conditions of inhibited photosynthesis (Medina-Sanchez et al., 2004). Competitive advantages of “UV-specialists” can influence phytoplankton composition (Sommaruga, 2001), with feedback to alpine zooplankton species (Williamson et al., 2010a). Moreover, characteristically low and highly variable water temperatures have been shown to affect lake biota directly, for example they mediate diatom silicification rate (Kuefner et al., 2020d). An important indirect effect is through the coupling of lake mixing and water temperature. Global change therefore is expected to have severe impacts on mountain lake ecosystems, with higher temperatures leading to less frequent and less profound mixing (Niedrist et al., 2018) that in turn promotes small celled planktic algae that have lower probability of subsiding of the euphotic zone under stable water conditions (Gunkel and Casallas, 2002, Rühland et al., 2015). Overall phytoplankton density was found to increase at higher water temperature and high release of dissolved organic carbon (DOC) in lakes, while both factors separately have the opposite effect (Weidman et al., 2014). The duration of ice cover has several indirect consequences for lake biota, with shorter ice cover causing an earlier onset of lake mixing and a longer

period of open water (Kirillin et al., 2012). There is some evidence that this may cause higher dissolved oxygen saturation in mountain lakes, especially as they shift from meromictic to dimictic state (Flaim et al., 2020, Catalan et al., 2002b). The snow cover in the catchment mainly determines the drainage of soil ions into the lakes by controlling mobilization of weathering products, which affects chemical properties of the lake. Consequently, high altitude lakes with long snow cover have less ionic runoff in the soil than lower altitude counterparts (Rogora et al., 2020).

Even though mountain lakes are generally shed from many direct anthropogenic pressures, impacts due to pasture, fish stocking, damming and tourism are frequent in some regions (Moser et al., 2019b). In addition to direct pressures, global environmental change is increasingly affecting mountain lakes. To assess these effects, the European Union (EU) set up the research programs ALPE, MOLAR and EMERGE. Starting in 2000, a large set of mountain lakes in Europe were systematically investigated, with a special focus on acidification. Lakes from the central Alps in Austria and Italy were considered, however no lakes of the Northern Alps as the main research focus was on acidification (Battarbee et al., 2002, Curtis et al., 2009). In the northern Alps, limestone bedrock prevails, which means the lakes are well buffered, and potential acidification effects are mitigated. However, northern European mountain lakes are indeed affected by global warming (Kuefner et al., 2020a) and through changes in water chemistry due to nitrate deposition (Bergstrom, 2010), which affects primary producers in lakes. In this region, shallow subalpine mountain lakes with elevated nutrient levels have been identified to be most susceptible to climate change impacts through both, direct impacts on lake processes and indirect impacts reflecting processes mediated by the catchment (Schindler, 2009, Kuefner et al., 2020c, Niedrist et al., 2018). With the EU projects mountain lake research in the European Alps has diversified including studies that investigate ecological thresholds (Catalan et al., 2009), catchment – lake interactions (Kamenik et al., 2001), impacts of glaciers on lakes (Sonnleitner et al., 2011), occurrence of persistent organic pollutants (Carrera et al., 2001) and ecosystem services (Schirpke et al., 2021a).

1.2 Diatoms: The most diverse group of algae

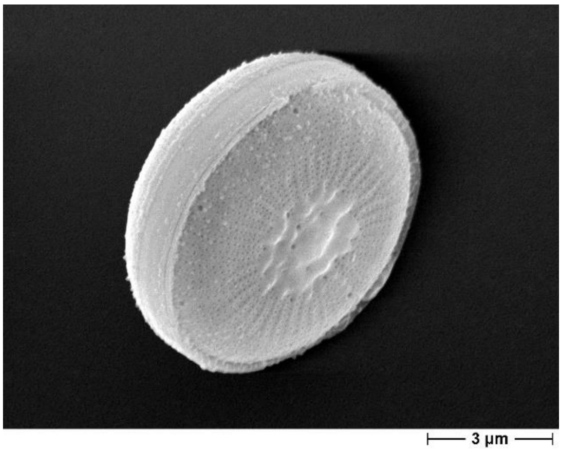

Figure 3: The diatom *Cyclotella cf. delicatula* under the scanning microscope. Some characteristic elements can be recognized such as the symmetrical valve structure and the lateral girdle band where both valves (Hypotheca and Epitheca) overlap.

Diatoms (Class Bacillariophyceae) are unicellular, eukaryotic algae, having a characteristic silica-based cell wall called frustule. Most diatoms have internal vacuoles for defence and buoyancy control. Characteristically, diatoms are covered in a bipartite frustule, composed of the hypotheca that overlaps with the epitheca (Figure 3). Each cell division leads to a diminished daughter cell as both halves of the frustule serve as the hypotheca for both daughter cells. This necessitates sexual reproduction at a critical cell size. The formerly proposed function of vacuoles to store nutrients during luxury consumption appears to matter only for few species such as *Asterionella formosa* (Behrenfeld et al., 2021). The origin of the word diatom comes from the Greek “diatomos”, meaning “cut in half” and referring to the two-part nature of the diatom cell. According to molecular clock data, the diatoms appeared at least 240 Mio. years ago and the oldest fossil records date back 190 Mio. Years (Sorhannus, 2007, Sims et al., 2006, Medlin et al., 1996). Diatoms colonized almost all aquatic environments, from marine to freshwater habitats, semiaquatic environments, soils, aerosols and even hot springs (Owen et al., 2008, Medlin, 2016, Mann, 1999). Aquatic diatoms can be divided into the following life forms: planktic diatoms float in the water column, benthic settle on various substrates and tychoplanktic alternate between the planktic and benthic life forms (Round et al., 1990).

Diatoms are one of the most important primary producers, contributing 40-45% of marine primary production (Yool and Tyrrell, 2003) and 20-25% of total global primary production (Falkowski et al., 1998). The majority is photoautotrophic, but obligate heterotroph forms exist (Round et al., 1990). The currently assessed species richness of diatoms is assumed to range from 10,000 to 12,000 (Mann and Droop, 1996), making them the most speciose group of unicellular eukaryotes. With 70%, most diatom taxa described so far are from freshwater and 83% of all diatoms of either freshwater or marine are benthic. Divergences in species richness among habitats are reflected by three times higher ratios of net diversification and net turnover (speciation and extinction) within freshwater diatoms compared to the marine environment, which can be contributed to salinity as the principial gradient and differences in underlying environmental, ecological and trait factors (Behrenfeld et al., 2021). Projections of the actual species richness range from 20,000 (Guiry, 2012) to 200,000 (Mann and

Droop, 1996). Generally, high species richness compared to other photosynthetic protists is probably due to the greater requirement for sexual reproduction in diatoms (a fortuitous consequence of the frustule): While speciation under asexual reproduction is highly reserved to mutations and gene transfer, more regular genetic recombination in sexual reproduction implies higher gene diversity and thus higher speciation potential (McDonald and Linde, 2002). In line with this, the most sexually active modern diatom lineages are also the most species-rich (Nakov et al., 2019).

High diatom species richness of up to 100,000 is likely because many regions such as the tropics or marine littoral zone to date remain largely unexplored and there is a huge potential for (pseudo)-cryptic variation (Souffreau et al., 2013) that will only be revealed through further genetic studies or crossing experiments (Mann and Vanormelingen, 2013). As (pseudo)-cryptic species are likely to coexist in many cases (Poulickova et al., 2010, Van den Wyngaert et al., 2015) this is a challenging task. However, refining diatom taxonomy through investigation of (pseudo)-cryptic species occurrence or, in contrast, identification of phenotypes among previously believed distinct morphospecies will be crucial for delimiting a correct number for diatom species richness. Moreover, this will enhance correct identification of species distribution patterns, endemism and cosmopolitism, topics that have been debated controversially (see next chapter) (Finlay, 2002, Shurin et al., 2009). In turn, this will help to delimitate the relative importance of various evolutionary mechanisms that lead to diatom diversification. For example, allopatric divergence including adaptive radiation is based on the distinct geographical distribution of a species caused by long-distance dispersal and subsequent isolation (Vanormelingen et al., 2008).

However, for most species complexes their evolutionary history is still poorly understood. For example, only recently the importance of allopatric speciation for the diversification of the soil diatom *Pinnularia borealis* through long-distance dispersal and colonization of novel geographic areas and subsequent evolution in isolation has been unveiled (Pinseel et al., 2020). Within this study 126 species belonging to the *P. borealis* complex were delimitated with an estimated species richness of 415 according to species accumulation curves. The results were based on applying genetic markers but were also reflected by divergent morphological and ecological characteristics. Diversification rates likely range between 0.09 to 0.30 events per lineage per Million years. Further studies point to similar high cryptic variation in other species formerly deemed cosmopolitan such as *Asterionella formosa* (Van den Wyngaert et al., 2015), *Sellaphora spp.* (Vanormelingen et al., 2013) and *Asterionellopsis glacialis* (Kaczmarska et al., 2014). Further research using species-level phylogenetic markers is needed to place these observed differentiations in an evolutionary context.

Another important feature of diatom populations is their high intraspecific variation, which helps them to endure environmental changes (Godhe and Rynearson, 2017, Andersson et al., 2021). This is especially relevant in light of human induced global environmental change, which can be expected to fuel selection processes among intraspecifically divers diatom populations (Wolf et al., 2019).

1.3 Developments in diatom population biology

1.3.1 A brief history of diatom research

The discovery of diatoms can be dated back to the year 1703 and was made possible through the invention of the microscope (Round et al., 1990). The systematic description of diatoms was pioneered by Müller (1783), and pursued by Ehrenberg (1843), Kützing (1844) and Hustedt (1930). In the first part of the 20th century, ecological studies and classifications including water properties were increasingly carried out as outlined by Patrick (1948).

At this time, the importance of water movement, physical variables such as water temperature, pH and turbidity, i.e. light intensity, and water chemical properties such as salinity, iron and nutrient concentration was already broadly recognized. Also geographic differences in the distribution of species and genera were recorded, for example Cleve and Möller (1878) found that 51% of the diatom flora of Franz Josef Land was present in Spitzbergen but only 26% in Lapland. Moreover, also temporal variation was investigated, demonstrating the importance of turbulent lake water conditions, exemplified by the seasonal occurrence of the planktic diatom *Melosira italica* (Lund, 1954). During this period, demonstration of coexistence of species with similar ecological requirements led to new insights into diatom population ecology (Small, 1950) and investigations on grazing pressure of the marine snails *Littorina* and *Limpet* emphasized the importance of diatoms as food source for higher aquatic organisms (Castenholz, 1961). Moreover, the development of diversity indices such as the Shannon-Wiener Index (Shannon, 1948), Simpson´s index (Simpson, 1949) and Margalef´s index (Hairston, 1959) enhanced the quantitative assessment of diversity patterns at different sites (McIntire and Overton, 1971) and helped to unveil relationships between diatom diversity and water chemical properties (Williams, 1964). It is no coincidence that the development of some of the essential principles of modern population ecology fall into this period. For example, the theory of island biogeography was developed through the study of the successive phase colonization (Macarthur, 1965). This theory could be applied to other habitats and was a basis for population ecology, which then evolved rapidly.

1.3.2 Setting the stage: Modern statistical techniques

A fundamental advance in understanding patterns within aquatic communities and thereupon develop and test ecological theory became possible through the implementation of multivariate statistical methods that can account for the multivariate nature within environmental and community datasets (Terbraak and Verdonschot, 1995). The basic feature of these methods is to use weighted averages of species occurrences, a concept already proposed by the pioneers in community ecology such as Ellenberg (1948) and Whittaker (in Gauch (1982). A distinction can be made between redundancy analysis which models a linear relationship between environment and species (Borcard et al., 1992) and canonical correspondence analysis which predicts an unimodal relationship (Terbraak and Verdonschot, 1995). Both methods produce synthetic environmental gradients that can be used to describe and visualize ecological preferences of species. Enhancements of these methods such as Monte-Carlo-Permutation tests and backward/forward selection procedures allow for detecting variables that significantly influence overall species composition. Another advance was the partitioning of the total variation of species abundances into independent components and measuring decay of assemblage similarity with increasing distance (geographical, environmental or other factors that may affect species) (Borcard et al., 1992). Both methods are complementary and enabled to deduce the relative importance of different constraints on diatom populations, such as local environment (e.g., (Soininen and Weckstrom, 2009), climate (e.g., Benito et al., 2018), isolation (e.g., Schmera et al., 2018), spatial distance (e.g., Plante et al., 2021) and phylogenetic distance (Morlon et al., 2011).

Current research suggests that procedures based on machine learning such as boosted regression trees, random forest, fully connected neural network and neural generalized additive models have a wide applicability and high power to model ecological patterns (Valletta et al., 2017, Moisen and Frescino, 2002, Segurado and Araujo, 2004). For example, they were used to detect global marine diatom diversity and to predict its future trend under a changing climate (Busseni et al., 2020) or to model silicification patterns of diatoms depending on water temperature (Javaheri et al., 2015).

1.3.3 Setting the stage: Modern diatom taxonomy

Together with new statistical methods, revisions in taxonomy, possible through molecular technics, set the stage for modern diatom population biology (see chapter 1.3.4). The current state of the knowledge is that distinct morphospecies were largely pooled in the globally used European freshwater diatom floras of Hustedt (1927-1966) and Krammer and Lange-Bertalot (1981-1996) (Vanormelingen et al., 2008). On the one hand, the global use of this identification literature leads either to an “enforced-fitting” of the European flora to other floras such as the Australis (Tyler, 1996), or to large amounts of unidentified taxa. For example, in a 2,735 sample study of US rivers 26% of all species could not be identified (Potapova and Charles, 2002). On the other hand, species pooling led to underestimation of the strong biogeographical component of many diatom taxa (Vanormelingen et al., 2008). After it became increasingly clear that there are many diatom strains with distinct taxa exhibiting different ecological characteristics, more than 1,400 new diatom taxa were described in the Iconographia Diatomologica (edited by Lange-Bertalot) between 1999 and 2008. Other studies into the taxonomy of diatoms are continually expanding the knowledge on geographical distribution patterns, ecological niches and species interactions (Vanormelingen et al., 2008). For example, refinements in taxonomy have clarified the long debated question of whether microbes (size < 1 mm) are ubiquitous across the globe (Finlay, 2002). This is not the case, as many examples for endemic diatom species have been proven (e.g., Shishlyannikov et al., 2018), while evidence for cosmopolites is restricted on few marine species (Vanormelingen et al., 2008). This is also true on a population level, for example the Antarctic and Arctic region have hardly any species in common (Spaulding et al., 2010). Furthermore, among freshwater diatoms large pure spatial effects mediating distance decay of similarity of assemblages have been detected on a continental scale (e.g., Potapova and Charles, 2002).

1.3.4 Concepts in population biology and their application to diatoms

Demonstration of endemism, distance decay of assemblage similarity and distinct biogeographical distribution in diatoms (see chapters 1.3.3) is highly relevant in studying the importance of dispersal for structuring populations, one of the core criteria in modern population biology. Thus, diatomology benefits from and, in turn, contributes to the development of new concepts in population biology. The most comprehensive and yet fundamental concept is the metacommunity framework (Leibold et al., 2004) as it comprises various ideas of population biology such as the importance of ecological niches, species interactions, stochasticity and dispersal. Accordingly, a metacommunity defines as a set of local communities that are linked by dispersal of multiple potentially interacting species (Figure 4).

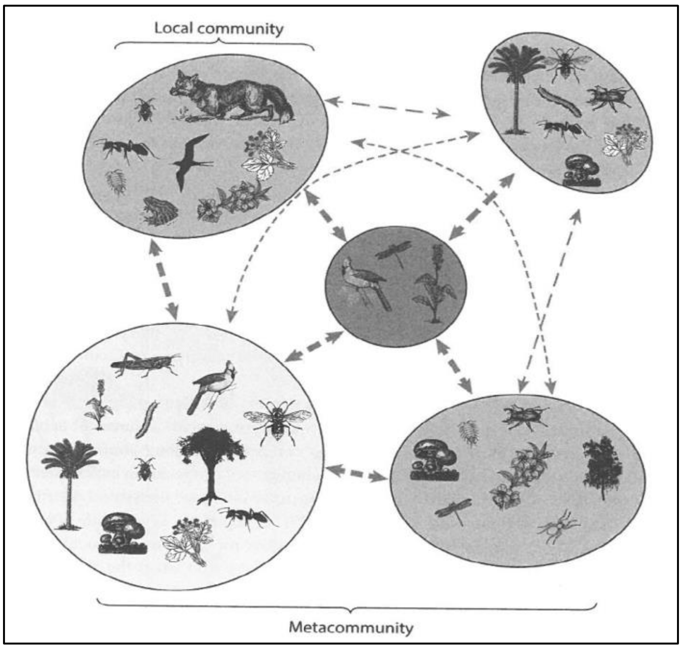

Figure 4: Features of a metacommunity (from Leibold and Chase (2018).

The following four paradigms are defined, each emphasizing different processes of potential importance in metacommunities: The neutral view, the patch-dynamic view, the species-sorting view, the mass effects view. In neutral theory, species are identical concerning interspecific interactions and they respond uniformly to the environment (Hubbell, 2001). Hence, demographic processes such as extinction are stochastic. Within the patch dynamics archetype, species reactions to the environment vary, but extinction is stochastic, and the environment is homogenous. The species sorting concept assumes that the environment is heterogenous and species react differently to environmental conditions. Moreover, local conditions regulate species demographic processes and adaptive abilities while species distribution can be limited. The mass effect framework expects that the environment is heterogeneous, local conditions regulate the competitive abilities of species and the demographic processes. Since dispersal is sufficient, each species can persist in any habitat where it can achieve positive population growth. Furthermore, very high dispersal rates can allow stable populations of species even under unfavourable conditions (Leibold and Chase, 2018) (Figure 5). For freshwater diatoms, varying importance of local environmental factors compared to geographical and historical constraints has been detected. This ratio is strongly mediated by the scale of the study area: At continental to global scale the importance of historical constraints and dispersal limitation expressed through spatial patterns is often stressed (Vyverman et al., 2007), while in regional studies local environmental influence predominates (reviewed in Soininen (2007). Thus, it is evident, that there exist multiple drivers on diatom assemblages acting simultaneously at different geographical and temporal scales. The local to regional perspective mainly reflects the species sorting archetype, i.e. the classical view that assemblages are ordered by the available niches and that all regional species can reach and colonize these niches. However, very high dispersal rates, corresponding to the mass effects archetype, were detected within regional diatom sets, leaving a spatial imprint on otherwise environmentally structured diatom community patterns (Leboucher et al., 2020, Jamoneau et al., 2018). In contrast, also dispersal limitation was prevalent on regional scales as indicated by exclusively spatially structured diatom assemblages (de Oliveira et al., 2020). This overlap of mechanisms has implications on a practical level. For example, spatial effects can distort results of diatom bioassessment indices as identified in a set of lake benthic diatoms from Norway (study area: 305 km^2) (Vilmi et al., 2016). To resolve this problem, the pioneering work by Leboucher et al. (2020) to detect mass effect species is an important basis and it was shown that excluding species influenced by mass effect fortifies the relationship between diatom indices and environmental conditions (Leboucher et al., 2021). The used approach relies on a species distribution modelling, with environmental and spatial factors computed from asymmetric eigenvector maps, coupled with negative co-occurrence patterns. However, a core challenge remains to distinguish between the forms of dispersal. Therefore, further assessments of diatom dispersal ability based on species traits, e.g. probability of wind, bird or insect mediated dispersal as a function of body size, habitat or attachment

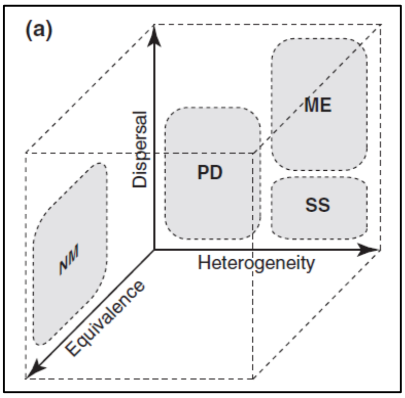

Figure 5: Processes that act within a metacommunity and define the relative strength of the four paradigms within the metacommunity concept: Patch dynamics (PD), mass effects (ME), species sorting (SS) and neutral model (NM) (from Leibold and Chase (2018).

probability are urgently needed (Cottenie, 2005). Resolving this issue will not only provide information for future bioassessment procedures but also contribute to better understand the global diatom evolution and their response to environmental change.

1.4 Diatom diversity within mountain regions

Biodiversity combines the words “biological diversity” and can be defined as the "full variety of life on Earth”. It considers the diversity of individuals within populations, the diversity of species within communities, and the range of ecological roles within ecosystems. It consists of three components: species diversity, ecosystem (or habitat) diversity and genetic diversity (Schmeller et al., 2017). The following chapters focus on *species diversity* of diatoms, hereafter referred to as “diatom diversity”, which in turn can be diverted into α, β, and γ diversity. α diversity describes species richness and is a measure derived from species presences or abundances measured at a specific site, β diversity considers the dissimilarity of species composition among sites, describing the abundances of species entities at all sites within a region and γ diversity refers to the total diversity within a region (Whittaker, 1965).

1.4.1 Diatom α, β and γ diversity

Along the elevational gradient decreasing α diversity has been detected for lotic and lentic aquatic habitats such as Chinese Himalayan plateau streams (Wang et al., 2011) or a Nepalian river (Ormerod et al., 1994). The former study also revealed a correlation of α diversity with the total nitrogen to total phosphorus ratio (TN/TP ratio) and, more specifically, a negative binomial relationship for evenness along the altitudinal gradient. Both studies point to an important role of species sorting mechanisms for diatoms along the elevational gradient that is reflected by the strong correlation of nutrient supply and species assemblage composition. Because TN and TP concentration depend mainly on geoclimatic variables (Kamenik et al., 2001) α diversity of diatoms is indirectly dependent on climatic conditions. However, the elevation dependent environmental gradient not contributes exclusively to diatom α diversity. For example, in Fenoscandinavian rivers along an elevational gradient of 21-877 meters above sea level only a weak richness-elevation relationship was detected. Accordingly, this diatom flora does not conform to Rapoport's elevational rule, predicting a general decrease of local species richness with elevation (Teittinen et al., 2016, Stevens, 1992, Rapoport, 1982). Instead, local environmental factors such as water depth and substrate size were of major importance. Generally, relying solely on species richness to describe a diatom community can be problematic due to the pronounced effects of undersampling. For example, for a set of 71 Swiss springs with a total of 539 diatom species, species richness increased monotonically with elevation. However, the Jaccard index for the measured compositional turnover showed a mean similarity of 70% between microhabitats, while the Chao index, which accounts for sampling artefacts, estimated a turnover of only 37%. This suggests that the counted 500 valves per sample (the commonly applied method) led to an undersampling of rare species (Taxbock et al., 2020).

Regional diatom β diversity in freshwater habitats appears to be mainly influenced by local environmental variables, that in turn are determined by geoclimatic conditions or geology and land use. This is indicated by shared effects of environment and space in variation partitioning (Soininen and Teittinen, 2019). Studies from the Tibetan plateau unveiled a u-shaped pattern for the local contribution to diatom β diversity (LCBD), which is a component of β diversity, along the elevational gradient. This pattern was mainly related to the changes in ambient temperature (Wang et al., 2020a). Moreover, changes in β diversity and the importance of environmental determinants have been found to depend on the presence of direct or indirect human impacts within a lake set in the Tibetan plateau (Wang et al., 2020b). Interestingly, indirect human impact primarily enhanced β diversity. However, in the long term a homogenization of diatoms in lakes was observed. This process has led to a decrease in overall species diversity. Generally, the emphasis of the local environment might be because until now the overarching contribution to diatom research in mountain regions has been made at the regional scale, probably because of the challenging sampling.

Across large mountain ranges, also pure spatial patterns were evident, pointing either to dispersal limitation or mass effects (Benito et al., 2018). Recently, also the imprint of historical legacies on diatom β diversity in mountain streams has been proven, pointing to an important role of biogeography for freshwater ecosystems that are found on mountains (Gonzalez-Trujillo et al., 2021).

A study of γ diatom diversity within a study region must be considered in a global context. Disproportional high regional diversity in mountain regions can be expected for several reasons:

1. It was found that low water temperatures in the Antarctic during the last 15 Mio. years resulted in high diatom speciation ratios. This is probably due to direct influence of temperature on metabolic rate and hence may also cause high diatom diversity and speciation rate in mountain environments (Crampton et al., 2016).
2. Studies investigating processes that lead to diatom speciation frequently identified allopatric speciation (Evans et al., 2009, Pinseel et al., 2020). This suggests that mountain lakes, even though relatively young compared to lowland rivers and oceans, are a hotspot for diatom speciation as dispersal boundaries are more pronounced here than in flat areas. This effect is enhanced through environmental divergence among habitats, as demonstrated for Patagonian mountain lakes (Fernandez et al., 2017).

3. The ecological divergence of mountain lakes (e.g., the variation of benthic habitats along the elevational gradient) probably enhances the potential for sympatric speciation, as demonstrated within soil diatoms (Rysanek et al., 2016).

1.4.2 Mountain lake diatom diversity in applied research

Diatoms are among the most used biological indicator organisms in mountain lakes (Smol et al., 2001). The basis for any paleolimnological interpretation of fossil diatoms in sediment records and for the inference of current ecological lake conditions is a sound understanding of the impact factors controlling diatom diversity and distribution (Hamilton, 2005), which is assessed by community-based measures (Winter et al., 2013). An approach to quantitatively model past environmental conditions is the application of transfer functions (Antoniades et al., 2005). These are based on a training set of diatom assemblages that should correspond to the environmental gradient of interest. However, it was shown that this approach is susceptible for secondary gradients, inhomogeneous sampling and analogue problems (if fossil diatoms are missed in the training set) (Juggins, 2013). An additional and previously hidden source for uncertainty, i.e. low predictive power, may arise from effects of species dispersal within the diatom training set as has been demonstrated for current bioassessment approaches (see chapter 1.3.4). Therefore, it may be worthwhile to test current training sets on spatial effects and eliminate species that are affected by mass effect or dispersal limitation (Leboucher et al., 2021).

1.4.3 Mountain lakes and diatom conservation

The conservation of lakes including mountain lakes has largely focused on mammals and invertebrates, mainly due to the broad knowledge on their distribution (Casamayor, 2017). However, the species diversity of diatoms probably exceeds that of higher trophic groups in most cases and so it is recommended to include these species in future conservation programs. This calls for the further development of regional diatom Red Lists (RL) such as the one that exists for Germany (Cantonati et al., 2022b, Hofmann et al., 2018). Besides of the degradation of mountain lakes through human recreational activity (Chapter 1.1) several other stressors impair diatom communities. These are fish stocking and increased cattle herding, leading to nutrient enrichment and top-down control effects (Tiberti et al., 2014a, Tiberti et al., 2014b, Schindler and Eby, 1997, Schindler et al., 1993, Schindler et al., 2001). Recently, also the introduction of alien diatom species has been problematized. For example, the bloom forming northern American diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt was found to have negative effects on invertebrate communities in New Zealand upland streams (Anderson et al., 2020) and was recently also detected in stream headwaters of the Picos de Europa mountain range in northern Spain (Gonzalez-Paz et al., 2021). Some of these human stressors lead to eutrophication and RL species were found to be highly representative of this process within springs (Cantonati et al., 2012, Cantonati et al., 2022b, Cantonati and Lange-Bertalot, 2010, Cantonati and Spitale, 2009, Hofmann et al., 2018) and lakes (Cantonati et al., 2011, Tolotti, 2001). Thus, identifying and preserving rare and restricted diatom assemblages, i.e. candidates for the Red List, not only contributes to sustain the high diversity within algal communities but also helps to preserve threatened freshwater habitats that are important to a broader range of taxa and general ecosystem functioning (Cantonati et al., 2022b, Juran and Kastovsky, 2019).

1.5 Objectives

This PhD thesis is embedded in a comprehensive "Mountain Lakes Project", which was started in 2016 at the Limnological Research Station Iffeldorf, Chair of Aquatic Systems Biology. The project deals with the effects of climate change on mountain lakes, including diatoms as indicators. This study covers most of the natural mountain lakes in the northern European Alps, whose diatom communities were recorded for the first time. Within the project, a subset of the lakes was characterized with paleolimnological methods, while this dissertation includes the full set of lakes and focuses on the study of recent diatom assemblage patterns.

The goal of this work was to investigate the drivers of diatom diversity for sedimentary, littoral and planktic assemblages in mountain lakes. A lake set with a large elevational gradient, resulting in strong differences of local environmental conditions was selected for the study. In addition, the highly rugged landscape has led to accentuated isolation among those lakes.

The diatom samples analysed were from lakes in the montane, subalpine to alpine zones. In parallel, the chemical and physical characteristics of the lakes important for diatoms were assessed, including the year-round continuous recordings of the lake bottom and surface temperatures.

The following general hypotheses were tested:

1. The composition of the lake diatoms is mainly mediated by local environmental factors and spatial factors play a minor role.
2. The relative importance of environmental factors for assemblages structure of sedimentary, littoral and planktic diatoms varies and determines patterns in α, β and γ diversity.
3. The diatom assemblages have high conservation value that is reflected by Red List taxa that are in turn reflected by ecological uniqueness and species richness.

The results should contribute to understanding the principal drivers of diatom assemblages composition on a regional scale in mountain environments, reveal their conservation value and potential human pressures. On this basis and considering ongoing global change the adaption of existing conservation strategies is discussed.

2 Material and Methods

2.1 Study Sites

The study includes 43 mountain lakes located in the northern European Alps in Bavaria (Germany) and Tyrol (Austria) (Figure 6). The study area comprises a longitudinal gradient of 220 km from the Berchtesgaden mountains in the east to the Allgäu in the west and a latitudinal gradient of 50 km.

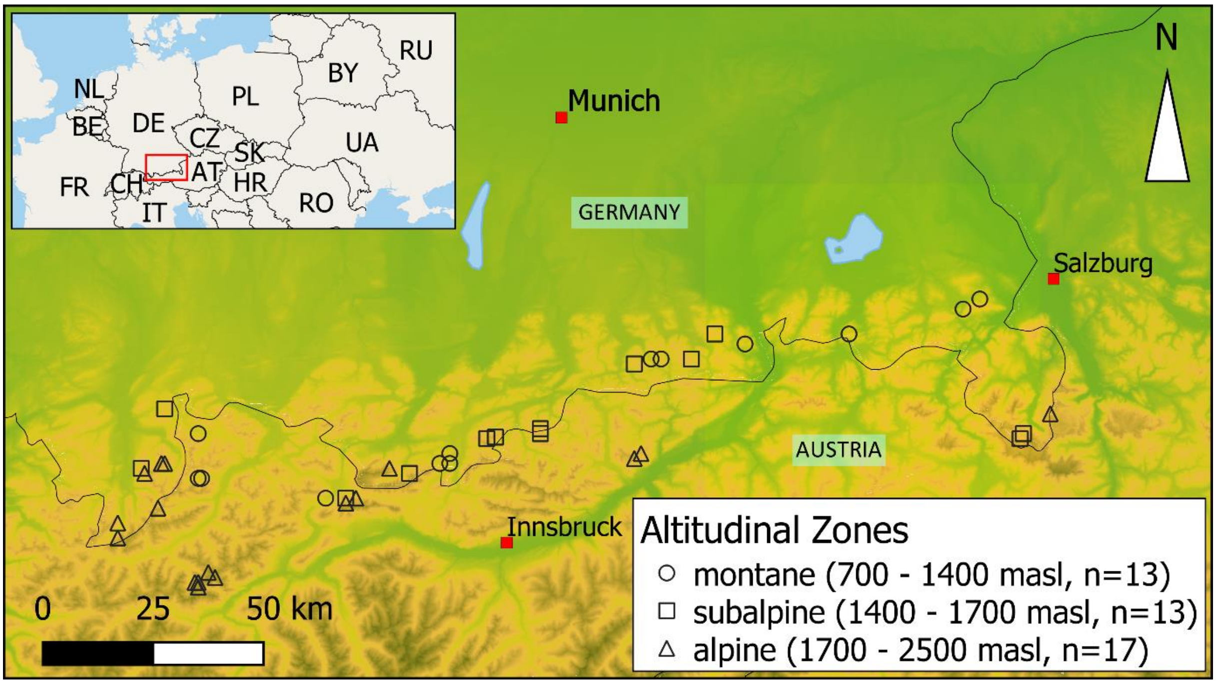

Figure 6: Location of the study site in the northern European Alps (adapted from Ossyssek et al., 2022).

The study lakes cover an elevational gradient from 760 to 2,469 masl, comprising the montane (750 – 1,400 masl), subalpine (1,400 – 1,700 masl) and alpine (1,700 – 2,500 masl) vegetation zone. Lake catchments of the montane zone are characterized by conifer-dominated forest (*Picea abies*, *Larix decidua, Acer pseudoplatanus* and *Fagus sylvatica*). The subalpine catchments are located at the ecotone from forest to grasslands characterized by patches of *Pinus mugo* and alpine catchments are dominated by alpine meadows (e.g. *Carex sempervirens*, *Rhododendrum hirsutum*, dwarf shrub communities), poorly developed soils and fellfields (Figure 7).

Figure 7: Examples for a montane lake (Lake Sieglsee, 1,207 m, left), a subalpine lake (Lake Seebensee 1,657 m, middle) and an alpine lake (Lake Laufbichlsee, 2,012 m, right).

Table 1: Overview of all sampled lakes. The individual altitudinal level, lake name and code, altitude, lake area, and sampling dates are given.

Alt. Level	Lake name	Code	Altitude (masl)	Area (ha)	1. Sampling	2. Sampling	3. Sampling
Montane	Falkensee	Fal	760	1.0	06-10-2017	06-10-2017	
	Bichlersee	Bic	955	1.4	09-06-2016	08-09-2016	13-09-2017
	Frillensee	Fri	973	1.2	17-07-2017	04-10-2017	
	Suttensee	Sut	995	1.4	07-06-2016	06-09-2016	
	Lautersee	Laut	1,013	12.0	15-07-2015	18-09-2015	
	Ferchensee	Fer	1,060	10.0	15-07-2015	18-09-2015	
	Mittersee	Mit	1,082	3.3	13-09-2016	08-10-2017	
	Wildensee	Wild	1,136	2.3	21-06-2016	15-09-2016	
	Taubensee	Tau	1,138	3.6	09-06-2016	08-09-2016	
	Höfersee	Hoef	1,192	0.6	24-08-2016	25-10-2016	19-09-2017
	Sieglsee klein	SieK	1,205	0.2	24-08-2016	26-10-2016	
	Sieglsee groß	SieG	1,207	0.8	24-08-2016	26-10-2016	21-08-2018
	Grünsee	GruW	1,393	2.3	08-06-2016	07-09-2016	
Subalpine	Röthensteiner See	Roe	1,450	1.0	07-06-2016	06-09-2016	
	Soinsee Süd	SoiS	1,458	4.0	06-07-2016	06-09-2016	13-09-2017
	Grünsee	GruO	1,474	3.5	20-06-2017	05-10-2017	
	Unterer Gaisalpsee	GaiU	1,508	3.5	26-07-2016	21-09-2016	
	Soinsee Nord	SoiN	1,520	0.3	05-07-2016	07-09-2016	
	Unterer Soiernsee	SoE	1,552	3.0	30-06-2016	05-10-2016	
	Oberer Soiernsee	SoW	1,558	3.0	30-06-2016	05-10-2016	
	Delpssee N	DelN	1,600	0.6	07-07-2016	01-09-2016	
	Delpssee S	DelS	1,600	0.2	07-07-2016	01-09-2016	
	Funtensee	Fun	1,601	2.5	20-06-2017	05-10-2017	
	Hörnlesee	Hoer	1,601	0.5	23-09-2016	09-10-2017	
	Seebensee	Seeb	1,657	6.3	22-06-2016	13-09-2016	
	Schachensee	Scha	1,680	3.0	04-07-2016	06-10-2016	
Alpine	Guggersee	Gug	1,725	0.1	25-07-2016	23-09-2016	
	Oberer Gaisalpsee	GaiO	1,769	0.8	26-07-2016	21-09-2016	
	Ziereiner See	Zie	1,799	3.0	04-07-2017	27-09-2018	
	Seeleinsee	Seel	1,809	0.4	21-06-2017	04-10-2017	
	Eissee	Eis	1,827	0.7	21-09-2016	10-10-2017	
	Drachensee	Dra	1,874	5.3	23-06-2016	13-09-2016	
	Engeratsgundsee	Eng	1,876	3.0	27-07-2016	22-09-2016	18-09-2017
	Brendlsee	Bre	1,903	1.5	22-06-2016	13-09-2016	
	Stuibensee	Stu	1,921	3.0	28-06-2016	15-09-2016	
	Laufbichelsee	Lauf	2,012	0.8	27-07-2016	22-09-2016	
	Gr. Rappensee	Rap	2,047	2.3	28-07-2016	20-09-2016	17-09-2017
	Grubersee	Grub	2,060	0.5	04-07-2017	03-10-2017	
	Unterer Seewiesee	SeeU	2,224	2.4	23-08-2016	17-10-2016	
	Auf der Lacke	Adl	2,294	1.9	23-08-2016	26-10-2016	
	Schiefersee	Schi	2,300	2.0	22-08-2016	25-10-2016	
	Mittlerer Seewiesee	SeeM	2,424	0.5	23-08-2016	18-10-2016	
	Oberer Seewiesee	SeeO	2,469	1.6	23-08-2016	18-10-2016	

While the formation of the vegetation zones naturally is constrained by annual local temperature and therefore by altitude, ordination, morphology and wind pattern (Korner, 2004, Korner, 2021), the actual ecotone between the subalpine and alpine region was shifted downward during prehistoric times due to deforestation to create alpine meadows for cattle herding or for generating timber (Pini et al., 2017). In turn, ongoing climate warming and abandonment of pastures lead to an upward shift of the ecotonal boundaries in current times (Cudlin et al., 2017).

2.2 Water sampling and processing

Each of the 43 included lakes was sampled at least two times during the ice-free period, i.e. in early summer and in autumn (Table 1). On the first sampling date, bathymetric measurements were conducted with an echo sounder (Lawrence HDS8, Oslo, Norway), and a buoy fixed with a rope on a stone was subsequently installed at the deepest point of each lake. Temperature loggers (Onset Pendant UA-001-64 HOBO, Bourne, MA) were mounted on the rope 0.5 m above the sediment surface and 0.5 m below the water surface (Figure 8).

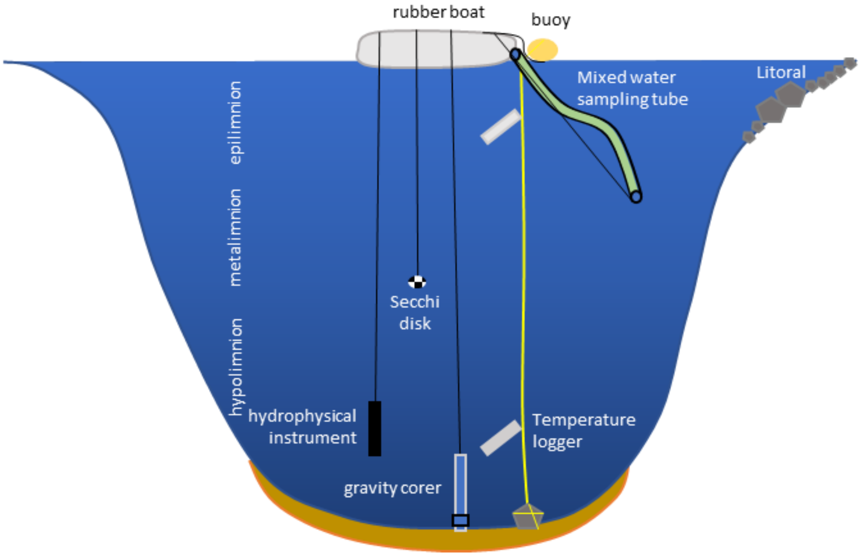

Figure 8: Overview of mountain lake sampling procedures containing the rubber boat, buoy, mixed water sampling tube, Secchi disk, hydrophysical instrument, gravity corer and temperature loggers.

On both sampling dates, physical parameters (temperature, oxygen saturation, pH and conductivity [at 25°C]) were measured with a multiprobe (WTW 350, Weilheim, Germany) at 1-m intervals at the deepest point of each lake. After measuring the Secchi depth of each lake, 0.5 L of a mixed water sample for hydrochemical analysis was collected with a hose sampler from the euphotic zone (Z_{Euph}), which was defined as $Z_{Euph} = 5 \times Z_{Secchi}^{0.5}$. Half of the sample was filtered onsite with 0.45 µm syringe filters for determination of major ions and nutrients, half of the sample was left unfiltered for determination of total phosphorus content. Both samples were stored in cleaned plastic bottles at 4 ° C before further processing. At the end of the second sampling day, the temperature loggers, together with the stones, were retrieved from the lakes (Figure 9).

Figure 9: The picture shows some central equipment of the lake sampling: Gravity corer, hose sampler and hydrophysical multiprobe as well as carriage systems. In the background, water samples are pre-processed on site using syringe filters. Photo credit: Lorenz Tschampel.

All chemical analysis were carried out at the Limnological Research Station Iffeldorf (LSI) of the Chair of Aquatic Systems Biology at Technical University Munich, Germany. Standard colorimetric methods using a Hitachi 150-200 photometer (Chiyoda, Japan) were applied to determine the concentrations of total phosphorus (Murphy and Riley, 1962), nitrate-N (Navone, 1964), ammonia-N (DIN, 1983) and silica. The content of major ions (calcium, magnesium, and sodium) was measured using a cation chromatograph (Thermo Scientific, ICS-1100, Waltham, USA) (Table 2).

Table 2: Averages and extreme values for the assessed chemical and physical parameters from the 43 lake set.

Parameter	Abbreviation	Minimum	Maximum	Mean	Median	Standard Deviation
Altitude (masl)	alt	760	2,469	1,598	1,600	429
Lake area (ha)	area	0.1	12	2.3	1.9	2.4
Maximum depth (m)	depth	1.3	20.7	7.8	5.5	5.9
Secchi depth (m)	secchi	1.3	11.3	4.6	4.2	2.5
Nitrate-N (mg/l)	NO_3	0.03	2.86	0.44	0.33	0.5
Total phosphorus (µg/l)	TP	1	20.41	6.92	6.62	4.6
Silicate-Si (mg/l)	Si	0.12	0.77	0.22	0.18	0.15
Ammonia-N (µg/l)	NH_4	3.84	126.85	36.45	25.29	27.49
Sodium (mg/l)	Na	0.1	2.11	0.38	0.23	0.42
Calcium (mg/l)	Ca	12.44	49.24	28.87	27.06	9.94
Magnesium (mg/l)	Mg	0.98	19.47	7.12	6.34	4.8
pH	pH	7.9	9	8.4	8.5	0.3
Oxygen (%)	O_2	5.1	129.8	93.4	96.9	23.8
Conductivity (µS/cm)	cond	121.4	536.7	226	208.6	78.2
Ø August bottom temperature(°C)	T_aug_bot	4.6	20.9	10	9.4	4
Ø August surface temperature (°C)	T_aug_surf	8.8	22.6	15.1	14.9	3.1

2.3 Diatom sampling and processing

Diatom samples were collected from the sediment surface, the littoral zone and the open water zone in all lakes. For obtaining sediment samples, a sediment core was collected using a gravity corer (Uwitec, Mondsee) and the uppermost centimetre of sediment was used for diatom analysis. Planktic diatoms were collected by taking one litre of water from the euphotic zone with the hose sampler (DIN, 2015a) and preserved with Lugol's solution (Throndsen, 1978a). Littoral diatoms were obtained from four to seven rocks – or other surfaces if no rocks were available – from depths between 20 and 50 cm. A new toothbrush and distilled water were used to scrub and rinse the biofilm of the stones. From all sampled lakes, periphytic diatom samples could be obtained at 34 sites. Sediment cores were hermetically sealed directly after recovering and all samples were kept at 4 °C until further processing.

To obtain planktic diatoms from the water samples these were filtered with 0.45 µm syringe filters and the residue on the filters was further processed (Nixdorf et al., 2014a). The residue on the filters, the sediment samples and the littoral samples were processed in the same way: Preparation of the diatoms was carried out according to van der Werff and Macan (1955). To analyse the composition of the diatom samples, 500 valves were identified in each case using a Leica DNM microscope (Wetzlar, Germany) at 1000-x magnification. Eleven of the 43 planktic samples were excluded from further analysis because they contained an insufficient number of valves. Taxa were counted at the species level or, if possible, at the subspecies level. Individuals that could not be identified were given working names. For diatoms with difficult morphology, especially centric diatoms, an electron microscope (Hitachi S-2300, Tokyo, Japan) was used under a magnification of 5,000 – 20,000. For preparation of the sample 50 µl of a sample dilution with reasonable distribution of diatoms was air dried onto a class cover slip (Ø 12 mm) and coated in gold with a Polaron SC502 Sputter Coater (Fisons Instruments, UK). Standard literature was used for identification (Krammer and Lange-Bertalot, 1991a, Krammer and Lange-Bertalot, 1991b, Krammer and Lange-Bertalot, 1997b, Krammer and Lange-Bertalot, 1997a, Krammer, 2000, Lange-Bertalot, 2001, Krammer, 2002, Lange-Bertalot et al., 2017).

2.4 Processing of data

All analysis were based either on raw community data (for predictive modelling approaches, e.g. in Chapter 3), Hellinger-transformed community data (for multivariate analysis of variance, e.g. in Chapter 5) or on metrics derived from the raw community data. These were species richness (α diversity), Shannon-diversity and β diversity. The latter was partitioned in its turnover and nestedness components and the contribution of single species and single sites was calculated (Baselga, 2013). For detailed information see Chapter 4 and 5. Moreover, based on the German Red List (RL) (Hofmann et al., 2018) for diatoms indices describing the richness, share and abundance share of RL taxa were calculated. For detailed information see Chapter 5.

2.5 Statistical methods

The statistical methods applied can be grouped into statistical tests, predictive modelling approaches and analysis of explained variance. Within these categories, methods were applied that can handle one-dimensional (“1”) or multidimensional patterns (“m”), i.e. the response of one variable or a set of variables (Table 3, Column D). The number of predictor variables can vary among the methods and is not further accounted for in this summary.

Moreover, within these categories methods were applied across a varying range of data, i.e. either to structures among environmental (“E”), spatial (“S”) and community (“C”) metrics or a combination (“co”) of them (Table 3, Column R). Table 3 contains all methods in the context that they were applied. Each of the methods is described in detail in the respective chapter (Chapter 3 - 5).

Table 3: The applied statistical methods can be assigned to statistical tests, predictive modelling approaches and analysis of variance. The methods were either applied in a one-dimensional (“1”) or multidimensional (“m”) context and on environmental, spatial and community data or on a combination of two or all datatypes.

D	R	Statistical test	Predictive modelling approach	Analysis of explained variance
1	**E**	Shapiro-Wilk-Test Kolmogorov-Smirnov-Test Levene´s-Test	Linear model	Pearson correlation
	S	Moran-Test of model residuals Moran´s I		
	C			Pearson correlation
	co		Linear model Generalized linear model Generalized additive model	Akaike Information Criterion
m	**E**			Principal component analysis
	S			Distance-based Moran´s eigenvector maps
	C			Principal component analysis
	co	Monte Carlo permutation test Mantel test Multivariate analysis of variance	Generalized linear model Generalized additive model	Redundancy analysis Variation partitioning

3 Identification of the ecological preferences of *Cyclotella comensis* in mountain lakes of the northern European Alps

A similar version of this chapter was published as: OSSYSSEK, S., GEIST, J., WERNER, P. & RAEDER, U. 2020. Identification of the ecological preferences of *Cyclotella comensis* in mountain lakes of the northern European Alps. Arctic, Antarctic, and Alpine Research, 52, 512-523.

Author contributions: This study was conceived by Stefan Ossyssek (SO) in consultation with Uta Raeder (UR), Jürgen Geist (JG) and Petra Werner (PW). On-site-measurements and laboratory analyses were carried out by SO. Diatom preparation and microscopic analyses was done by SO. Statistical analysis, visualisation and data interpretation was conducted by SO. The manuscript was drafted by SO and continuously refined, improved and edited by UR, JG and PW.

3.1 Abstract

Planktic diatom ecology in the mountain lakes of the northern European Alps has only been studied sparsely so far. To fill this knowledge gap, the driving parameters of planktic diatom assemblage composition in the euphotic zones of twenty lakes located between 955 and 2,060 masl were assessed. The mean August water temperature, concentration of major ions, total phosphorus and lake physical parameters explained significant amounts of variation within the diatom assemblages, as identified by redundancy analysis and consecutive backward selection. *Cyclotella comensis* was the most abundant taxon in these oligotrophic (<17 total phosphorus µg/L), phosphorus (P) limited, stratified study lakes, particularly when the calcium concentration was high (>35 mg/L). The results of generalized linear models and generalized additive models further revealed that August surface temperature, thermocline depth, and nitrate-N positively and significantly influenced *C. comensis* growth. These results shed light on the interplay between physical and chemical parameters as important drivers of *C. comensis* abundance in temperate mountain lakes. They may aid in the interpretation of past and the prediction of future climate-driven changes in planktic diatom composition in these lakes.

3.2 Introduction

Mountain lakes are often remote, and their catchments are therefore less affected by anthropogenic factors than the catchments of other lakes. This makes mountain lakes good sentinels for the study of environmental change (Catalan et al., 2013). As long-term monitoring data on water properties are often lacking, temporal changes are usually inferred through abiotic and biotic remains in lake sediments (Smol et al., 2002). In palaeolimnological studies, diatoms are well-established indicator organisms (Dixit et al., 1992, Scherer, 2002) as their silica cell walls are preserved well in lake sediments and their characteristic cell structure allows for species identification by light microscopy (Scherer, 2002). Diatoms have previously been used as indicators of pH, salinity, nutrient levels, mixing regimes and light conditions (Curtis et al., 2009, Flower and Battarbee, 1983, Lotter et al., 1997, Lotter et al., 1998, Saros et al., 2016, Winder et al., 2009). However, interpretation of palaeolimnological results requires in-depth knowledge of the relationships between environmental factors and diatom distribution (Smol et al., 2002).

A common approach to lake core analysis is the collection of training sets containing surface sediment samples with diatom assemblages representing the current state of lakes (e.g. Hall & Smoll, 1992). Whilst this approach has yielded valuable insights, it presents some limitations in terms of interpretation, as surface sediment samples commonly represent several years and many life cycles of diatoms whereas chemical measurements are usually only taken once. Hence, the need for better integration of ecological information in paleoecology is increasingly acknowledged (Davidson et al., 2018).

Little is known about what controls the abundant planktic diatom *Cyclotella comensis* across ecological gradients (Saros and Anderson, 2015). This species is an important component of many temperate lakes and shows pronounced reactions to climate change (Reavie et al., 2017, Rühland et al., 2008, Rühland et al., 2015, Winder et al., 2009). In terms of the distribution of this taxon, the interplay between environmental drivers such as lake temperature (Livingstone and Dokulil, 2001), mixing patterns (Kraemer et al., 2015), nutrient composition and turbidity (Whitehead et al., 2009) as well as competition with other planktic taxa (Jäger et al., 2008, Stomp et al., 2011) are important.

Within the northern European Alps, only one comprehensive study investigating the ecology of planktic diatoms including *C. comensis* exists (Wunsam et al., 1995). The lakes sampled in that study were mostly located at elevations below 1,500 masl, although many lakes in the region are found at higher elevations. Therefore, the present study examined the ecological preferences of planktic diatom assemblages in 20 mountain lakes, with special emphasis on the ecology of *C. comensis*. This study was designed to survey lakes along an elevational gradient from 955 to 2,060 masl. As the pH and total phosphorus (TP) gradients were short, it was hypothesised that changes in water temperature would influence planktic diatom assemblage composition along with concomitant changes in water chemistry (Reavie et al., 2017), i.e. nitrate concentration and turbidity.

3.3 Study Sites

The 20 study lakes are located in Bavaria (Germany) and Tyrol (Austria) along a longitudinal gradient of 220 km and a latitudinal gradient of 50 km (Figure 10).

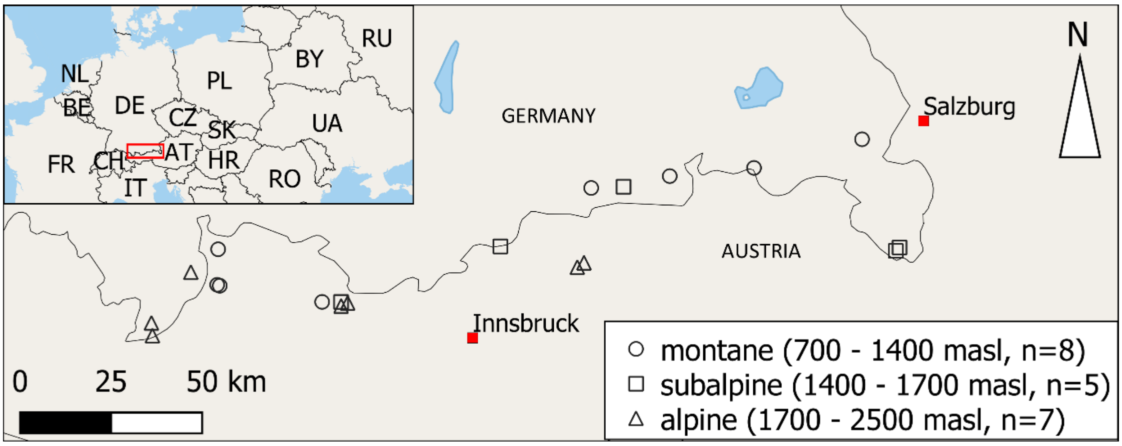

Figure 10: Geographical and zonal locations of the sampled lakes in the northern Alps in Austria and Germany. Background map based on Natural Earth data (2020).

Most of the lakes were formed by cirque glaciers. Typically, they are small (< 7 ha) and shallow (< 20 m) (Table 4), consisting of one main basin. Two of the lakes are karstic; they are nearly round and have a smaller surface area to volume ratio than lakes of glacial origin. The elevation of the 20 lakes ranged from 955 to 2060 masl (Table 4). Eight of the lakes were located in montane forest (750–1,400 masl), five were located in subalpine forest (1,400–1,700 masl) and seven were located in alpine meadows and rock basins (1,700–2,500 masl). In the study region, the montane forest is dominated by beech (*Fagus sylvatica*), spruce (*Picea abies*) and maple (*Acer pseudoplatanus*), whilst the subalpine forest mainly consists of spruce and—at the ecotone between forest and bare meadows—of pine (*Pinus mugo ssp. mugo*). In alpine meadows, shrubs (e.g. *Rhododendron hirsutum*), sedge meadows (e.g. *Carex sempervirens*) and fellfields predominate.

3.4 Methods

Sampling and laboratory procedures

The 20 lakes were sampled twice during the ice-free period, once between June and middle of August and once between August and November 2016. On the first sampling date, bathymetric measurements were taken with an echo sounder (Lawrence HDS8, Oslo, Norway) and a buoy fixed with a rope on a stone was subsequently installed at the deepest point of each lake. Temperature loggers (Onset Pendant UA-001-64 HOBO, Bourne, USA) were mounted on the rope 0.5 m above the sediment surface and 0.5 m below the water surface. Temperature data were recorded at 30 minute intervals between the first and second sampling date. On both sampling dates, physical parameters (temperature, oxygen saturation, pH and conductivity (at 25 °C)) were measured with a multiprobe (WTW 350, Weilheim, Germany) at 1 m intervals from the deepest point of each lake. After measuring the Secchi depth of each lake, 0.5 l of a mixed water sample was collected with a hose sampler from the euphotic zone (Z_{Euph}), which was defined as $Z_{Euph} = 5 \times Z_{Secchi}^{0.5}$ (DIN, 2015b). One half of the water sample was filtered (0.45 µm) on-site to analyse dissolved ions and the remaining sample was left unfiltered to analyse the concentration of TP. Both samples were stored at 4 °C for further processing in the laboratory. Another litre of water was taken from the euphotic zone with the hose sampler and preserved with Lugol's solution to analyse planktic diatom communities (Throndsen, 1978b). At the end of the second sampling day, the temperature loggers, together with the stones, were retrieved from the lakes. All chemical analyses were carried out in the laboratory of the Limnological Research Station in Iffeldorf. Standard colorimetric methods were applied using a Hitachi 150-200 photometer (Chiyoda, Japan) to determine the concentrations of TP (Murphy and Riley, 1962), nitrate-N (Navone, 1964), ammonia-N (DIN, 1983) and silica (DIN, 1983). The concentrations of major ions (calcium, magnesium, sodium) were measured using a cation chromatograph (Thermo Scientific, ICS-1100, Waltham, USA).

Planktic diatom samples were concentrated with 0.45 µm syringe filters before further processing (Nixdorf et al., 2014b). Diatoms were prepared according to van der Werff and Macan (1955). To analyse the composition of the diatom samples, 500 valves (including broken valves representing more than half of a complete valve) were identified in each case using a Leica DNM microscope at 1000× magnification. Taxa were counted at the species level. Standard literature was used for identification (Krammer and Lange-Bertalot, 1991a, Krammer and Lange-Bertalot, 1991b, Krammer and Lange-Bertalot, 1997b, Krammer and Lange-Bertalot, 1997a, Krammer, 2000, Krammer, 2002, Lange-Bertalot, 2001, Lange-Bertalot et al., 2017).

Data analysis

The atomic N/P ratios in lake water were calculated to determine pelagic nutrient limitation status by using the DIN/TP ratio (Bergström, 2010, Kolzau et al., 2014). Our dataset included only concentrations of nitrate-N and ammonia-N; nitrite-N was not measured. Therefore, the real DIN/TP ratio is probably higher than the results suggest. However, as nitrite occurs only at very low amounts under aerobic conditions, and the conditions in the euphotic zones of the sampled lakes were mostly aerobic, this bias is probably negligible. Moreover, all lakes were found to be P-limited and integration of nitrite-N would have shifted the N/P ratio further in this direction. The lake mixing regime was assessed by calculating thermocline depth and buoyancy frequency at the thermocline and within the epilimnion based on temperature profiles using the R package "rLakeAnalyzer" (Winslow et al., 2019). Sodium was excluded from further analysis as it could only be detected in a few samples.

With the obtained set of 19 abiotic parameters, a Pearson correlation matrix with Bonferroni-adjusted probabilities was computed (Haynes, 2013) using the R package "corrplot" (Wei and Simko, 2017a). For significantly correlated parameters, coefficients of linear regression models were included. To identify relationships among environmental variables, principal component analysis (PCA) was carried out with the datasets of 19 variables (Terbraak and Prentice, 1988). Before analysis, all environmental variables except pH and elevation were log transformed to correct for non-normal distribution (pH is a log scale and elevation showed a normal distribution). Further, the parameters were normalised by subtraction of the mean and division by the standard deviation for each variable (Oksanen et al., 2018).

The share of species with planktic life cycles was higher than 10% in all assemblages. For all calculations, benthic or tychoplanktic species were excluded and relative abundances were calculated based on the sum of obligate planktic species (Table S 2). Before numerical analysis, the dataset was Hellinger transformed (Prentice, 1980) and the obtained Hellinger distance matrices were used for PCA (Legendre and Gallagher, 2001). Before constrained analysis, variance inflation factors (VIFs) were calculated for the environmental data with the R package "usdm" (Naimi et al., 2014). To evaluate collinearity problems, the function "vifcor" of the "usdm" package was applied. According to the obtained results, no variable had collinearity problems. To evaluate whether diatom distribution followed a linear or unimodal trend, detrended correspondence analysis (DCA) was applied (Hill and Gauch, 1980). For gradient lengths < 3, linear constrained methods are considered appropriate; for gradient lengths between 3 and 4, linear or unimodal methods can fit; for higher gradient lengths, unimodal methods should be used (Terbraak and Prentice, 1988). The DCA gradient length was 3.51 for the first axis and 2.91 for the second axis. Based on the results of DCA and VIFs, an initial redundancy analysis (RDA) with the 14 initially measured variables was computed. The significance for the whole model and for the first and second RDA axis was assessed by means of a Monte Carlo permutation test with 999 permutations; all tests were significant ($p < 0.01$). For further evaluation of the importance of each single explaining variable, backward selection was applied (Blanchet et al., 2008). With the selected variables, another RDA was performed. As p-values decrease and R^2 values increase with the number of explanatory variables, adjusted model values (R^2_{adj}) were obtained through Bonferroni–Holm correction (Haynes, 2013). All models and each of the first two axes were significant as inferred by Monte Carlo permutation tests ($p < 0.01$). The explanatory potential and significance value of each single variable was obtained by setting the variable as the sole explanatory variable with all other variables as covariables in another round of Monte Carlo permutation tests. All multivariate analyses were carried out with the R package "vegan" (Oksanen et al., 2018).

To evaluate the correlation between environmental variables and *C. comensis,* generalised linear models (GLMs) were applied. For parameters with a significant influence on *C. comensis* based on GLM results and for further assumed important ecological drivers, generalised additive models (GAMs) were applied using the R package "gam" (Hastie, 2019). GAMs were used instead of GLMs when the responses of *C. comensis* to interacting parameters were assumed to be non-linear. All data analysis was carried out using the free statistics software R (version 3.6.3) (R Core Team, 2013).

3.5 Results

Physical and chemical features

The lakes were shallow (maximum depth 20.7 m, median depth 7.6 m) and small (< 6.4 ha). While most of the lakes can be assumed to stratify during summer, i.e. the sampling period, at least four of the lakes probably mix irregularly as they are very shallow (< 4 m) (Table 4). The Secchi depths of the lakes ranged from 1.5 m to 11.3 m (median = 4.6 m). At seven sites, the Secchi depth was equal to the maximum lake depth, i.e. light reached the bottom of the lake. The pH levels ranged from 7.9 to 9.0 (n = 20), reflecting the high concentration of alkaline earth ions; concentrations reached 49.2 mg/l for Ca^{2+} and 18.4 mg/l for Mg^{2+}. Accordingly, electrical conductivity averaged 251.5 µS/cm (reference temperature = 25 °C). The maximum conductivity level, which was more than 500 µS/cm, was recorded in one of the karstic lakes ('SieG'), which was strongly influenced by groundwater. Nitrate-N and TP concentrations were generally low with a mean of 0.39 mg/l and 6.1 µg/l, respectively, classifying most lakes as oligotrophic according to Vollenweider (1968). Based on N/P ratios, all lakes were P-limited (N/P > 43; *sensu* Klausmeier et al., 2004) and all but two lakes ('Eng', 'Rap') were co-limited by silica (Si/N < 1.12; *sensu* Brzezinski (1985). The ammonia -N concentration was low in most lakes (median 26.7 µg/l) but showed a wide range (3.8–126.9 µg/l), possibly due to oxygen depletion in the hypolimnion of a few lakes. The means of the average August surface and bottom water temperatures were 15.1 °C and 9.4 °C, respectively.

Table 4: Descriptive metrics of the measured and calculated environmental variables of the twenty-lake set.

Parameter	Abbre-viation	Min.	Max.	Mean	Me-dian	SD
Elevation (masl)	alt	955	2,060	1,491	1,537	373
Lake area (ha)	area	0.1	6.4	2.2	1.9	1.9
Maximum depth (m)	depth	1.5	20.7	9.3	7.4	6.4
Secchi depth (m)	secchi	1.5	11.3	5.3	4.6	2.91
Nitrate-N (mg/l)	NO3_N	0.03	0.93	0.39	0.41	0.27
Total phosphorus (µg/l)	TP	1.0	17.0	6.1	4.8	3.6
Silicate (mg/l)	Si	0.12	0.77	0.25	0.18	0.20
Ammonia-N (µg/l)	NH4_N	3.8	126.9	36.8	25.0	40.0
Calcium (mg/l)	Ca	14.97	49.24	31.62	30.53	9.29
Magnesium (mg/l)	Mg	1.42	18.40	6.90	5.20	4.60
pH value	pH	7.9	9.0	8.4	8.5	0.3
Conductivity (µS/cm)	cond	150.6	536.7	251.5	222.2	93.0
Ø August bottom temperature	T_B	4.5	18.4	9.4	8.8	4.0
Ø August surface temperature	T_S	8.8	22.6	15.1	14.5	3.8
Thermocline depth (m)	TCL	0.17	6.5	2.2	1.3	2.0
Ø Buoancy frequency Hypolim.	BFe_mean	0.0001	0.0067	0.001	0.001	<0.001
Buoancy frequency Thermocl.	BF_TCL	0.0001	0.0067	0.001	0.001	<0.001
Atomic Si to N ratio	Si_N	0.07	4.30	0.58	0.27	0.93
Atomic N to P ratio	N_P	44.38	4,442.2	890.8	537.4	1,173.9

The chemical parameters of the 20 study lakes varied along the elevation gradient, which was mainly correlated with PCA axis one (λ = 4.59, 24.17%) (Figure 11). Elevation was negatively correlated with conductivity, ammonia-N, nitrate-N, the N/P ratio, the August surface temperature and the Ca and Mg concentrations. It was positively correlated with pH and the Si/N ratio (Figure S 1, Figure S 2). The second PCA axis (λ = 3.97, 20.91%) was positively correlated with lake depth and Secchi depth, but negatively correlated with August surface and bottom temperatures, thermocline depth and buoyancy frequency. The positive correlation between lake depth and Secchi depth was highly significant and can be explained by seven lakes that had equal Secchi depths and maximum depths (Table S 1).

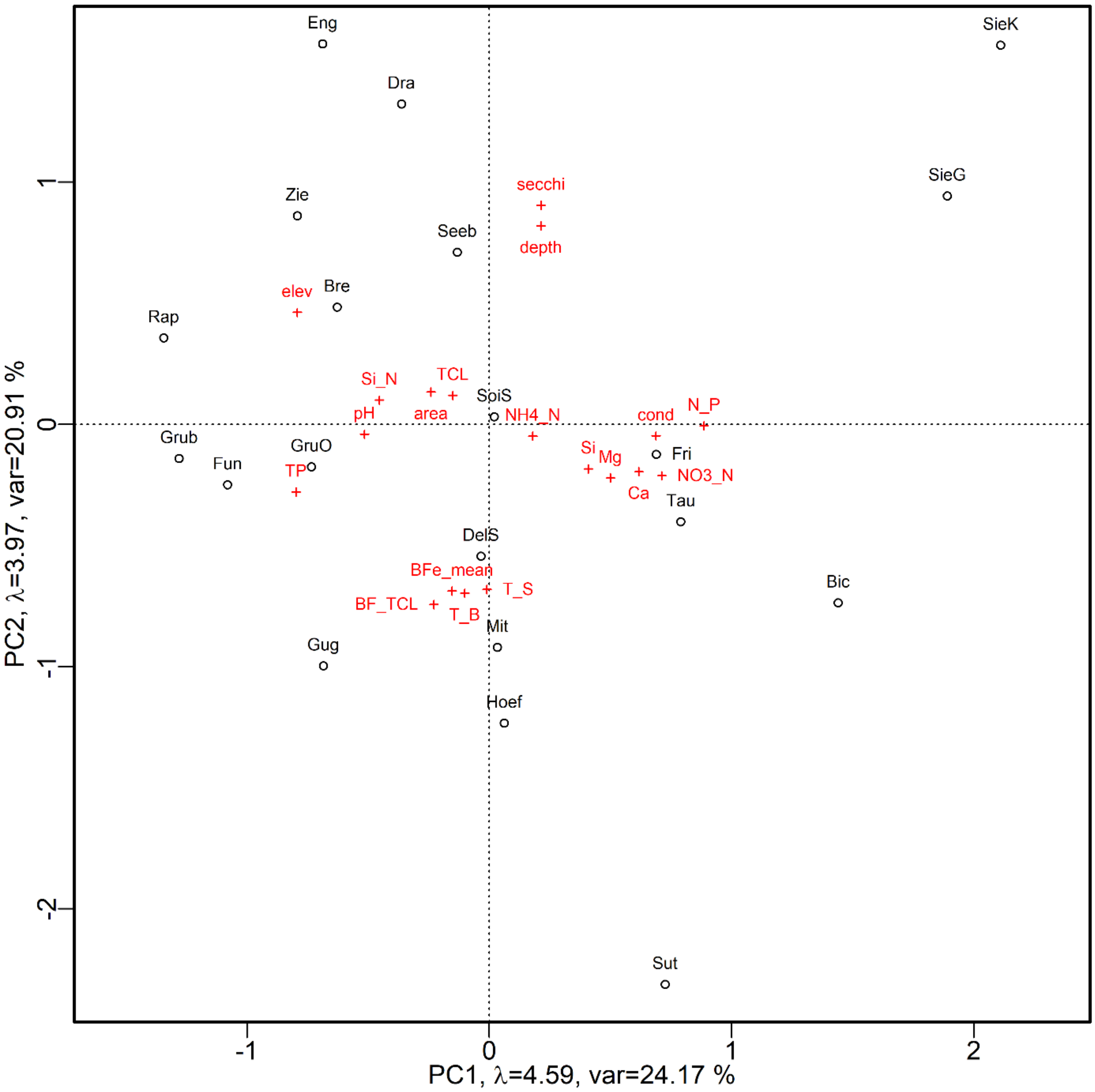

Figure 11: Principal component analysis correlation biplot for nineteen environmental variables measured in twenty mountain lakes in the northern European Alps. Principal components 1 and 2 (PC1, PC2) are plotted. λ indicates eigenvalues, var indicates percentage of explained variance. For variable and lake abbreviations, see Table S 1.

Bottom water temperature decreased significantly with maximum lake depth and Secchi depth and was positively correlated with surface water temperature. Buoyancy frequency at the thermocline and within the epilimnion were negatively correlated with Secchi depth, whilst thermocline depth was not correlated with any of the measured variables. Correlations among nutrients were significant for nitrate-N and ammonia-N (positive), nitrate-N and TP (negative), ammonia-N and Ca (positive) and nitrate-N and Ca (positive).

Diatom assemblages

Obligate planktic taxa occurred with relative abundances of 10.4% to 100% (median = 79.8%, n = 20) (Table S 2). Of the 14 identified planktic taxa, *C. comensis* was the most abundant (33 % of all planktic taxa, present in 10 lakes, abundance range = 0.4%–100%, median = 19%). Also abundant were *Fragilaria nanana* (21%), *Fragilaria delicatissima* (12%), *Discostella woltereckii* (10%), *Fragilaria gracilis* (8%) and *Discostella stelligeroides* (7%) (Table S 2).

Diatom–environment relationships

Variation in planktic taxa distribution was significantly influenced by the August surface temperature, lake area, Ca concentration, Secchi depth, Mg concentration, August bottom temperature and TP, which explained 11.6%, 7.6%, 6.6%, 5.3%, 5.2%, 5.1% and 4.6% of variation, respectively. The adjusted R^2 value of the full RDA model was 37.8 (Table 5).

Table 5: Adjusted R2 values for a planktic diatom RDA model with backward selected variables. Explained variance and p values were inferred from Monte Carlo permutation test.

Dataset	Variable	var. (%)	p
Plankton	**T_S**	11.6	0.001
n=20	**area**	7.6	0.007
R^2= 60.7 %	**Ca**	6.6	0.009
R^2_{adj} = 37.8	**secchi**	5.3	0.025
	Mg	5.2	0.026
	T_B	5.1	0.027
	TP	4.6	0.052

For the planktic diatom dataset, the first constrained RDA axis (λ = 0.172, var = 29.99%, p = 0.001) was negatively correlated with August surface and bottom temperature and TP. The second axis (λ = 0.079, var = 12.26%, p = 0.001) was negatively correlated with Mg concentration and positively correlated with Secchi depth and lake area (Figure 12). The RDA biplot revealed a preference of *C. comensis* for warm, calcium-rich lakes, whilst *Fragilaria nanana* showed the opposite preference. *Discostella woltereckii* was abundant in lakes with high Secchi depths, whilst *Fragilaria delicatissima* showed a preference for magnesium-rich waters (Figure 12).

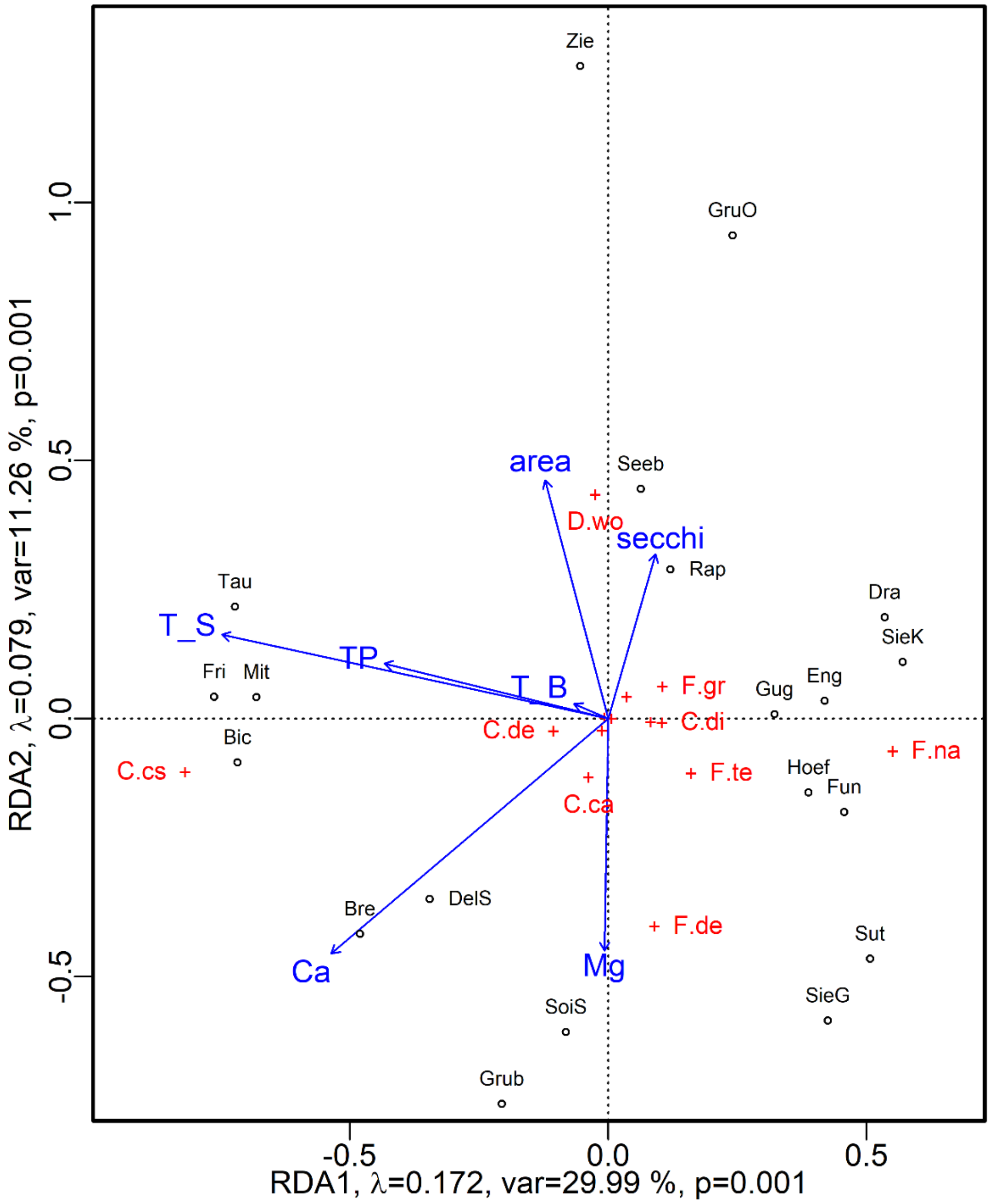

Figure 12: RDA correlation biplot of species scores and environmental parameters that significantly and independently influenced diatom taxon composition as determined by backward selection applied to RDA models for planktic diatom assemblages of twenty lakes. For variable, species, and lake abbreviations, see Table S 1and Table S 2.

The results of the GLMs confirmed the tight coupling of *C. comensis* abundance and August surface temperature ($p = 0.025$, $R^2 = 0.66$) and further revealed a significant positive influence of thermocline depth on *C. comensis* abundance ($p = 0.047$, $R^2 = 0.41$) (Figure 13). None of the models including the other parameters significantly predicted *C. comensis* abundance; however, high relative abundances of *C. comensis* were found in samples with Ca values above 35 mg/l, Secchi depths of 4 to 5 m and nitrogen-N levels of 0.5 to 1 mg/l. GLMs were also applied to all other taxa in the dataset; however, no model identified a significant correlation between these taxa and any of the measured variables.

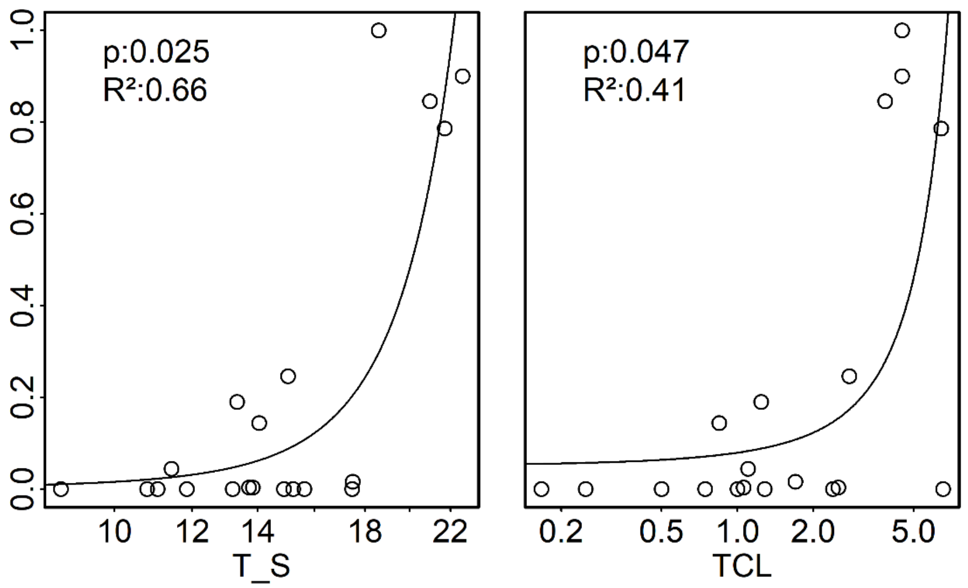

Figure 13: Relative abundances of *Cyclotella comensis* plotted against August surface temperature and thermocline depth. R^2 values and p values are given for generalized linear models; model prediction curves are plotted for significant models ($p < 0.05$). For abbreviations and units, see Table 4.

According to the GLM analysis, the relative abundance of *C. comensis* was significantly correlated with August surface temperature and thermocline depth. The GAMs also included nitrate-N as it was deemed to have an effect on *C. comensis* based on literature. For all three parameters, a significant GAM was found, with thermocline depth having the lowest AIC score and highest R^2_{adj} (Table 6).

Table 6: Model coefficients for generalized additive models for abundance of *Cyclotella comensis* in response to environmental variables that proved to be important for *Cyclotella comensis* abundance based on GLM results and are known to be ecologically important factors influencing the taxon. For abbreviations see Table 4.

Model	F value	p	R^2_{adj}	AIC
T_S	34.27	< 0.001	0.941	215.3
TCL	55.15	< 0.001	0.963	206.3
NO3_N	4.854	0.013	0.421	257.9
log(NO3_N)	3.946	0.017	0.507	256.0
Secchi	1.655	0.201	0.210	264.7
T_S + TCL			0.864	230.0
T_S	6.082	0.020		
TCL	6.570	0.002		
T_S + NO3_N			0.930	218.6
T_S	17.619	< 0.001		
NO3_N	4.793	0.018		
TCL + NO3_N			0.88	228.7
TCL	20.221	< 0.001		
NO3_N	6.774	0.021		

All combinations of parameters produced higher AIC scores, with August surface temperature and nitrate-N scoring lowest among all model combinations. The models suggested a pronounced increase in *C. comensis* abundance at lake surface temperatures above 18 °C and nitrate-N values above 0.8 mg/l (Figure 14).

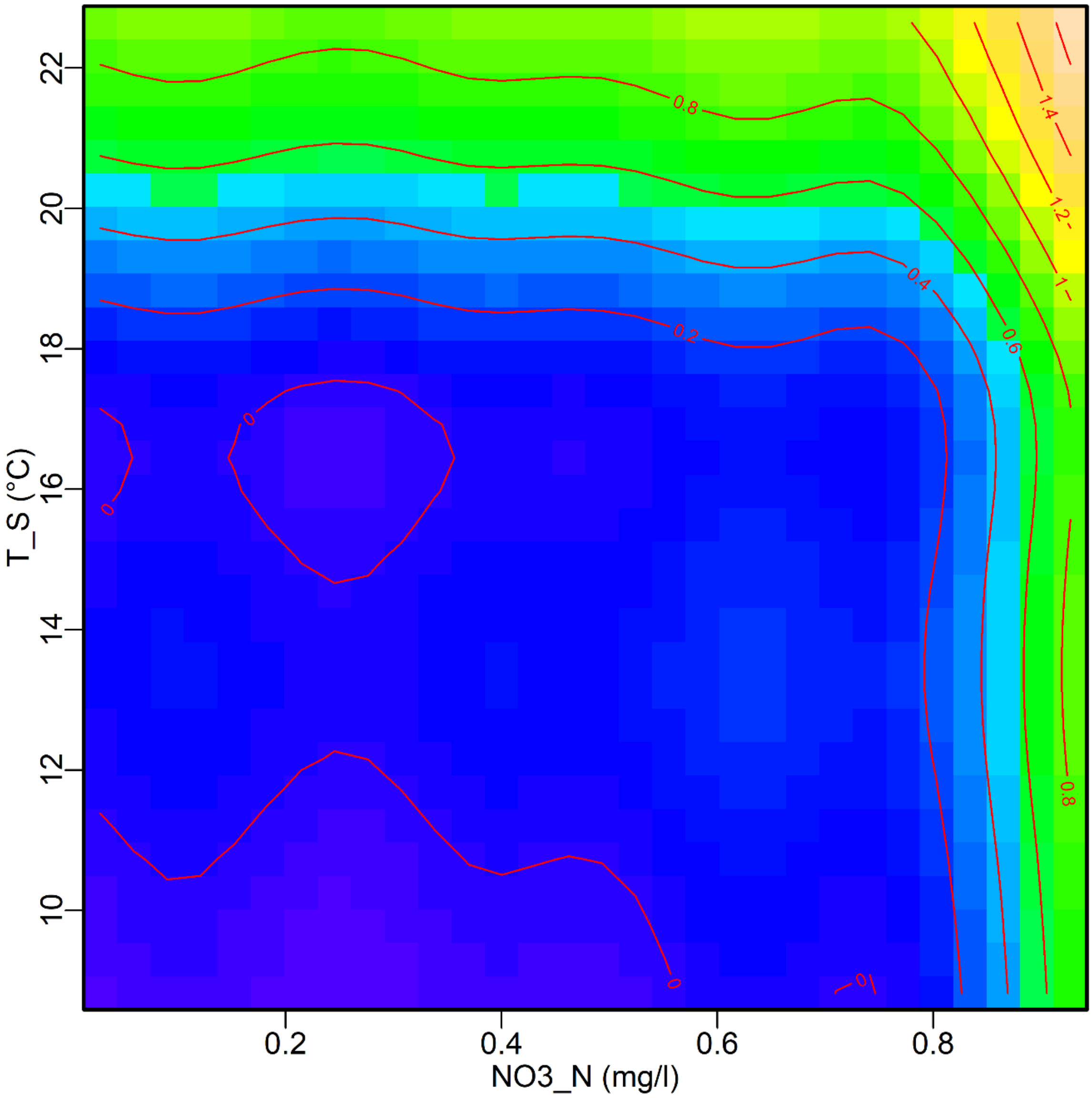

Figure 14: Generalized additive model results for the relative abundance of *Cyclotella comensis* and its interaction with August surface temperature and nitrogen-N. For model scores, see Table 6.

Cyclotella comensis was also particularly dominant in the planktic diatom assemblages when August surface water temperatures and nitrate-N concentrations were high (Figure 15).

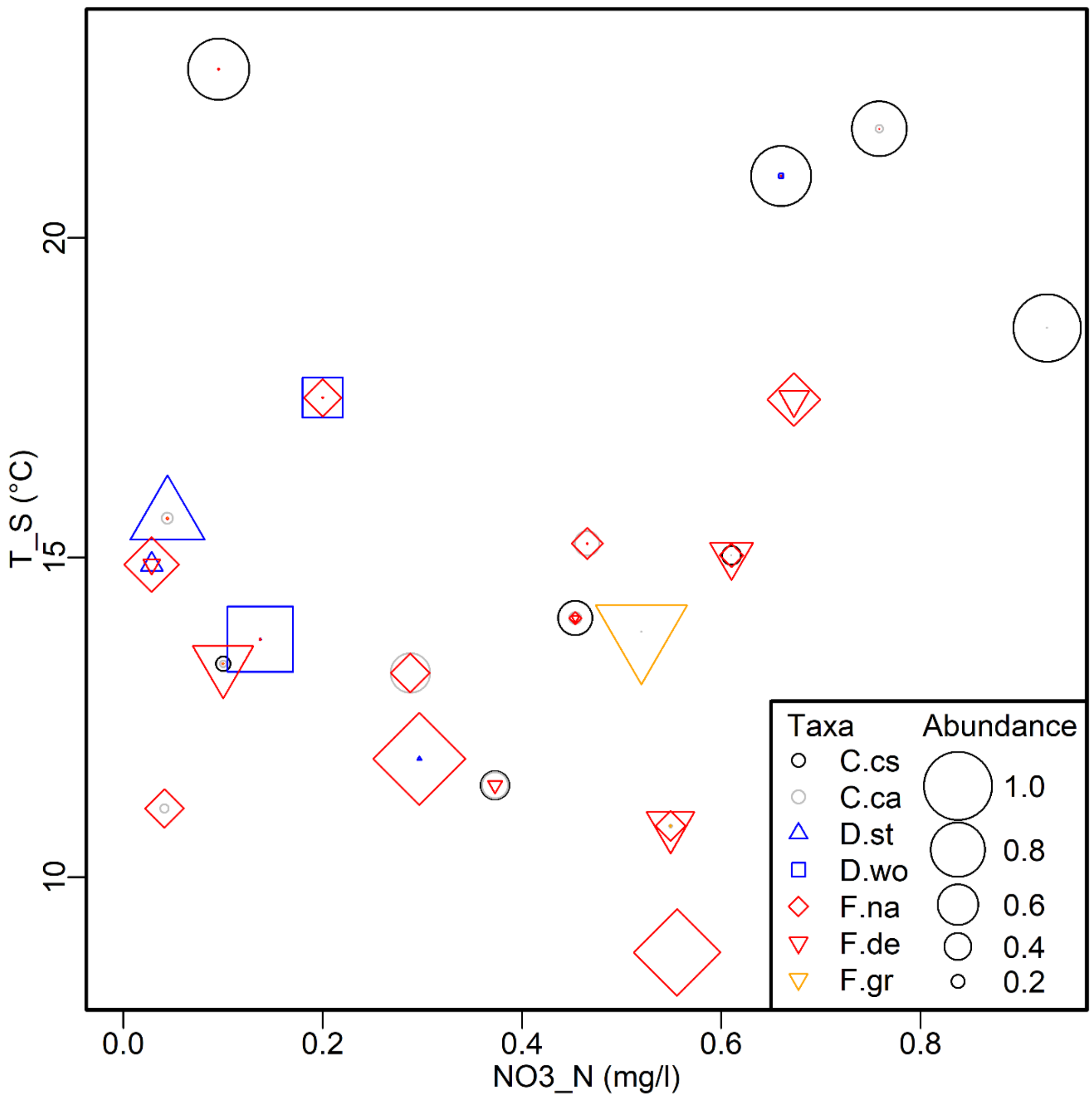

Figure 15: Scatterplot depicting relative abundances of the most frequent taxa in the data along the nitrate-N gradient and the August surface temperature gradient. The plotted taxa represent 93 percent of all counts. For species abbreviations, see Table S 2.

3.6 Discussion

Cyclotella comensis occurred at high abundance in the plankton communities of alkaline montane lakes with high August surface temperatures (> 18 °C) and thermocline depths of 4 to 5 m. The lakes were P-limited but rich in nitrogen (> 0.8 mg/l), giving high N/P ratios. Further, most of the lakes had intermediate Secchi depths (4–5 m, range = 1.5–11.3 m). The ecology of *C. comensis* has been the subject of numerous studies involving the combination of palaeolimnological lake data and recent observations (Lotter and Bigler, 2000), the compilation of training sets (Catalan et al., 2009, Curtis et al., 2009, Hall and Smol, 1992, Wunsam et al., 1995, Werner and Smol, 2006), investigations of *in situ* growth (Williamson et al., 2010a) and mesocosm experiments (Jäger et al., 2008).

Apart from one study that found *C. comensis* under slightly acidic conditions (Battarbee, 1984), this taxon prefers alkaline conditions with an optimum pH between 8 and 9 (Saros and Anderson, 2015, Scheffler et al., 2005, Werner and Smol, 2006). In line with this, all study lakes were alkaline in the present study (pH range = 7.9–9.0, median = 8.5), and *C. comensis* was especially abundant at the higher end of the Ca^{2+} gradient (35–49 mg/l; range = 15–49 mg/l, median = 27 mg/l).

Cyclotella comensis is generally rare at TP concentrations above ca. 10 µg/l (Hall and Smol, 1992, Ramstack et al., 2003, Saros et al., 2012, Saros and Anderson, 2015, Werner and Smol, 2006, Wunsam et al., 1995). In the present study, the taxon occurred only in one lake with a TP concentration above 10 µg/l (range = 1–17 µg/l, median = 5 µg/l). The results are in line with those of the only other comprehensive study on lake diatom ecology within the study region, which identified a TP optimum of < 15 µg/l for *C. comensis* (range = 2–266 µg TP/l) (Wunsam et al., 1995).

Despite the insights into *C. comensis* ecology that the present results provide, the responses of this taxon to environmental changes remain unclear in some respects. In particular, the interaction of epilimnetic water temperature with *C. comensis* (and the *Cyclotella sensu lato* complex in general) remains controversial, as there are various examples of increasing abundances of these taxa with higher temperatures (e.g. the present study, Pienitz et al., 1995, Catalan et al., 2002, Koinig et al., 2002), whilst there is also evidence for the opposite pattern (Weckstrom et al., 1997). Various studies have noted that increases in *C. comensis* abundance with increasing water temperature may reflect indirect limnological factors, such as interactive effects between water temperature and thermocline depth (Catalan and Fee, 1994, Catalan et al., 2002a, Huisman and Weissing, 1995, Huisman et al., 1999). The results of the present study demonstrate that thermocline depth has a significant effect on the abundance of *C. comensis* (Figure 13; GLM: $p = 0.047$, $R^2 = 0.41$; GAM: $p < 0.001$, $R^2_{adj} = 0.963$, lowest AIC among all significant parameters). The thermocline depth in small lakes in turn depends on several factors, including water temperature (Catalan et al., 2002), turbidity (Sadro and Melack, 2012, Strock et al., 2017) and fetch (France, 1997). In our dataset, none of the assessed variables, including mean August water temperature, were significantly correlated with thermocline depth (Table S 1). This finding indicates that multiple drivers may be relevant and that a single dominating driver of *C. comensis* abundance seems unlikely. However, turbidity and fetch were not assessed in the present study. Therefore, further research in these lakes should consider the importance of factors that control thermocline depth separately.

Interestingly, the results of the GAMs indicate interactive effects between thermocline depth, nutrients and *C. comensis* abundance ($F_{TCL} = 20.221$, $F_{NO3} = 6.774$, $p_{TCL} < 0.001$, $p_{NO3} = 0.021$, $R^2_{adj} = 0.88$, AIC = 228.7). The positive interactive effect of thermocline depth and nitrogen on *C. comensis* growth may be attributed to weaker phosphorus upcycling from the hypolimnion (Jager et al., 2010);

phosphorus is mostly released through internal hypolimnetic processes. Nitrogen input, in contrast, mainly comes from external sources (Rogora et al., 2018a, Schwefel et al., 2019). It was found that an increase in the N/P ratio can select for small centrics that have competitive advantages due to more effective nutrient uptake mechanisms (Malik et al., 2017, Tolotti et al., 2007, Tolotti et al., 2012). In experiments in which light and nutrient concentrations were varied, *Cyclotella bodanica* and *C. radiosa* showed especially high growth rates under P-limitation and moderate to low light conditions, but required sufficient nitrogen; i.e. their growth declined under colimitation of nitrogen (Malik et al., 2017). This can be explained by the fact that nitrogen is an important component of the light harvesting apparatus of these taxa, which supports sustained growth even under P-limitation. An increase in phosphorus can even be detrimental as it increases susceptibility to photoinhibition (Litchman, 2003). Hence, it is likely that increased thermocline depths offer superior nutrient conditions for *C. comensis,* leading to competitive advantages within the phytoplankton assemblage (Catalan et al., 2002a, Cantin et al., 2011, Jager et al., 2010, Jäger et al., 2008, Huisman et al., 2004, Williamson et al., 2010b). Under climate change, extreme precipitation events will become more frequent (Gobiet et al., 2014) and thus external input of nitrogen compounds into the study lakes will likely increase. Furthermore, the input of atmospheric nitrogen into high altitude lakes is increasing and it is likely that this trend will continue (Catalan et al., 2013). As a result, *C. comensis* may become more abundant in lakes at higher elevations within the study region.

This study further demonstrated a significant positive correlation between August surface water temperature and the relative abundance of *C. comensis* (Figure 13; GLM: $p = 0.025$, $R^2 = 0.66$; GAM: $F_{T\_S} = 34.27$, $p < 0.001$, $R^2_{adj} = 0.941$, AIC = 215.3). Epilimnetic water temperature was found to be correlated with various parameters that may in turn be relevant to *C. comensis* growth. These include the duration of ice cover (Catalan et al., 2002, Koinig et., 2002, Sorvari et al., 2002), the strength of summer stratification (Catalan et al., 2013, Korhola et al., 2002, Reavie et al., 2017, Rühland et al., 2008, Rühland et al., 2015, Saros et al., 2016b, Thompson et al., 2005), elevation and consequently catchment characteristics (e.g. Kamenik et al., 2001, Livingstone et al., 1999) as well as light availability (Malik et al., 2017, Saros and Anderson, 2015, Tolotti et al., 2012, Winder et al., 2009). All of these parameters in turn influence lake biogeochemical cycling (Catalan et al., 2002a, Catalan et al., 2002c). Based on the data of the present study, buoyancy frequency within the epilimnion (which corresponds to the strength of summer stratification) did not significantly influence *C. comensis* growth. However, August surface water temperature was negatively correlated with elevation, implicating possible interactions with variables that were not assessed, such as the duration of ice cover, which in turn depends on catchment characteristics and can influence light availability. Further research should integrate these possible secondary effects to further specify the influence of epilimnetic temperature on *C. comensis*.

3.7 Conclusions

The present study underscores the potential of the diatom *C. comensis* to be used as an indicator of rising lake temperatures under elevated nitrate concentrations. *Cyclotella comensis* abundance is indicative of relatively deep thermoclines, whereas the strength of summer stratification was not an important driver of *C. comensis* abundance within the sampled lakes. At present, the conditions in montane lakes of the northern European Alps are especially favourable for *C. comensis*. As temperatures rise, the tree line will shift upwards, catchment vegetation and soil formation will enhance and extreme precipitation events will become more frequent. All of these consequences of climate change will lead to higher input of organic compounds, including nitrate, into mountain lakes. Therefore, it is possible that *C. comensis* will also increase in abundance and possibly dominate lake plankton in subalpine or even alpine lakes in the future, if thermoclines are sufficiently deep and epilimnetic water temperatures continue to rise.

4 Sedimentary, planktic and littoral diatom metacommunities in mountain lakes of the northern European Alps show divergent assembly patterns

A similar version of this chapter is currently under review in Hydrobiologia.

Author contributions: This study was conceived by Stefan Ossyssek (SO) in consultation with Uta Raeder (UR) and Jürgen Geist (JG). On-site-measurements and laboratory analyses were carried out by SO. Diatom preparation and microscopic analyses was done by SO and Andrea Maria Hofmann (AMH). Statistical analysis, visualisation and data interpretation was conducted by SO. The manuscript was drafted by SO and continuously refined, improved and edited by UR, JG and AMH.

4.1 Abstract

This study analysed diversity patterns of sedimentary, littoral and planktic diatoms in 43 mountain lakes in the northern European Alps and identified processes that contribute to these patterns. Linear regression models showed a significant increase of sedimentary α-diversity with lake area and conductivity, and a negative trend along the elevational gradient, while the littoral diatom α-diversity increased significantly with conductivity and lake water temperature. Planktic diatom α-diversity significantly increased in shallow and small lakes. August water temperature, total phosphorus, conductivity, and lake depth explained a significant part of the variation and were significantly correlated with pairwise β-diversities in the data sets, but spatial and shared effects were more important for planktic and littoral diatoms. A null-model approach revealed that the structure of littoral and planktic assemblages was predominantly stochastic. In contrast, sedimentary diatoms were formed by both deterministic and stochastic processes. Abundant and widespread species contributed a large part to the assemblage β-diversity. The results point to a stronger role of niche assembly in sedimentary than for littoral and planktic diatoms. Dispersal limitation, in turn, is likely to contribute to the spatial patterns and stochastic assembly processes observed for littoral and planktic diatoms.

4.2 Introduction

Understanding the spatio-temporal patterns of diatom diversity is one of phycologists' most important goals. Species richness, i.e. α-diversity, and differences among local community composition, in other words β-diversities, contribute to a region's species diversity (Whittaker, 1972). Different patterns of diatom diversity were found for the two components. For example, there is evidence that harsh environmental conditions can lead to species-poor diatom assemblages in streams (Bae et al., 2011), while stream diatom β-diversity showed an unimodal relationship with altitude across several biogeographical regions (Wang et al., 2020a). Other studies highlight the importance of disturbance (Teittinen et al., 2016) and nutrients for stream diatom richness (Wang et al., 2011). Diatom diversity in lakes is known to be influenced by various local environmental factors such as total phosphorus, i.e. nutrient level (Rodriguez-Alcala et al., 2020) and pH (Pither and Aarssen, 2005). Moreover, the role of spatial factors for β-diversity patterns is more pronounced in lakes than in streams (Vilmi et al., 2017), with the importance of dispersal limitation increasing in more isolated lakes and ponds (Heino et al., 2015, Shurin et al., 2009). However, few studies have compared the diversity patterns of lake assemblages.

Single diatom assemblages from lakes are commonly used for biomonitoring or as paleolimnological proxies. In this context, it is important to ask if different assemblages within a lake respond to the same environmental drivers and if the influence of environmental and spatial constraints is consistent among assemblages. In a 468-lake set in the USA, Winegardner et al. (2015) found that environmental and spatial variables explained a similar part of the variance in sedimentary and planktic assemblages. They also found that productivity-related variables structured both sets of communities. Studies from tropical reservoirs are in line with these findings (Bartozek et al., 2019, Zorzal-Almeida et al., 2017). In turn, for planktic and benthic diatoms across south American lakes, a dominant role of spatial and topographical factors was detected, especially in mountain regions (Benito et al., 2018). Such analyses are still lacking for European lakes.

Consequently, this paper aimed to investigate if α- and β-diversity patterns are congruent among sedimentary, littoral and planktic diatoms in the mountain lakes of the northern European Alps. The relative contribution of local environmental variables and spatial predictors was evaluated and the importance of stochastic versus deterministic processes was measured. These complementary approaches were used to disentangle the effects of unmeasured yet important environmental factors and dispersal processes that both may lead to spatial patterns in community structure (Heino and Soininen, 2005, Soininen et al., 2007). Even though β-diversity results may be context-dependent, dispersal processes' strength depends on spatial scale (Graco-Roza et al., Leboucher et al., 2019, Soininen, 2007) and isolation (Ramos-Jiliberto et al., 2009); differences among assemblages may be representative for mountain regions elsewhere. Dispersal processes include dispersal limitation and excessive dispersal, so-called "mass effects". The latter may homogenise communities, and it was recently shown that some specific taxa may be affected more than others (e.g., Benito, Fritz, Steinitz-Kannan, Velez, McGlue, 2018, Blanco et al., 2020, Jamoneau, 2018, Leboucher, 2020). Thus, dispersal limitation and mass effects may operate simultaneously but may be disentangled by examining the individual species' contribution to β-diversity.

Based on the approaches mentioned, the following hypotheses were tested:

1. Along the altitudinal gradient, diatom α-diversity decreases as environmental conditions become harsher at higher altitudes, selecting for a few adapted species

2. The influence of spatial variables is weaker with sedimentary diatoms than with littoral and planktic diatoms due to the integration of introduced diatoms across several seasons

3. Dispersal limitation contributes to spatial patterns among littoral and planktic diatoms because most lakes are isolated

4.3 Study sites

The 43 study lakes are in Bavaria (Germany) and Tyrol (Austria) and span a longitudinal gradient of 220 km and a latitudinal gradient of 50 km (Figure 16).

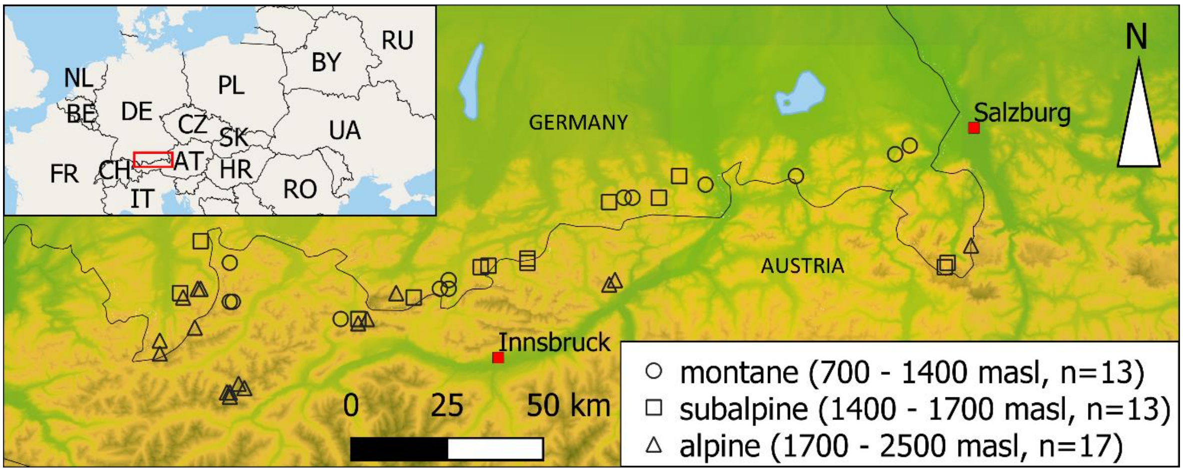

Figure 16: Geographical and zonal locations of the selected lakes in the northern Alps in Austria and Germany. Background map is based on SRTM Data.

Most lakes of this study are located on carbonate bedrock and are well-buffered, as reflected by their pH of between eight and nine (Table S 3). The altitudinal gradient comprises the vegetation zones of montane forest (750 – 1,400 masl), subalpine forest (1,400 – 1,700 masl) and alpine meadows (1,700 – 2,500 masl). In this region, the montane forest is dominated by beech (*Fagus sylvatica*), spruce (*Picea abies*) and maple (*Acer pseudoplatanus*); the subalpine forest mainly consists of spruce and pine at the ecotone to bare meadows (*Pinus mugo ssp. mugo*). In alpine meadows, shrubs (e.g., *Rhododendron hirsutum*), grasslands (e.g., *Carex sempervirens*) and fellfields mostly predominate.

Most lakes were formed by cirque glaciers and are typically small (< 3 ha) and shallow (<10 m) (Table S 3) with a single deep zone. Two of the lakes are karstic; they are nearly round and deeper than the other lakes in relation to their surface. Six of the lakes are polymictic, and macrophytes are found in 26 of the 43 lakes sampled.

4.4 Methods

Sampling and laboratory procedures

The 43 lakes were sampled twice during the ice-free period: once between June and mid-August and once between August and November. Thirty-six lakes were investigated In 2016 and seven in 2017. On the first sampling date, lake bathymetry was determined with an echo sounder (Lawrence HDS8, Oslo, Norway) and subsequently, a buoy was installed, attached by rope to a stone at the deepest point of each lake. Temperature loggers (Onset Pendant UA-001-64 HOBO, Bourne, USA) were mounted on the rope 0.5 m above the ground and 0.5 m below the water surface. During most of the ice-free period, the loggers in the lakes were exposed to assess the temperature regime and the lake's mixing type. On both sampling dates, physical variables (temperature, oxygen saturation, pH and electrical conductivity at 25 °C) were measured with a multiprobe (WTW 350, Weilheim, Germany) in one-metre steps above the deepest point of each lake. After measuring the Secchi depth, 0.5 litres of a mixed water sample - comprising the euphotic zone (CEN, 2015) - was collected with a hose sampler. One half of the water sample was filtered (0.45 µm) on-site and stored at 4 °C together with the unfiltered rest until further processing at the laboratory.

Another litre of water was taken from the euphotic zone with the hose sampler and preserved with Lugol's solution to analyse planktic diatom communities (Throndsen, 1978b). Planktic samples could only be taken from every lake on the first sampling date. Periphytic diatom assemblages were assessed by scraping off the diatom communities of five stones at depths of between 20 cm and 50 cm in the northern and southern littoral zone of each lake with a single-use toothbrush (DIN, 2014). At nine sites, no stones were present in the littoral zone. On the second sampling date, sediment cores were taken from the deepest point of each lake with a gravity corer (Uwitec, Mondsee, Austria) to assess the sedimentary diatom communities from all 43 lakes according to Kuefner et al. (2020a). Hence, three diatom assemblages could be sampled: planktic diatoms from the open water, periphytic diatoms from the northern littoral zone and sedimentary diatoms (the uppermost centimetre of each sediment core) from the deepest point of each lake.

All chemical analyses were carried out at the laboratory of the Limnological Research Station Iffeldorf at the Technical University of Munich, Germany. Standard colorimetric methods using a Hitachi 150-200 photometer (Chiyoda, Japan) were applied to determine the concentrations of total phosphorus (Murphy and Riley, 1962), nitrate-N (Navone, 1964), ammonia-N (DIN, 1983) and silica. The concentrations of major ions (calcium, magnesium, and sodium) were analysed using a cation chromatograph (Thermo Scientific, ICS-1100, Waltham, USA).

Planktic diatom samples (1 L) were filtered with 0.45 µm syringe filters, and the residue on the filters was further processed (Nixdorf et al., 2014a). The uppermost centimetre of each sediment core was used to assess the sedimentary diatom assemblages present. The residue of the filters of the planktic samples, the sediment samples and the littoral samples were processed in the same way: preparation of the diatoms was carried out according to van der Werff and Macan (1955). A total of 500 valves were identified in each case using a Leica DNM microscope (Wetzlar, Germany) at 1000-x magnification to analyse the composition of the diatom samples. Eleven of the 43 planktic samples were excluded from the data analysis because they contained an insufficient number of valves. Taxa were counted at the species level and where possible, at the subspecies level. Individuals that could not be identified were given working names. Standard literature was used for identification (Krammer and Lange-Bertalot, 1991a, Krammer and Lange-Bertalot, 1991b, Krammer and Lange-Bertalot, 1997b, Krammer and Lange-Bertalot, 1997a, Krammer, 2000, Lange-Bertalot, 2001, Krammer, 2002, Lange-Bertalot et al., 2017).

Data analysis

For each sample of the three assemblages, α-diversity was computed as species richness and Shannon diversity. Both measures of α-diversity were included as they are frequently used in the context of conservation (Spellerberg and Fedor, 2003) but may reveal different patterns along environmental gradients (Stirling and Wilsey, 2001). Differences in mean α-diversity among the assemblages were assessed with the Wilcoxon Test as diversities were not distributed normally (Wilcoxon, 1945). Relations between environmental variables and α-diversity measures were investigated using linear regression models and multiple R^2-values were calculated for significant models.

The mean and pairwise β-diversity of diatom communities was calculated for sedimentary, littoral and planktic assemblages for abundance and incidence data, based on the method proposed by Baselga and Orme (2012). For the abundance data, the multiple-site Bray-Curtis dissimilarity (β_{tot}) was computed and then partitioned into its “abundance balanced variation” (β_{bal}) and “abundance gradients” (β_{gra}) components (Baselga, 2017). For incidence data, β-diversity was calculated as a Simpson diversity (β_{sim}) and then partitioned into its component for turnover (representing the Sorensen dissimilarity which measures species replacement) (β_{sor}) and nestedness (representing the nestedness component of the Sorensen dissimilarity, reflecting species loss) (β_{sne}) following Baselga (2010). The contribution to abundance and incidence-based β-diversity (SCBD) of each species was assessed according to Legendre and De Caceres (2013). The relationship between SCBD-values and species abundance and occurrence was modelled using polynomial regression models.

The β-diversity variation among lakes was investigated by distance decay analysis (Dray, 2020). The effect of spatial, environmental and altitudinal distance on total β-diversity ($β_{tot}$, $β_{sim}$) and its components ($β_{bal}$, $β_{gra}$, $β_{sor}$, $β_{sne}$) was investigated with partial Mantel tests (Borcard et al., 1992). Significance levels and r-values were calculated for each combination while controlling for the other distance matrices to obtain the exclusive effect values of the factor of interest. The decay of assemblage similarity with spatial, altitudinal and environmental distance was assessed by fitting negative exponential functions using the "decay.model" function in the "beta part" package (Baselga and Orme, 2012). Distance decay analysis of the abundance and incidence data was complemented with variation partitioning to investigate the proportion of variance explained by environmental and spatial variables using Euclidean distances (Borcard et al., 1992).

To choose the environmental variables used in distance decay analysis and variation partitioning, separate redundancy analysis (RDA) models for sedimentary, littoral and planktic diatom assemblages were computed based on Hellinger-transformed assemblage data (Legendre and Gallagher, 2001). Only variables with variance inflation factors less than five for all data sets were included in the RDAs. VIF´s were calculated and variables were selected with the "step.vif" function in the "usdm" R package (Naimi, 2017). The same ten variables were selected for each dataset and used for all further calculations. Pearson correlations were calculated for these variables, and p-values were Bonferroni-Holm-corrected. Based on the results, correlation plots were produced using the "corrplot" function to identify significantly correlated variables (Wei and Simko, 2017b). All variables except for altitude and pH were log transformed and the full data set was scaled before RDA using the "scale" function in "vegan." Only variables that were identified by forward selection using the "ordiR2step" function in "vegan" ($p < 0.05$) were incorporated into the final environmental distance matrix (Blanchet et al., 2008). The altitudinal distance matrix used in distance decay analysis and variation partitioning was calculated based on Euclidean distances between sites. Distance-based Moran´s eigenvector maps (db MEM) based on the geographical coordinates of the lakes were used in variation partitioning (Dray et al., 2006) to explore spatial effects. Eigenvectors were selected using the "mem.select" function in the "ade4" R package. This function runs a forward selection based on R^2-values after a global test of significance (Bauman et al., 2018). The significance of each MEM was assessed with the "moran.randtest" function that computes Moran´s index and calculates p-values using random permutations. To measure the relative strength of stochastic versus deterministic processes, a null-model approach was applied using the "tNST" function in the "NST" R package (Ning et al., 2019). Null-models were calculated for all three diatom data sets and abundance data using the Bray-Curtis distance and incidence data using the Jaccard index. This function produces results ranging from 0 to 100, with values below 50, indicating a prevalence of deterministic processes and values above 50, denoting stochasticity. The results for the data sets were compared by ANOVA, PANOVA and

PERMANOVA with 1000 resampling runs. All the analyses were computed using version 3.6.6 of the "R" free statistics software, except for NST analysis, which was conducted using version 4.1.3 (R Core Team, 2013). Data curation was facilitated using the "dplyr" package (Wickham and François, 2014).

4.5 Results

Environmental variables

Variables with VIFs < 5 were altitude ("alt"), lake area ("area"), lake depth ("depth"), nitrate ("NO3"), total phosphorus ("TP"), silicate ("Si"), pH, conductivity ("cond"), August bottom temperature ("ABT") and August surface temperature ("AST"). A significant negative Pearson correlation was found in all data sets between conductivity and altitude, conductivity and pH and ABT and depth ($p < 0.05$, Figure S 15).

α-diversity

The mean species richness and Shannon diversity were significantly higher for sedimentary and littoral diatom assemblages than for planktic assemblages (Wilcoxon Test, $p < 0.001$; Figure 17).

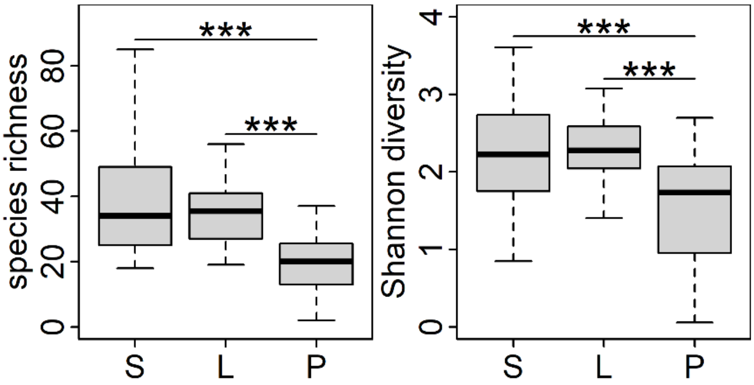

Figure 17: Boxplots for species richness and Shannon diversity in sedimentary ("S", n=43), littoral ("L", n=34) and planktic ("P", n=32) diatom assemblages. Asterisks indicate significantly higher mean values for sedimentary and littoral data compared to planktic data (Wilcoxon Test: $P < 0.001$).

Species richness of sedimentary samples was negatively correlated to altitude ($p = 0.02$, $R^2 = 0.10$) and positively correlated to area ($p < 0.001$, $R^2 = 0.21$), depth ($p = 0.02$, $R^2 = 0.10$) and conductivity ($p = 0.01$, $R^2 = 0.12$). Positive correlations were detected between littoral diatom richness and conductivity ($p = 0.04$, $R^2 = 0.10$), ABT ($p < 0.001$, $R^2 = 0.22$) and AST ($p = 0.01$, $R^2 = 0.18$), while a negative correlation was found for planktic diatom richness and depth ($p = 0.01$, $R^2 = 0.17$, Figure S 5). The Shannon diversity of sedimentary diatom assemblages was positively correlated with area ($p = 0.04$, $R^2 = 0.08$) and positively correlated with conductivity ($p = 0.04$, $R^2 = 0.10$) for littoral diatoms. The Shannon diversity of planktic diatoms was negatively correlated to area ($p < 0.001$, $R^2=0.21$) and depth ($p < 0.001$, $R^2 = 0.24$, Figure S 6).

β-diversity and community assembly

The β-diversities among the lakes were generally high (β_{tot}: 0.925 - 0.964), and the component for the balanced variation and turnover always accounted for the main part of the total β-diversity (Table 7).

Table 7: Mean β-diversity values for abundance and incidence data for sedimentary ("S"), littoral ("L") and planktic ("P") diatom assemblages.

	β_{tot}	β_{gra}	β_{bal}	β_{sor}	β_{sne}	β_{sim}
S	0.964	0.002	0.962	0.954	0.022	0.932
L	0.925	0.003	0.922	0.926	0.020	0.906
P	0.954	0.007	0.947	0.942	0.033	0.909

Significant variables of the RDA models chosen by forward selection ($p < 0.05$) were TP, AST, and depth for sedimentary and planktic diatom assemblages. Conductivity and AST had a significant effect on littoral diatoms (Table 8).

Table 8: Percent of explained variance ("Var."), F-values and p-values based on Monte Carlo permutation tests for variables selected by forward selection for sedimentary ("S"), littoral ("L") and planktic ("P") diatom communities.

	ANOVA			
	Variable	**Var. (%)**	**F**	**p**
S	depth	2.7	1.83	0.013
	TP	3.7	2.51	0.002
	AST	2.9	1.96	0.006
L	cond	2.1	1.87	0.016
	AST	2.7	2.41	0.005
P	depth	6.1	3.06	0.006
	TP	5.2	2.63	0.006
	AST	4.0	2.04	0.025

Mantel tests and regression models produced similar results when comparing species dissimilarity with environmental, geographical, and altitudinal distance (bold values in Table 9). For five combinations, either Mantel tests or regression models indicated a significant correlation (grey shading in Table 3). The abundance- and incidence-based dissimilarity of all assemblages increased significantly with increasing environmental distance. Planktic assemblages were significantly less similar with increasing lake distance, while for littoral diatoms, this was only true for the components representing Simpson diversity and abundance gradients. Dissimilarity of sedimentary incidence data significantly decreased with altitudinal distance (Table 9, Figure S 7 - Figure S 12).

Table 9: Model statistics for partial Mantel tests and exponential regression models for the distance decay of β-diversity along with environmental distance, geographical distance, and altitudinal distance for sedimentary ("S"), littoral ("L") and planktic ("P") assemblages. Statistical tests and regression models were calculated for pairwise β-diversity values derived from incidence data (βsor) and its components for turnover and nestedness (βsim, βsne) as well as for abundance data (βtot) and its components for balanced variation and abundance gradients (βbal, βgrad). p = P-value, r = Mantel r-value, ps. R^2= pseudo R^2. Bold font (of numbers) indicates the significance of both the Mantel test and the exponential regression model, and grey shading indicates the significance of either the Mantel test or the exponential regression model.

	S				**L**				**P**			
	Mantel Test		**Regression**		**Mantel Test**		**Regression**		**Mantel Test**		**Regression**	
	p	**r**	**p**	**ps. R^2**	**p**	**r**	**p**	**ps. R^2**	**p**	**r**	**p**	**ps. R^2**
	environmental distance											
β_{sim}	**0.001**	**0.019**	**0.044**	**0.010**	0.103	0.125	0.200	0.016	0.242	0.041	0.520	0.002
β_{sne}	0.743	0.452	0.002	0.510	0.194	0.082	0.360	0.006	0.342	0.025	0.800	0.001
β_{sor}	0.001	0.091	0.060	0.010	**0.007**	**0.226**	**0.010**	**0.052**	0.148	0.083	0.340	0.007
β_{bal}	**0.007**	**0.166**	**0.010**	**0.027**	**0.018**	**0.204**	**0.020**	**0.042**	**0.014**	**0.170**	**0.010**	**0.032**
β_{grad}	0.779	-0.051	0.500	0.003	0.770	-0.103	0.550	0.008	0.362	0.029	0.750	0.001
β_{tot}	**0.005**	**0.171**	**0.010**	**0.029**	**0.026**	**0.193**	**0.030**	**0.038**	**0.002**	**0.215**	**0.010**	**0.048**
	geographical distance											
β_{sim}	0.324	0.023	0.122	0.009	**0.024**	**0.153**	**0.043**	**0.024**	**0.004**	**0.173**	**0.004**	**0.031**
β_{sne}	0.536	-0.008	0.198	0.005	0.998	-0.139	0.045	0.019	0.504	-0.009	0.887	0.001
β_{sor}	0.319	0.024	0.283	0.004	0.089	0.095	0.148	0.009	**0.008**	**0.223**	**0.008**	**0.054**
β_{bal}	0.320	0.023	0.679	0.001	0.380	0.001	0.765	0.001	**0.001**	**0.287**	**0.001**	**0.100**
β_{grad}	0.530	-0.008	0.904	0.001	**0.001**	**0.150**	**0.001**	**0.201**	0.999	-0.187	0.037	0.034
β_{tot}	0.320	0.024	0.653	0.001	0.117	0.004	0.218	0.009	**0.002**	**0.230**	**0.001**	**0.063**
	altitudinal distance											
β_{sim}	0.060	0.095	0.030	0.017	0.297	0.042	0.244	0.008	0.158	0.055	0.276	0.004
β_{sne}	0.408	0.009	0.995	0.001	0.487	-0.003	0.689	0.001	0.687	-0.037	0.649	0.001
β_{sor}	**0.019**	**0.138**	**0.006**	**0.032**	0.234	0.054	0.032	0.021	0.301	0.036	0.496	0.003
β_{bal}	0.131	0.065	0.094	0.009	0.979	-0.155	0.498	0.003	0.286	0.036	0.322	0.005
β_{grad}	0.972	-0.103	0.059	0.012	0.926	-0.129	0.101	0.024	0.494	-0.008	0.979	0.001
β_{tot}	0.156	0.060	0.116	0.008	0.991	-0.178	0.337	0.006	0.268	0.039	0.212	0.006

The contribution of individual species to β-diversity (SCBD) correlated well with species abundance and the number of lakes (N_{lake}) for all data sets using species incidence and abundance data, except for sedimentary and littoral species incidence data (Figure S 13, Figure S 14). The most abundant species had above-average SCBD-values, indicating that these species do not homogenise diatom metacommunities. Selected eigenvectors based on Hellinger-transformed abundance data were MEM 1 (Sed., $p_1 = 0.008$), MEM 3 and 12 (Lit., $p_3 = 0.024$, $p_{12} = 0.041$) and MEM 1,2,6 and 7 (Pla., $p_{1,2,6} =$

0.006, p_7 = 0.042) for sedimentary, littoral, and planktic assemblages, respectively. Based on incidence data MEM 3 and 5 (Sed., p_3 = 0.020, p_5 = 0.009), MEM 1,2,3 and 12 (Lit., p_1 = 0.49, p_2 = 0.007, p_3 = 0.022, p_{12} = 0.009) and MEM 1,2 and 9 (Pla., $p_{1,9}$ = 0.005, p_2 = 0.002) were selected for sedimentary, littoral, and planktic assemblages, respectively.

Results for variation partitioning confirmed the principal patterns detected by distance decay analysis. The forward selected variables explained a significant part of variance for all assemblages. The MEMs selected had a greater explanatory power for littoral and planktic assemblages than for sedimentary diatoms. This also accounted for explained variation through shared effects. Unexplained variation was generally lower when using abundance data (Table 10).

Table 10: Variation partitioning results for the pure and shared fraction (indicated by "+") of variance explained by environmental ("E"), spatial ("S") and altitudinal ("A") distance as well as unexplained variance ("U") for abundance and incidence data of sedimentary ("S"), littoral ("L"), and planktic ("P") diatom assemblages.

	Abundance			**Incidence**		
	S	**L**	**P**	**S**	**L**	**P**
E	5	1	7	2	3	4
S	1	2	8	1	4	5
A	0	0	1	1	0	2
E + S	0	3	5	0	0	2
E + A	1	4	0	0	2	0
S + A	0	0	1	0	0	0
E + S + A	0	0	3	1	0	1
U	91	91	78	95	90	87

Null models based on abundance and incidence data indicate a strong stochastic influence on littoral and planktic communities. Assembly processes were significantly different for sedimentary diatoms, showing a more balanced deterministic and stochastic influence (Table 11).

Table 11: NTS results ("NTS"), standard deviation ("SD") as well as the F-statistic and p-values for ANOVA, PANOVA and PERMANOVA for pairwise comparison of NTS-values for sedimentary ("S"), littoral ("L") and planktic ("P") assemblages based on Bray-Curtis distance ("BC") and Jaccard index ("JA"). Bold font (of numbers) indicates significance ($p < 0.05$).

Group 1	**Group 2**	**NTS 1**	**NTS 2**	**SD 1**	**SD 2**	Δ_{NTS1_NTS2}	**F**	p_{anova}	p_{panova}	p_{perm}
S_{BC}	L_{BC}	0.492	0.901	0.059	0.039	-0.409	107.658	**< 0.001**	**0.001**	**< 0.001**
S_{BC}	P_{BC}	0.492	0.796	0.059	0.074	-0.304	10.014	**0.001**	**0.004**	**0.001**
L_{BC}	P_{BC}	0.901	0.796	0.039	0.074	0.105	7.063	**0.008**	0.211	0.453
S_{JA}	L_{JA}	0.606	0.893	0.071	0.049	-0.287	330.712	**< 0.001**	**0.004**	**< 0.001**
S_{JA}	P_{JA}	0.606	0.768	0.071	0.079	-0.162	74.999	**< 0.001**	0.106	**0.035**
L_{JA}	P_{JA}	0.893	0.768	0.049	0.079	0.125	6.441	**< 0.001**	0.126	0.469

4.6 Discussion

We compared the patterns of diatom α- and β-diversity for sedimentary, littoral and planktic assemblages within a 43-lake set across the montane, subalpine and alpine region in the northern European Alps. Diatom α-diversity was correlated to altitude, lake depth and area, water temperature and conductivity. The variables explaining a significant portion of community composition were total phosphorus, AST and lake depth for sedimentary and planktic diatoms, as well as AST and conductivity for littoral diatoms. Spatial descriptors and spatial distance were important in explaining littoral and planktic diatom community structure, and stochastic community assembly dominated in both groups. In contrast, deterministic and stochastic processes were equally important for sedimentary diatoms and spatial patterns were subordinate.

Niche assembly

Our hypothesis that α-diversity decreases with altitude holds true for sedimentary diatom richness, but other variables additionally explained the variation in α-diversity for all data sets. This underpins the high variability in local diatom diversity patterns along the elevational gradient. For example, in subarctic mountain ponds (Heikkinen et al., 2022) and streams (Teittinen et al., 2016), no significant richness-elevation pattern was found, while an unimodal relationship was detected for a different set of subarctic ponds (Teittinen et al., 2017) and a monotonic positive relationship was found for Swiss mountain springs (Taxbock et al., 2020). Combined with these studies, our findings point to the importance of additional mechanisms that act independently of altitude in forming local diatom diversity.

The positive correlation of conductivity with littoral and sedimentary α-diversity that was detected probably reflects an influence of alkalinity because, in our dataset, the concentration of calcium and magnesium correlated highly with conductivity (Ossyssek et al., 2022b). This is in line with the monotonic increase of benthic diatom richness with alkalinity in US streams (Smucker and Vis, 2011), the decrease of diatom richness in fens along a gradient from calcareous to mineral-poor conditions in the western Carpathians (Frankova et al., 2009) and the increase in epilithic diatom richness with conductivity in Swiss mountain springs (Taxbock et al., 2020). The important role of alkalinity in diatom community structure is beyond doubt (e.g. Wilson & Gajewski, 2002), and the classification of diatom indicator taxa according to the alkalinity of lakes suggests species-specific optima (Jarvinen et al., 2013). Based on the positive correlation of alkalinity and dissolved inorganic carbon (i.e. HCO_3^- under near-neutral pH values), Baattrup-Pedersen et al. (2022) suggest that species-specific alkalinity preferences may be coupled to different HCO_3^- uptake efficiencies. Moreover, carbon metabolism in diatoms depends on phosphorus limitation and is species-specific, potentially influencing niche partitioning among taxa (Brembu et al., 2017). Thus, it is likely that alkalinity has a direct effect on diatom α-diversity. However, we do acknowledge that the intercorrelation of conductivity and elevation may mask a direct effect of elevation on diatom richness, as suggested by Teittinen et al. (2017).

For sedimentary diatoms, the correlation of lake area and depth with α-diversity likely reflects an influence of increasing habitat diversity, which was correlated to diatom richness in streams and springs (Smucker and Vis, 2011, Taxbock et al., 2020). Sedimentary assemblages integrate diatoms from the whole lake including the pelagic and littoral zone through taphonomic processes (Smol et al., 2001) and thus reflect the diversity of habitats that is likely to increase with lake size. For planktic diatoms, the correlation of lake depth and AST probably reflect an effect of lake mixing conditions on α-diversity, indicated by the high number of benthic species in shallow and polymictic lakes. In turn, deep and warm lakes, that tend to be stratified, are frequently dominated by one or only a few taxa (Ossyssek et al., 2020). Our results further show that Shannon diversity and species richness are not interchangeable as a measure of α-diversity, as they are correlated with different environmental variables in some cases. This calls for the application of both measures in diatom studies to assure better comparability. Overall, our results only give a weak indication of the elevational structuring of diatom richness in mountain lakes in the northern European Alps and reveal different processes that control α-diversity among sedimentary, littoral and planktic assemblages.

As hypothesised, sedimentary diatom β-diversity was mainly explained by the local environment, while spatial effects were more important for littoral and planktic diatoms. The results are in line with previous research that found environmental filtering effects for sedimentary diatoms in temperate lakes, which may be attributed to the long-term integration of environmental conditions through sedimentary assemblages (Verleyen et al., 2009, Winegardner et al., 2015). The concordance of environmental predictors for sedimentary and planktic assemblage composition reflects the results of previous studies of north American lakes (Winegardner et al., 2015) and tropical reservoirs (Bartozek et al., 2019, Zorzal-Almeida et al., 2017). Accordingly, the paleolimnological investigations of diatoms reliably reflect environmental constraints for pelagic diatom assemblages and vice versa, supporting previous paleolimnological studies from the lake set (Hofmann et al., 2021, Kuefner et al., 2020a, Kuefner et al., 2020b). AST was the sole variable correlating with β-diversity among all assemblages, possibly reflecting a direct effect of AST on diatom silicification among the study lakes (Kuefner et al., 2020d). Influence on planktic and sedimentary community composition may be through different diatom buoyancy. Secondary effects of AST and lake depth may be through the coupling of water temperature and lake morphology with lake mixing patterns (Niedrist et al., 2018, Read et al., 2011), which influence planktic community composition in the study lakes (Ossyssek et al., 2020). In turn, pure environmental effects were low for littoral diatoms, and a shared effect of environment and altitude was more important. This suggests an influence of unmeasured variables intercorrelated with altitude and AST. The significant correlation of TP with the sedimentary and planktic diatom β-diversity reveals a sensitive reaction of the assessed assemblages towards nutrient conditions that ranged from ultraoligotrophic to mesotrophic. These findings confirm previous results, suggesting an influence of anthropogenic pressure on the share and abundance of Red List species (Ossyssek et al., 2022b).

Spatial patterns

The significant correlation between spatial distance and littoral and planktic β-diversity, as well as the explained variation by the selected eigenvector maps reflect either spatial structures among unmeasured variables that influence diatom composition or dispersal effects (Leibold and Chase, 2018). The NTS index indicated a strong influence of stochastic processes for littoral and planktic assemblages. These include stochastic birth-death occurrence, i.e. ecological drift, dispersal processes, and historical contingency (Ning et al., 2019). Ecological drift may indeed be relevant for diatoms, but this has not yet been directly proven (Remmer et al., 2019). Historical contingencies are known to influence diatom communities, but they ought to influence sedimentary assemblages even stronger than littoral and planktic diatoms (Gonzalez-Trujillo et al., 2021). Thus, the NTS results suggest that dispersal processes contribute to the observed stochasticity within littoral and planktic diatoms. Dispersal limitation or mass effects can lead to spatial structures of β-diversity and stochasticity (Leibold and Chase, 2018). Evidence for a prevalence of mass effects in planktic and littoral diatom communities remains scarce, and even in regions where high migration rates can be expected, only slight indication of mass effects was found (Michels et al., 2001, Cottenie, 2005). In our dataset, the contribution of the most abundant species to β-diversity was above average. If mass effects influenced these species, this fact ought to lead to the homogenisation of assemblages, being associated with a lower contribution of these species to overall β-diversity. However, mass effects among adjacent lakes cannot be excluded, and they may also influence less abundant species (Bried and Vilmi, 2022, Leboucher et al., 2020). In our study, three pairs of lakes were within the same water basin, so they are more likely to be influenced by mass effects than the other lakes were. However, it appears unlikely that this would result in a strong stochastic effect across the whole lake set. More generally, the high overall β-diversity of planktic and littoral diatoms and the significance of the component that represents species loss (β_{Sim}) when using incidence data, further point to dispersal limitation rather than to mass effects. As a result, different evidence suggests a contribution of dispersal limitation to littoral and planktic diatom β-diversity, confirming our initial hypothesis.

Residual variation

Explained variation of variation partitioning for the sedimentary, littoral and planktic abundance data set was relatively low (9 %, 9 %, and 22 %, respectively), and it was even lower for incidence data (5 %, 10 %, and 13 %, respectively). Such a low amount of explained variation is not unusual in studies investigating diatom metacommunity structure, and it lies within the range of values reported by other studies for diatoms within Europe (6 – 27 %) (Kernan et al., 2009, Szabo et al., 2018, Szabo et al., 2019, Teittinen et al., 2017). The inclusion of further environmental variables may increase the explanatory power of the investigated assemblages (Soininen et al., 2021). For sedimentary and planktic diatoms, further important variables may be total organic and inorganic carbon and dissolved organic carbon (DOC) (Vinebrooke and Leavitt, 1999), which are known to be influenced by catchment variables such as land cover (Kamenik et al., 2001) and which may thus vary within our dataset that spans a variety of vegetation zones. Therefore, adding those environmental variables can potentially enhance the explanatory power of pure environmental effects or of shared effects of environment and altitude. For sedimentary diatoms, this is only likely to reinforce the principal pattern detected, namely that environmental gradients are an important driver of diatom metacommunity structure. For planktic and littoral diatoms, the importance of the environmental component may increase, and pure spatial effects may decrease if additional environmental variables are spatially structured. An increase in explanatory power can be expected for littoral diatoms if the microhabitat structure is taken into account (Pla-Rabes and Catalan, 2018). More generally, interspecific interactions do shape diatom community patterns through nutrient competition (Manoylov, 2009), parasitism (Kagami et al., 2007), or grazing (Wigdahl-Perry et al., 2017). Including the composition and density of other biotic groups should also increase the explained variation.

Another factor that may help explain diatom patterns in the study lakes is that of historical legacies (Vyverman et al., 2007). These may lead to priority effects that have already been documented for ostracods (Castillo-Escriva et al., 2017), aquatic plants (Garcia-Giron et al., 2021) and zooplankton (Mergeay et al., 2011, Leibold et al., 2010). In our dataset, such processes may be caused by the introduction of fish (Hobbs et al., 2016, Chen et al., 2011, Ossyssek et al., 2022b) or land-use changes (Martin et al., 2017). Identifying lakes that have been affected by such events and transferring the analytical scheme of this study to downcore assemblages may help interpret historical legacies, yet there are doubts about the completeness and correctness of such information, affecting the ability to track responses of biotic assemblages over time.

A methodological source of residual variation within our study may be that not all samples were collected in the same year. Some seasonal effects such as snow and duration of ice cover or longer-term weather phenomena may have had different effects in the two years of sampling. The impacts on the communities sampled will be greater for littoral and planktic diatoms because sedimentary samples cover several years of sedimentation, levelling out annual patterns. With regard to littoral and planktic diatoms, the measured variables may reflect longer-term ecological constraints. For example, nutrient content may mirror heavy rain events (Stockwell et al., 2020). However, it cannot be excluded that annual phenomena have changed environmental variables such as turbidity, which was not measured. Moreover, previous events may have triggered community-level changes, leading to priority effects (Vass and Langenheder, 2017) that will also increase residual variation.

4.7 Conclusions

This study sheds light on the factors controlling diatom metacommunity structure in the mountain lakes of the northern European Alps. In contrast to our hypothesis, elevation was of minor importance for α-diversity. In turn, alkalinity may be more important for local littoral and sedimentary diatom diversity, while habitat diversity and lake stratification may influence sedimentary and planktic diatom α-diversity, respectively. As expected, sedimentary diatom β-diversity was mainly controlled by environmental factors, while planktic and littoral diatom communities also revealed spatial constraints. Dispersal limitation likely contributed to the β-diversity patterns of littoral and planktic diatoms, substantiated by the importance of stochastic effects for both groups. In practice, the minimal spatial impact on sedimentary diatoms suggests that they are reliable bioindicators for total phosphorus, surface water temperature and lake depth, while the results for littoral and planktic diatoms may be confounded through stochastic assembly processes. In future studies, the inclusion of water chemical measurements of carbon compounds, the assessment of other biotic groups, and historical legacies may explain increased variance.

5 Diatom Red List species reveal high conservation value and vulnerability of mountain lakes

A similar version of this chapter was published as: OSSYSSEK, S., HOFMANN, A. M., GEIST, J. & RAEDER, U. 2022a. Diatom Red List species reveal high conservation value and vulnerability of mountain lakes. Diversity 2022, 14, 389.

Author contributions: This study was conceived by Stefan Ossyssek (SO) in consultation with Uta Raeder (UR) and Jürgen Geist (JG). On-site-measurements and laboratory analyses were carried out by SO. Diatom preparation and microscopic analyses was done by SO and Andrea Maria Hofmann (AMH). Statistical analysis, visualisation and data interpretation was conducted by SO. The manuscript was drafted by SO and continuously refined, improved and edited by UR, JG and AMH.

5.1 Abstract

Mountain lakes are unique and often isolated freshwater habitats that harbour a rich biotic diversity. This high conservation value may be reflected by diatoms, a group of algae that is known for its reliability as a bioindicator, but which has not been studied extensively in mountain lakes of the northern European Alps. In this study, the conservation value of these lakes was assessed by characterizing the number, share, and abundance of diatom Red List (RL) taxa and their relationship with environmental variables, diatom α and β diversity (assemblage uniqueness). For this purpose, linear regression models, generalized linear models, and generalized additive models were fitted and spatial descriptors were included when relevant. Of the 560 diatom taxa identified, 64 % were on the RL and half of these were assigned a threat status. As hypothesized, a decreasing share of RL species in sediment and littoral samples at higher trophic levels was reflected by higher total phosphorus content and lower Secchi depth, respectively. Species-rich lakes contained a high number of RL taxa, contrasting our hypothesis of a logarithmic relation-ship. In turn, RL abundance increased with uniqueness, confirming our initial hypothesis. However, some of the most unique sites were degraded by fish stocking and contained low abundances of RL species. The results demonstrate the importance of oligotrophic mountain lakes as habitats for rare freshwater biota and their vulnerability in light of human impact through cattle herding, tourism, damming and fish stocking. Additional conservation efforts are urgently needed for mountain lakes that are still underrepresented within legal conservation frameworks. Species richness and uniqueness reflect complementary aspects of RL status and thus should be applied jointly. Uniqueness can indicate both pristine and degraded habitats, so that including information on human impacts facilitates its interpretation.

5.2 Introduction

In light of the global biodiversity crisis, it is crucial to prioritize conservation on a global, regional, and local scale so that limited resources can be used effectively (Mittermeier et al., 1998, Darwall and Vie, 2005, Groom et al., 2012, Knight et al., 2008, Geist, 2015, Geist, 2011). While aquatic biodiversity in freshwater habitats is decreasing rapidly (Dudgeon et al., 2006), conservation measures lag behind those taken to preserve and restore terrestrial and marine ecosystems (Darwall et al., 2011). Within the European Union, the “Water Framework Directive” (WFD) that was implemented in 2000 aims to prevent the deterioration and enhance the status of aquatic ecosystems (EEA, 2021). WFD Annex II provides a non-mandatory minimum size limit for reporting the ecological status of lakes of 50 ha, which is applied by most member states (Kristensen and Globevnik, 2014). Accordingly, of the presumed 600,000 lakes and ponds in Europe (EEA, 1994), the ecological status was reported for less than 20,000 lentic water bodies (EEA, 2018). This low sufficiency in reporting for small lakes can be assumed to be accompanied by a lower degree of restoration measures applied at these sites. However, small lakes are known to have a disproportionately high biodiversity relative to their size (Biggs et al., 2017). This may be due to their collective higher habitat diversity compared to a single large lake, as demonstrated for littoral macroinvertebrates (Martinez-Sanz et al., 2012). This is especially true for small and isolated mountain lakes, which contribute to the overall biodiversity through their highly adapted biota (Sommaruga, 2001, Casamayor, 2017). Due to their remoteness, many of these environmentally unique lakes are still pristine (Ortiz-Alvarez et al., 2018). This makes mountain lakes important sentinels for indirect pressures due to global change (Moser et al., 2019a). In turn, dramatic consequences for these ecosystems can arise through direct pressures, such as cattle herding (Tiberti et al., 2014a), hut construction (Hofmann et al., 2021) and tourism (Dynowski et al., 2019), which often lead to the eutrophication of mountain lakes, while fish stocking disturbs their food webs and internal nutrient recycling (Tiberti et al., 2014b, Schindler et al., 2001, Detmer and Lewis, 2019, Ventura et al., 2017, Selene et al., 2020). These direct pressures may be amplified by climate change (Hofmann et al., 2021, Tolotti et al., 2012, Kuefner et al., 2020a, Rogora et al., 2018b, Oleksy et al., 2020), which is particularly pronounced in mountain regions such as the European Alps (Gobiet et al., 2014, Rosbakh et al., 2014). Therefore, it is important to preserve undisturbed oligotrophic mountain lakes and to restore degraded ones.

Diatoms (class Bacillariophyceae) are considered bioindicators that mirror ambient habitat conditions, including nutrient levels (Schönfelder et al., 2002), pH (Weckstrom et al., 1997) and water temperature (Kuefner et al., 2020b). They reliably indicate eutrophication (Bennion et al., 2004), acidification (Battarbee, 1984), and consequences of climate change (Kuefner et al., 2020a). Moreover, diatoms constitute a significant portion of algal biodiversity, with a known species richness of 10,000–12,000

(Round et al., 1990). Projections of the actual diversity range from 20,000 (Guiry, 2012) to 200,000 (Mann and Droop, 1996). This known yet still hidden diversity, along with their indicator function, makes diatoms ideal conservation targets within aquatic ecosystems.

The recently updated Red List for diatoms in Germany (Hofmann et al., 2018) can be a valuable reference to assess the conservation value of mountain lakes. The threat status of RL species incorporates their spatial restrictedness, rarity, as well as long- and short-term population trends and thus the likelihood of their local extinction. On a continental scale, rare taxa may simply be captured by conserving species-rich regions (Myers et al., 2000), whereas it may be more important to preserve high β diversity to prevent species extinction on a regional scale (Drinan et al., 2013, Lukacs et al., 2013). A high restrictedness and rarity of a taxon should lead to a high contribution to the uniqueness of a site, which in turn reflects its local contribution to β diversity (Legendre and De Caceres, 2013). This is especially important in small lakes with typically high turnover rates, i.e. high β diversity (Martinez-Sanz et al., 2012). Consequently, RL species may be effectively conserved by targeting unique assemblages. However, this approach requires the investigation of additional environmental parameters since uniqueness may also reflect degraded habitats (Legendre and De Caceres, 2013, Socolar et al., 2016, Tonkin et al., 2016). Generally, a high number and share of RL diatoms is indicative of rare freshwater habitats (Juran and Kastovsky, 2019), which are typically oligotrophic or dystrophic in central Europe (Cantonati et al., 2022b). Diatoms can therefore help to identify important refugia for a broader group of threatened freshwater species. Mountain waters are naturally oligotrophic habitats. Accordingly, the application of the diatom RL in the southern European Alps has revealed high shares of RL taxa in mires (Cantonati et al., 2011), springs (Mogna et al., 2015), streams (Falasco et al., 2016) and lakes (Tolotti, 2001). This has allowed important insights concerning the interaction between diatoms and catchment geology (Cantonati and Lange-Bertalot, 2006, Cantonati et al., 2020), water chemistry (Cantonati and Spitale, 2009), bryophytes (Mogna et al., 2015), stream flow regime (Falasco et al., 2016, Falasco et al., 2019) and geodiversity (Cantonati et al., 2020). The conservation value remained mostly unknown, especially regarding the updated RL from 2018, for lakes from the northern European Alps. Hence, the aim of this study is (1) to identify the environmental correlates of RL species in this region and (2) to investigate whether α diversity and uniqueness of diatom assemblages reflects the richness, share and abundance of Red List diatoms (hereafter called “RL indices”). Specifically, we hypothesize that: (1) lake trophic status is negatively correlated with RL indices based on previous findings for springs, mires and lakes from the southern Alps; (2) a positive logarithmic correlation exists between diatom α diversity and RL species richness. This is based on the assumed increasing diatom species richness with lake trophic level (Leira et al., 2009, Tilman et al., 1982, Velghe et al., 2012), which will in turn lead to a lower share of RL taxa (Hypothesis 1). Finally, we hypothesize (3) that the uniqueness of diatom assemblages has a positive correlation with RL indices and is highest in either unimpaired and environmentally unique lakes or in impaired lakes.

5.3 Study sites

Most lakes in this study are located on lime bedrock and therefore are well-buffered, as reflected by their pH values of between 8 and 9 (Table 12 and Table S 3). The altitudinal gradient comprises the vegetation zones of montane forest (750–1400 masl), subalpine forest (1,400–1,700 masl) and alpine meadows (1,700–2,500 masl, Figure 18).

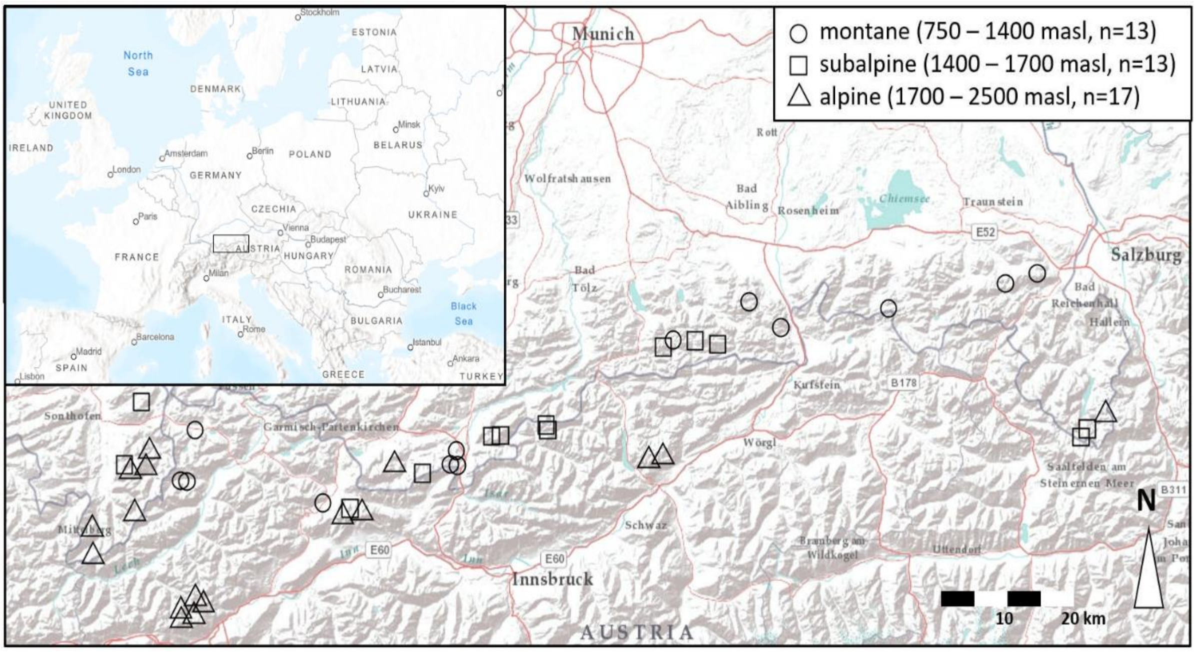

Figure 18: The 43 study lakes are spread across the Bavarian and Tirolian Alps in Germany and Austria, spanning a longitudinal gradient of c. 220 km and a latitudinal gradient of c. 50 km.

Most lakes were formed by cirque glaciers, they are typically small (<3 ha) and shallow (<10 m), consisting of one main basin (Table 12). Two of the lakes are karstic, they are almost round and deeper compared to their surface area than the other lakes. One of these lakes ("SieG") can be considered an outlier in terms of water chemistry due to a strong groundwater influence, resulting in a very high conductivity. Depending on the mountain group, different geological settings can be found in the dataset. A rough structuring reveals that the studied lakes in the "Berchtesgadener Alpen", "Chiemgauer Alpen", "Rofangebirge", "Karwendel" and "Mieminger Kette" are mainly on limestone that consists of calcium carbonate ($CaCO_3$), while in the "Lechtaler Alpen" they are on dolomite ($CaMg(CO_3)_2$). In the "Wettersteingebirge", they are partly on dolomite and partly on limestone and in the "Allgäu" and "Bayerische Voralpen" limestone, dolomite and marl are often closely interlaced. Seven lakes are stocked with fish according to personal communications of the lake owners or publicly available data. Various lakes are influenced by either intensive cattle herding (traces of trampling and excretion near the lake), tourism, damming, or a combination of these factors based on observations in the field. The relative strength of these influences is not known.

Table 12: Ecologically important morphological, physical and chemical parameters were assessed for 43 mountain lakes in the northern European Alps ranging from 760 to 2469 masl. The dashed box indicates an outlier lake that is strongly influenced by groundwater inflow. ABT = August bottom temperature, AST = August surface temperature. For abbreviations of other variables see Table S1. Abbreviations of the main bedrock type ("Geo."): Ls = Limestone, Do = Dolomite, Ma = Marvel, Mi = Mixed. Abbreviations of the mountain regions ("Reg.") are from west to east: A = Allgäu, L = Lechtaler Alpen, M = Mieminger Kette, W = Wettersteingebirge, K = Karwendel, R = Rofangebirge, V = Bayerische Voralpen, C = Chiemgauer Alpen, B = Berchtesgadener Alpen. Human impact is denoted by "+": F = Fish stocked lakes, C = Intensive cattle herding, T = Nearby touristic infrastructure, D = Dammed lakes.

	Alt.	**Area**	**Depth**	**Sec.**	**NO_3**	**TP**	**Si**	**NH_4**	**Na**	**Ca**	**Mg**	**pH**	**Cond**	**O_2**	**ABT**	**AST**	**DIN:TP**	**Geo.**	**Reg.**	**F**	**C**	**T**	**D**
Lake	**masl**	**ha**	**m**	**m**	**mg/L**	**µg/L**	**mg/L**	**µg/L**	**mg/L**	**mg/L**	**mg/L**		**µS/cm**	**%**	**°C**	**°C**							
Fal	760	1.0	15.0	7.0	1.84	9.0	0.18	17.0	2.11	42.3	6.7	8.0	266.3	96	5.8	12.8	205.4	Ls	C				
Bic	955	1.4	11.0	4.4	0.76	4.3	0.77	32.3	0.30	49.2	14.7	7.9	360.2	61	8.4	21.7	185.7	Mi	V	+			
Fri	973	1.2	5.5	4.6	0.93	7.2	0.15	83.7	0.48	39.6	5.4	8.6	224.3	110	13.9	18.6	140.1	Ls	C				
Sut	995	1.4	1.5	1.5	0.67	4.8	0.76	60.8	1.62	41.2	6.7	8.0	280.7	82	14.1	17.5	153.2	Mi	V				
Laut	1,013	12.0	18.0	6.0	0.21	13.5	0.25	50.8	0.10	46.1	16.0	8.6	310.0	102	8.2	16.0	19.3	Do	W	+		+	
Fer	1,060	10.0	19.5	6.8	0.33	10.1	0.21	43.0	0.10	47.2	18.1	8.1	304.0	102	7.4	15.6	36.9	Do	W	+		+	
Mit	1,082	3.3	4.7	4.7	0.10	7.5	0.13	34.0	1.23	38.5	18.4	8.2	345.8	101	18.4	22.6	17.4		W				
Wild	1,136	2.3	2.4	2.4	0.22	8.6	0.19	53.6	0.35	31.6	19.5	8.6	296.8	77	20.9	21.2	31.4	Do	W				
Tau	1,138	3.6	14.6	4.3	0.66	4.4	0.20	126.9	0.49	40.4	4.1	8.0	246.8	64	5.0	21.0	177.4	Ls	C	+			
Hoef	1,192	0.6	1.9	1.9	0.47	3.1	0.14	5.3	0.14	20.7	10.1	8.8	220.6	64	14.3	15.2	153.1		A				
SieK	1,205	0.2	11.3	11.3	0.56	1.0	0.23	99.4	0.36	38.6	10.8	8.2	382.4	130	7.4	8.8	655.2		A				
SieG	1,207	0.8	20.2	9.5	0.55	1.0	0.24	3.8	0.51	39.1	11.8	8.1	536.7	118	5.8	10.8	552.8		A				
GruW	1,393	2.3	5.8	3.7	0.18	14.1	0.18	19.9	0.29	29.7	3.2	8.1	198.6	99	14.0	20.3	13.8	Ma	V		+		
Roe	1,450	1.0	7.6	1.5	2.86	20.4	0.18	78.1	0.86	28.9	3.2	8.2	248.1	120	6.0	16.4	144.2	Ls	V		+		
SoiS	1,458	4.0	8.2	3.2	0.61	7.9	0.27	13.4	0.33	29.8	3.9	8.3	222.1	112	7.3	15.0	78.7	Ma/Ls	V	+			
GruO	1,474	3.5	6.9	5.0	0.20	8.3	0.13	60.8	0.10	26.5	1.4	8.5	194.5	112	14.1	17.5	31.3	Ls	B				
GaiU	1,508	3.5	4.1	3.8	0.25	12.0	0.29	9.6	0.18	16.4	10.1	8.9	198.3	72	13.4	16.3	21.3	Do	A				+
SoiN	1,520	0.3	4.7	4.2	0.77	10.8	0.24	13.9	0.37	36.3	6.8	8.2	251.8	115	5.4	13.4	72.5	Mi	V				+
SoE	1,552	3.0	5.5	4.5	0.61	3.9	0.18	49.3	0.10	31.1	6.6	8.8	177.7	123	7.5	15.0	168.2	Ls	K				
SoW	1,558	3.0	11.5	7.0	0.36	4.5	0.16	82.9	0.10	30.2	6.3	8.3	204.2	91	14.7	14.5	97.8	Ls	K	+		+	
DelN	1,600	0.6	1.3	1.3	0.37	5.7	0.38	15.1	0.39	35.1	2.8	8.2	223.3	81	11.9	12.6	67.7	Ls	K				
DelS	1,600	0.2	4.2	4.2	0.45	4.6	0.23	16.6	0.22	40.5	5.0	8.8	177.2	67	9.3	14.1	101.9	Ls	K				

Hoer	1,601	0.5	1.8	1.8	0.34	17.3	0.21	20.4	0.37	24.7	1.0	7.9	225.2	90	11.8	15.3	21.1	Mi	A		+		
Fun	1,601	2.5	4.5	3.5	0.03	10.3	0.13	44.3	0.10	31.3	4.3	8.4	274.4	91	10.3	14.9	7.0	Ls	B			+	
Seeb	1,657	6.3	18.4	6.9	0.52	4.5	0.14	23.3	0.14	27.0	4.4	8.8	165.9	82	6.8	13.8	121.6	Ls	M				
Scha	1,680	3.0	4.4	3.8	0.49	7.2	0.17	19.8	0.10	27.1	4.9	8.7	167.1	114	12.6	16.8	71.2	Ls	W				
Gug	1,725	0.1	1.9	1.9	0.29	4.6	0.23	10.6	0.86	15.0	10.3	9.0	207.3	100	11.8	13.2	64.7	Do	A				
GaiO	1,769	0.8	2.9	2.7	0.15	3.7	0.24	25.3	0.18	14.6	7.0	8.5	201.0	114	9.5	16.3	46.8	Do	A				
Zie	1,799	3.0	15.1	5.0	0.14	7.6	0.15	26.7	0.10	22.5	1.6	8.2	219.8	107	6.7	13.7	21.5	Ls	R				
Seel	1,809	0.4	5.4	5.4	0.59	7.9	0.12	31.5	0.10	23.8	1.0	8.7	134.2	93	12.4	14.9	79.3	Ls	B				
Eis	1,827	0.7	3.9	3.9	0.24	1.1	0.21	23.3	0.36	16.0	3.6	8.2	192.7	96	6.4	10.4	247.6	Ma	A				
Dra	1,874	5.3	20.7	10.3	0.30	4.0	0.19	19.6	0.10	26.8	3.1	8.6	157.7	97	4.9	11.9	79.9	Ls	M				
Eng	1,876	3.0	17.3	10.4	0.04	4.7	0.59	27.0	0.31	19.8	7.2	8.2	235.6	89	4.9	11.1	14.4	Do	A	+			
Bre	1,903	1.5	6.2	6.2	0.37	6.6	0.12	14.0	0.10	26.7	2.8	8.6	150.6	90	4.6	11.4	58.5	Ls	M				
Stu	1,921	3.0	5.1	5.1	0.25	7.7	0.12	19.6	0.10	23.3	1.6	8.8	126.0	112	12.4	16.7	35.4	Ls	W				
Lauf	2,012	0.8	5.6	3.7	0.13	3.8	0.22	24.9	0.19	12.4	6.3	8.3	168.2	99	9.4	14.7	39.1	Do	A				
Rap	2,047	2.3	7.8	5.0	0.04	9.2	0.17	15.9	0.23	21.2	9.3	8.6	205.1	101	11.0	15.6	6.5	Do/Ma	A				
Grub	2,060	0.5	3.5	3.2	0.10	17.0	0.15	17.8	0.18	37.9	2.6	8.6	222.4	73	9.4	13.3	6.9	Ls	R				
SeeU	2,224	2.4	1.7	1.4	0.07	2.5	0.25	21.4	0.99	19.8	9.1	8.8	208.6	113	16.1	17.0	35.7	Do/Ma	L				
Adl	2,294	1.9	1.7	1.7	0.15	1.0	0.13	30.3	0.32	19.4	9.2	8.5	159.6	94	14.0	14.7	183.3	Do	L				+
Schi	2,300	2.0	5.5	3.3	0.34	1.0	0.14	45.7	0.29	19.8	10.1	8.3	164.7	47	7.2	13.1	390.4	Do	L				
SeeM	2,424	0.5	4.1	4.1	0.20	1.5	0.13	67.8	0.14	17.6	9.9	8.7	137.8	122	10.6	11.5	173.2	Do	L				
SeeO	2,469	1.6	13.1	5.8	0.11	7.3	0.18	67.9	0.23	15.4	5.5	8.6	121.4	71	5.5	12.9	24.8	Do	L				

5.4 Methods

Sampling and Laboratory Procedures

The 43 lakes were sampled twice during the ice-free period, once between June and mid-August and once between August and November. Hence, 36 lakes were investigated in 2016 and seven lakes in 2017. On the first sampling date, lake bathymetry was determined with an echo sounder (Lawrence HDS8, Oslo, Norway) and a buoy was subsequently installed, fixed to a stone at the deepest point of each lake by a rope. Temperature loggers were mounted on the rope, (Onset Pendant UA-001-64 HOBO, Bourne, MA, USA) 0.5 m above the ground and 0.5 m below the water surface. To assess the temperature regime and the mixing type of the lakes, the loggers were exposed in the lakes during most of the ice-free period. Physical parameters (temperature, oxygen saturation, pH and electrical conductivity at 25 °C) were measured with a multiprobe (WTW 350, Weilheim, Germany) in one-meter steps above the deepest point of each lake on both sampling dates. After measuring the Secchi depth, 0.5 L of a mixed water sample was collected with a hose sampler from the euphotic zone (CEN, 2015). One half of the water sample was filtered (0.45 µm) on-site and stored at 4 °C together with the unfiltered rest until further processing in the laboratory. Another liter of water was taken from the euphotic zone with the hose sampler and preserved with Lugol’s solution to analyze planktic diatom communities (Throndsen, 1978b). Periphytic diatom assemblages were recorded by scraping the diatom communities off five stones, each taken at depths between 20 cm and 50 cm in the northern and southern littoral zone of each lake, with a single-use toothbrush (DIN, 2014). Out of all of the sampled lakes, periphytic diatom samples could be obtained at 34 sites, while no stones were available at nine sites. On the second sampling date, sediment cores were taken from the deepest point of each lake with a gravity corer (Uwitec, Mondsee, Austria) to record the sedimentary diatom communities from all 43 lakes (Kuefner et al., 2020a).

All chemical analyses were carried out in the laboratory of the Limnological Research Station Iffeldorf of the Technical University of Munich, Germany. Standard colorimetric methods were applied to determine the concentrations of total phosphorus (Murphy and Riley, 1962), nitrate-N (Navone, 1964), ammonia-N (DIN, 1983), and silica (Nanocolor silica test, Macherey-Nagel, Düren, Germany). The concentrations of major ions (calcium, magnesium, and sodium) were measured using a cation chromatograph (Thermo Scientific, ICS-1100, Waltham, MA, USA).

Planktic diatom samples (1 L) were filtered with 0.45-µm syringe filters and the residue on the filters was further processed (Nixdorf et al., 2014a). The uppermost centimeter of each sediment core was used to assess the sedimentary diatom assemblages. The residue on the filters of the planktic samples, the sediment samples and the littoral samples were processed in the same way: The diatoms were prepared according to van der Werff and Macan (1955). To analyze the composition of the diatom samples, 500 valves were identified in each case using a Leica DNM microscope (Wetzlar, Germany) at 1000× magnification. Eleven of the 43 planktic samples were excluded from the data analysis because they contained an insufficient number of valves. Taxa were counted at the species level and, if possible, at the subspecies level. Individuals that could not be identified were given working names. Standard literature was used for identification (Krammer and Lange-Bertalot, 1991a, Krammer and Lange-Bertalot, 1991b, Krammer and Lange-Bertalot, 1997b, Krammer and Lange-Bertalot, 1997a, Krammer, 2000, Lange-Bertalot, 2001, Krammer, 2002, Lange-Bertalot et al., 2017).

Data Analysis

Since periphytic diatom assemblages can vary significantly within a lake (Pla-Rabes and Catalan, 2018, Rimet et al., 2016), littoral samples from the northern and southern shore of each lake were pooled to obtain a more representative indication of the periphytic diatom assemblage. All statistical analyses were computed for the sedimentary data set (N = 43), the littoral data set (N = 34) and the planktic data set (N = 32) analogously.

The following parameters were computed to capture the conservation value of each sample using the current German Red List for diatoms (Hofmann et al., 2018). Community indices were calculated based on the taxa with a status higher than “not in danger/insufficient data” (RL_D), overall species richness per sample (N), overall abundance per sample (Ab) and overall abundance of all RL_D (Ab_{RL}):

N_rl = sum of RL_D

share_rl = N_rl / N

rel_share_rl = Ab_{RL} / Ab

weight_rl = rel_share_rl weighted by Red List class

Diatoms were assigned weighting factors ranging from 1 to 7, according to the threat category ranging from “warning list” to “threatened by extinction”, to calculate the weight_rl. Environmental predictor variables were selected based on their variance inflation factors (VIF). These were calculated with the “vif” function from the R package “usdm” (Naimi, 2017). To reduce multicollinearity among environmental predictors, only variables with VIFs less than five were included for each individual dataset. Shannon diversity was calculated within the “vegan” (Oksanen et al., 2007) package in R. The uniqueness of diatom assemblages was calculated as the local contribution to beta diversity (LCBD) at each site for Hellinger-transformed abundance data using the R package “beta.part” (Legendre and De Caceres, 2013). This approach is neutral with regard to ecological prerequisites (e.g., α and γ diversity) and allows the mathematically correct identification of assemblages’ uniqueness within a larger metacommunity. The total variance of a community matrix (Var(Y)) equals the overall β diversity

(BD_{Total}). This value is the total sum of squares (SS_{Total}; the sum of squared deviation for all sites and species from the mean) divided by n_{Sites}—1. The LCBD value for each sampling unit is derived by dividing the sum of squares of each site (SSi) by the total sum of squares (SS_{Total}). Accordingly, large LCBD values indicate a high contribution of a site to the overall β diversity. LCBD was partitioned in the component reflecting species substitution (Replacement; "Repl") and the component reflecting species loss (Nestedness; "Nest") (Baselga, 2013). The replacement component was the main contribution to BD_{total} for all datasets (sediment: 99.5 %, $BD_{total\_sed} = 0.385$; littoral: 99.6 % $BD_{total\_lit} = 0.282$; plankton: 97.0 %, $BD_{total\_pla} = 0.359$).

In order to test and visually verify the strength of the correlation between RL indices and the selected environmental and community-based predictor variables, a correlation plot was generated using the "corrplot" package in R (Wei and Simko, 2017b). To account for multiple testing, *p*-values were Bonferroni-corrected a priori. Previous work revealed pure spatial effects and shared effects of environmental and spatial variables on diatom communities within the lake set (Ossyssek et al., 2022a). Therefore, the spatial influence on all response and predictor variables was assessed by calculating Moran's I autocorrelation coefficient based on latitudes and longitudes recorded for each lake using the R package "ape" (Paradis et al., 2004).

The normal distribution of response variables was tested by the Shapiro–Wilk test in the "vegan" package. Linear models (hereafter called "LMs") were applied for normally distributed variables that were spatially structured according to Moran's I p-values. The spatial structure of model residuals was tested with the "lm.morantest" function from the "spdep" package (Bivand and Wong, 2018). No spatial structure of the residuals was detected in any of the computed LMs. If variables had a non-normal distribution and no spatial autocorrelation was indicated, generalized linear models (hereafter called "GLMs") were applied within the "vegan" package. Diagnostic plots were checked for structures within model residuals. Generalized additive models (hereafter called "GAMs") were developed, and spatial predictors were included (longitude and latitude) within the package "mgcv" (Wood, 2011) in cases of non-normal distributed and spatially autocorrelated variables. Variables were fitted with smoothers and k values and regression splines were fitted to increase model suitability. Non-significant variables were excluded until each predictor was significant. Reduced and original models were compared based on Akaike information criterion (AIC) (Akaike, 1974) and the most parsimonious model was selected.

5.5 Results

Briefly, 560 diatom taxa were recorded across the three diatom assemblages of the 43-lake dataset and 360 taxa (64 %) were on the German diatom RL. Of these, 184 (51 %) were assigned a threat status ranging from "warning list" to "threatened by extinction". Across the subsets, 276, 240 and 139 taxa were on the RL for sedimentary, littoral and planktic assemblages, respectively. Of these 135, 122 and 64 species were assigned a threat status for sedimentary, littoral, and planktic assemblages, respectively (Figure S 17).

Significant and ecologically meaningful correlations between RL indices and predictor variables were revealed by Pearson correlations (Figure 19). TP was significantly and negatively correlated with share_rl for all assemblages. Both variables were spatially structured (Moran's $p < 0.05$, Figure 20a), but no such structure was found in the LM residuals ($p = 0.175$, Table 13), suggesting that the spatial structure of both variables was congruent. LMs confirmed the correlation between TP and share_rl for sedimentary diatoms ($p = 0.002$, $R^2 = 0.20$, Figure 21a, Table 13).

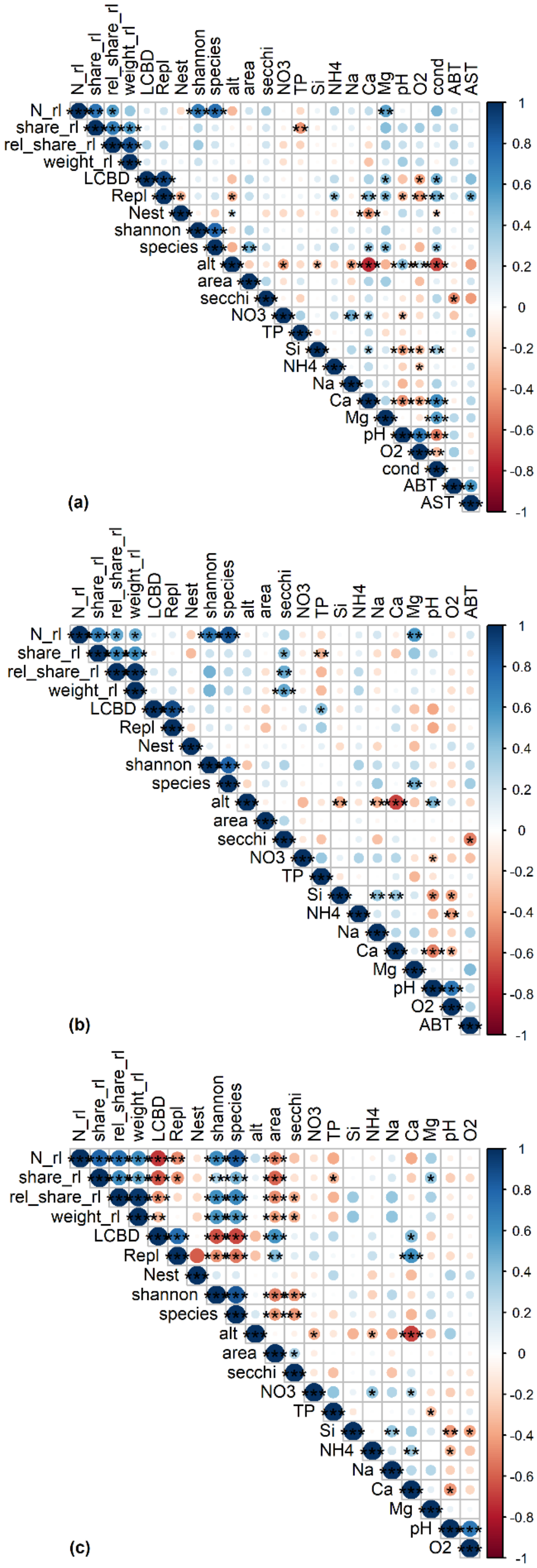

Figure 19: Correlations plots for the (a) sedimentary (N = 43), (b) littoral (N = 34) and (c) planktic (N = 32) diatom dataset. Abbreviations of environmental parameters are explained in Table S1. Asterisks: *** ≙ p-value < 0.001; ** ≙ p-value < 0.01; * ≙ p-value < 0.05. Point color refers to the Pearson correlation coefficient.

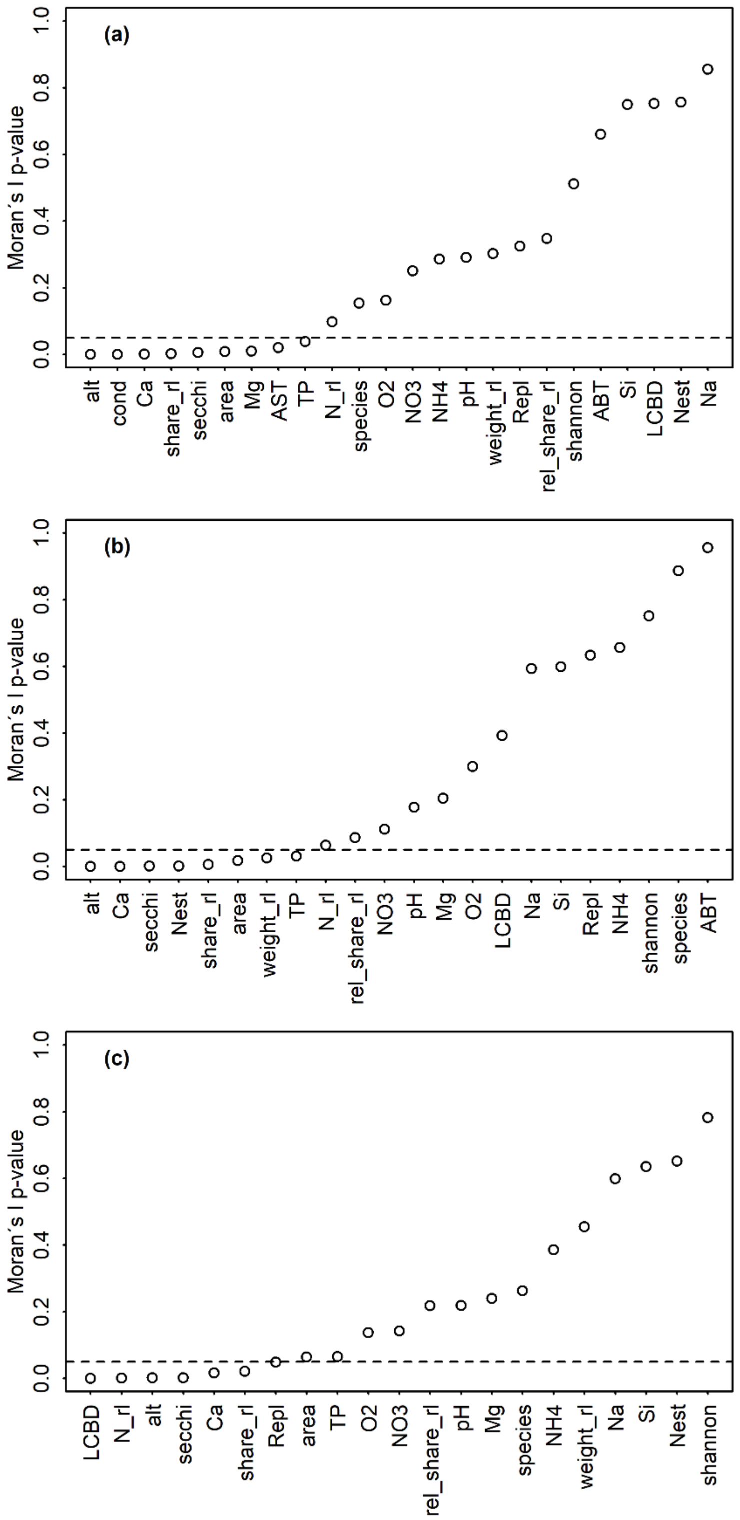

Figure 20: Moran's I p-values for RL indices, assemblage indices and environmental variables plotted in increasing order for the (a) sedimentary (N = 43), (b) littoral (N = 34) and (c) planktic (N = 32) dataset. The horizontal dashed line marks a p-value of 0.05, with lower values indicating spatial autocorrelation based on longitudes and latitudes. Abbreviations of environmental parameters are explained in Table S 3.

For littoral diatoms, the correlation of TP with share_rl became non-significant in the LM when Secchi depth was included ($p_{TP} = 0.182$; $p_{secchi} = 0.029$, Table 13), probably reflecting the intercorrelation of both variables as predictors of the lake's trophic state. After excluding TP, the LM confirmed the positive correlation of share_rl and Secchi depth for the littoral assemblages ($p = 0.009$, $R^2_{adj} = 0.17$, Figure 21b, Table 13). Both variables were spatially structured (Moran's $p < 0.05$, Figure 20b) but model residuals were not, indicating congruence of their distribution in space ($p = 0.607$, Table 13). TP was not correlated with any other variable in the dataset and Secchi depth was only correlated with August bottom temperature, which was not significantly correlated with any other variable (Figure 19). The significant correlation of TP and share_rl within planktic assemblages turned out to be mediated by the longitude of the sampled lakes ($p_{lon} < 0.001$, $p_{lat} = 0.117$, $p_{TP} = 0.327$), and the final model incorporated longitude as the sole predictor ($p < 0.001$, $R^2 = 0.34$) (Table 13, Figure 21c). Accordingly, a marked increase of share_rl could be observed in the "Allgäu" and "Lechtaler Alpen" lakes in the western part of the study region (Figure 21c, left of the vertical dashed line; see Table 12 for background information). Finally, magnesium content was positively correlated with RL indices for all datasets, and it was intercorrelated with conductivity in the sedimentary dataset and with TP in the planktic dataset ($p < 0.05$) (Figure 19 and Figure S 16).

Table 13: A significant correlation was detected based on linear regression models (LMs) between the share of RL species (share_rl) and total phosphorus (TP) and Secchi depth (secchi) for sedimentary and littoral assemblages, respectively. For planktic assemblages, share_rl significantly decreased with longitude (lon) based on GAMs. p-values for the Moran-test of LMs residuals and AIC values are given where relevant. Within GAMs, inclusion of smoothers is indicated by placing the predictor within "s()".

Response share_rl	$p_{Shapiro}$	**Model Type**	**Predictor**	p_{model}	R^2_{adj}	**Res. Df**	$p_{lm.moran}$	**AIC**
Sediment	0.098	LM	TP	0.002	0.20	41	0.175	
Littoral	0.931	LM	TP	0.056	0.08	32	0.908	
		LM	TP + secchi	TP: 0.182 secchi: 0.029	0.19	31	0.923	
		LM	secchi	0.009	0.17	32	0.607	
Plankton	0.02	GAM	s(lon) + s(lat) + s(TP)	lon: <0.001 lat: 0.117 TP: 0.327	0.38	19		−38.4
		GAM	s(lon)	<0.001	0.34	27		−41.3

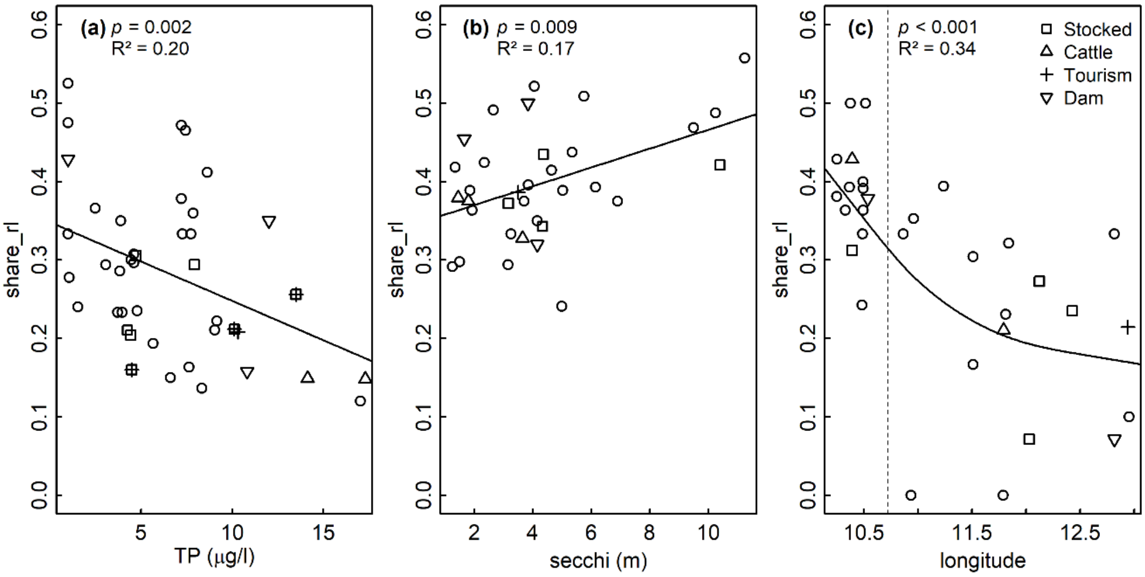

Figure 21: A significant correlation was detected based on LMs between the share of RL species (share_rl) and total phosphorus (TP) and Secchi depth (secchi) for (a) sedimentary and (b) littoral assemblages, respectively. A significant decrease of share_rl with longitude (lon) was found for planktic assemblages (c) based on GAMs.

GAMs and LMs confirmed the significant and positive correlation between species richness and N_rl, as indicated by Pearson correlations for sedimentary diatoms ($p < 0.001$, $R^2_{adj} = 0.56$) and littoral diatoms ($p < 0.001$, $R^2_{adj} = 0.74$), respectively (Table 14, Figure 22a,b). Both variables were not spatially structured within the sedimentary dataset (Moran's I $p > 0.05$). No spatial structure was observed in the model residuals ($p = 0.219$) for the littoral dataset, and GAMs revealed an increase of RL species richness (N_rl) for planktic diatoms, with overall species richness and a negative correlation of N_rl with longitude ($p < 0.001$, $R^2 = 0.81$) (Table 14, Figure 22c).

Table 14: A significant correlation between the number of RL species (N_rl) and species richness was detected for all assemblages based on LMs, GLMs and GAMs. For planktic assemblages, longitude (lon) was additionally correlated to N_rl. p-values for the Moran-test of the linear model residuals and AIC values are given where relevant. If smoothers were included in GAMs, this is indicated by placing the predictor within "s()".

Response N_rl	$p_{Shapiro}$	**Model Type**	**Predictor**	p_{model}	R^2_{adj}	**Res. Df**	$p_{lm.moran}$	**AIC**
Sediment	<0.001	GLM	species	<0.001	0.56	41		
Littoral	0.083	LM	species	<0.001	0.74	32	0.219	
Plankton	0.092	GAM	s(lon) + s(lat)+ s(species)	lon: 0.008 lat: 0.826 species: <0.001	0.80	28		−63.00
		GAM	s(lon) + s(species)	lon: <0.001 species: <0.001	0.81	29		−63.02

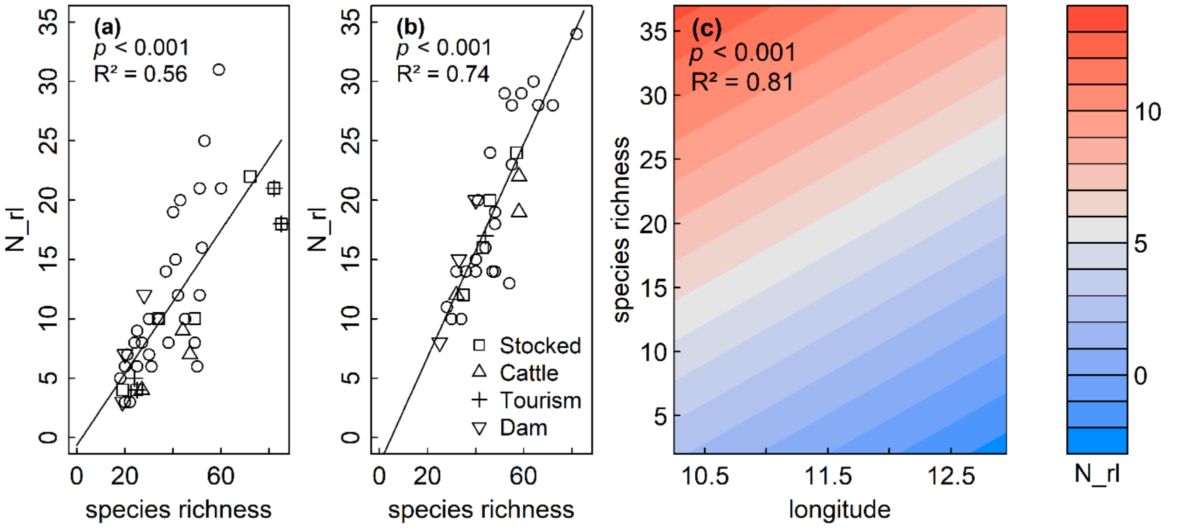

Figure 22: The number of Red List species (N_rl) increased with species richness for sedimentary (a), littoral (b) and planktic (c) assemblages. Longitude (lon) was additionally negatively correlated to N_rl for planktic assemblages. The color indicates the number of RL taxa.

A positive correlation of assemblage uniqueness (LCBD) and rel_share_rl was revealed by GAMs for sedimentary diatoms ($p = 0.049$, $R^2 = 0.07$). Omitting one outlier lake with extremely high conductivities due to groundwater influence (SieG, Table 12), high LCBD values resulted in an increasing and a decreasing branch of rel_share_rl values along the LCBD gradient (Figure 23a). A common feature of five lakes of the lower branch (Bic SoW, Tau, Laut, Fer) was that they are impacted by fish introduction and in three cases (SoW, Laut and Fer) by huts, hotels, or restaurants on the shoreline. The negative relationship between LCBD and rel_share_rl for planktic assemblages ($p = 0.010$, $R^2 = 0.18$, Table 15, Figure 23c) probably reflects the intercorrelation of LCBD with species richness ($p < 0.001$), which in turn was highly correlated with rel_share_rl ($p < 0.001$, Figure 19). No significant correlation of uniqueness and RL indices was found for the littoral diatoms ($p > 0.05$, Table 15, Figure 23b).

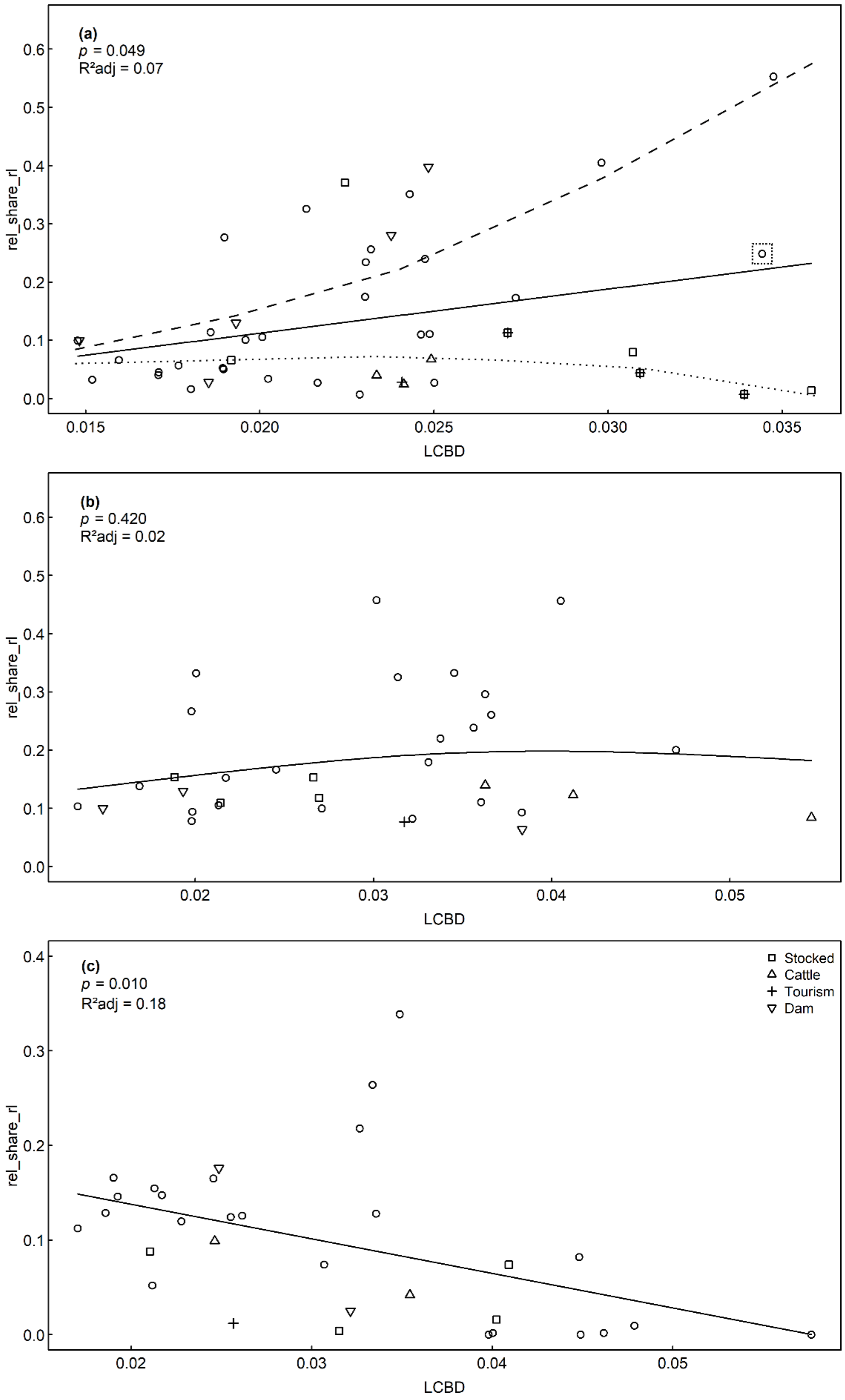

Figure 23: The abundance share of RL species (rel_share_rl) increases with higher uniqueness (represented by the local contribution to β diversity, LCBD) for sedimentary (a) and decreases for planktic assemblages (c), while no significant trend was found for littoral assemblages (b). The assumed trend for unimpaired and impaired lakes is indicated by a dashed and dotted line respectively for the sedimentary dataset. The dotted box indicates one outlier lake with a strong influence of groundwater (SieG, Table 12).

Table 15: A significant correlation between the abundance share of RL species (rel_share_rl) and the local contribution to β diversity (LCBD) was revealed by GAMs for sedimentary and planktic assemblages.

Response Rel_Share_rl	Model Type	Predictor	p_{model}	R^2_{adj}	Res. Df
Sediment	GAM	LCBD	0.049	0.07	41
Littoral	GAM	LCBD	0.420	0.02	32
Plankton	GAM	LCBD	0.010	0.18	30

5.6 Discussion

This study revealed a high proportion and abundance of endangered diatoms in naturally oligotrophic, fishless mountain lakes and underlined their vulnerability to eutrophication. This finding could be observed for sedimentary, littoral and planktic assemblages, supporting the broad applicability of the German Red List (RL) for diatoms (Hofmann et al., 2018) and confirming previous research on the effects of eutrophication on mountain waters (Cantonati et al., 2022a). A new approach was taken by comparing the uniqueness of assemblages and diatom RL indices. Unique sedimentary assemblages revealed either pristine lakes with high abundances of RL taxa or lakes with fish stocking and low RL species abundance. In turn, α diversity reflected only RL richness, but not the share or abundance of RL taxa, thereby losing important information on mountain lake conservation value.

Nutrients and the Share of Red List Diatoms

Previous research associated high numbers of RL diatom taxa with oligotrophic or dystrophic freshwater habitats (Cantonati et al., 2022b), reflecting the general rarity of these environments in central and southern Europe (Juran and Kastovsky, 2019). In mountain regions such as the European Alps, oligotrophic habitats are still abundant, but they are often threatened by eutrophication. This is especially true of springs (Cantonati and Lange-Bertalot, 2010) and lakes (Tolotti, 2001). Our results substantiate these findings by revealing a negative correlation of the share of RL taxa with TP for sedimentary assemblages. Moreover, a positive correlation between Secchi depth and RL share was found for littoral assemblages. Both findings indicate the suppression of oligotraphentic diatom taxa at higher trophic levels. In the lakes of our dataset, the elevated TP levels of three subalpine lakes (Roe, Hoer, GruW; Table 1), which were surrounded by pastures, are likely caused by intensive cattle herding. Strong trampling of the grass layer and excrements near the lakes probably led to the observed eutrophication (Tiberti et al., 2014a). Another important nutrient source includes mountain huts and touristic infrastructure, such as hotels and restaurants (Hofmann et al., 2021, Muri et al., 2018, Sienkiewicz and Gasiorowski, 2016), associated with four lakes in our dataset (Laut, Fer, Fun, SoW; Table 1). Furthermore, damming can lead to soil mineralization, possibly leading to the eutrophication of two subalpine lakes (GaiU, SoiN) in our dataset, while a dammed, high-altitude lake (Adl) remained nutrient poor. This may be related to the thin soil layer in the alpine region (Kuefmann, 2003) and the consequently lower mineralization potential. In contrast to previous research on RL diatoms in springs (Cantonati et al., 2022b), the negative correlation of trophic level and share of RL taxa was attributed to TP rather than nitrate. This difference may be due to phosphate limitation of the study lakes, indicated by DIN/TP ratios above 3.4 (Bergström, 2010) (Table 1, range: 7–655). If nitrite had been measured as a further component of DIN in addition to nitrate and ammonium, the N/P ratios would have been even higher. High concentrations of inorganic nitrogen in mountain lakes are related to atmospheric dry and wet deposition (Rogora et al., 2008, Muri et al., 2013, Rogora et al., 2012). This atmospheric input may be less pronounced in springs due to their smaller surface. Springs may therefore be nitrogen co-limited, causing stronger responses to a shift in nitrate concentrations. Moreover, some of the studies that identified nitrate as an important correlate of RL indices did not include TP measurements (Angeli et al., 2010), which may be autocorrelated with nitrate. Nevertheless, there is empirical evidence that elevated nitrate levels caused by direct loadings are not always concomitant with an increase of TP in springs (Cantonati et al., 2020). Overall, our findings confirm the hypothesized negative correlation between the RL share and the trophic state, while the number of RL taxa and abundance were not correlated. Our conclusions are in line with those of previous work, namely that mountain waters need to be better protected from human-induced nutrient inputs to conserve rare diatom taxa and thereby sustain valuable habitats for a broader range of biota. An unexpected observation was the positive correlation of magnesium (Mg) with RL richness across all assemblages (Figure S 16). Mg is known to influence diatom community composition, e.g., in springs from the Apennines (Cantonati et al., 2020) or in petrifying springs from Lower Belgium (Denys and Oosterlynck, 2015). Moreover, some diatoms are closely bound to alkaline conditions with high Mg contents, such as *Achnanthidium dolomiticum* Cantonati & Lange-Bertalot (Cantonati and Lange-Bertalot, 2006, Cantonati et al., 2017). Generally, we found high Mg contents in lakes with dolomite-dominated catchments, corresponding to the chemical composition of dolomite ($CaMg(CO_3)_2$). This probably explains the higher number of RL taxa in the western region, which is rich in lakes on dolomite bedrock. Previous studies have found a correlation between geodiversity and biodiversity of springs (Cantonati et al., 2020) and streams (Karna et al., 2019). In our dataset, RL richness was positively correlated with total diatom richness, suggesting a possible indirect effect of geodiversity on RL diatom richness. These results indicate the need for further research on the potentially important role of dolomite-dominated catchments for diatom α diversity.

Uniqueness as an Indicator of Fish Stocking

The correlation of RL species abundance and uniqueness was relatively weak for sedimentary assemblages ($R^2 = 0.07$). This does not necessarily indicate that the metric is of no use for detecting rare and restricted taxa, but reflects the potential of LCBD to indicate both pristine and disturbed sites: For fish in the Doubs river in France, the highly unique sites were either undisturbed and environmentally unique and corresponded to headwaters with steep slopes or impaired by eutrophication (Legendre and De Caceres, 2013). As hypothesized, a similar pattern was found for the sedimentary diatom assemblages in our dataset. Whereas the abundance share of RL taxa generally increased from low to moderate LCBD values, the most unique sites showed pronounced differences with respect to RL abundances: a group of lakes that is stocked with fish was highly unique, but had low RL abundances (< 10%), while no direct human pressures are known for two other highly unique lakes, reflected by very high RL abundances (> 40%). This picture is exemplified by the extreme difference in RL abundance between the adjacent lakes SoE (rel_share_rl: 40.5%) and SoW (rel_share_rl: 0.7%), which are only about 100 m apart. During hut construction in 1866 on the shore of SoW, the lake was stocked with *Salvelinus alpinus* Linné. SoE was not stocked as it experiences strong changes in water level of up to 9.5 m (Hofmann et al., 2021), probably contributing to its ecological distinctness (Hofmann et al., 2020, Cantonati et al., 2009). This suggests that ecological uniqueness is indicative within sedimentary diatom assemblages for degraded or pristine and environmentally unique sites. Importantly, not all pristine sites were unique, reflecting the context dependency of the metric (Tonkin et al., 2016): unaffected sites with low TP were frequent in our data set. Therefore, only those lakes that were additionally distinct, e.g., due to water level fluctuations, had unique assemblages. This is also reflected by one outlier lake ("SieG") that has been strongly influenced by groundwater and is very deep relative to its surface, probably leading to lower RL abundances in the sedimentary assemblage.

Our results confirm the hypothesized potential of LCBD to identify assemblages from pristine lake that are environmentally distinct and those from degraded lakes. Thus, a sound interpretation of the LCBD index is only possible when backed up with basic environmental data and information on human influence. If this is the case, it can be helpful in detecting complex ecological interactions, such as the effects of fish stocking in mountain lakes.

Degradation related to fish stocking may be due to either a change of the nutrient cycle, i.e. bottom-up effects (Schindler et al., 2001), top-down control due to the selective impact on planktic and benthic invertebrates (Jeppesen et al., 2000, Jeppesen et al., 2003, Brooks and Dodson, 1965, Carpenter et al., 1987), or through a combination of both (Benndorf et al., 2002). Of the seven fish-stocked lakes in our dataset, only those lakes that are additionally impacted by intensive tourism ("Lau", "Fer") were TP enriched. This indicates that predation is mainly on zooplankton rather than zoobenthos for the stocked lakes, which would cause the additional introduction of benthic nutrients into the open water (Schindler et al., 2001), manifested in elevated TP levels. Permanent fish stocking can contribute to the eutrophication of lakes through the addition of biomass that will be recycled after the fish die (Threlkeld, 1988). Moreover, Pastorino et al. (2020) found more than 80% of terrestrial invertebrates in the stomach of introduced *Salvelinus fontinales* Mitchill from an alpine mountain lake, possibly leading to additional allochthonous biomass input. However, these processes should also be reflected in the TP level, and thus appear of minor importance in the study lakes that are mainly at lower elevations. Nonetheless, fish feeding on zooplankton also leads to a transfer of nutrients to algae from previously inaccessible sources, i.e. nutrients stored within the zooplankton (Carpenter et al., 1992, Schindler et al., 1993). As a consequence, primary production will increase (Schindler et al., 2001). The observed low RL abundances in the fish-stocked lakes may be due to this eutrophication effect, which cannot be detected by TP measurements as the total phosphorus content in the pelagic zone remains unchanged. The stocked lakes in our dataset commonly contained moderate to high abundances of the benthic diatoms *Staurosirella pinnata* (Ehrenb.) D.M.Williams and Round and *Staurosira venter* (Ehrenberg) Cleve & Moeller that are tolerant to low light intensity (range of summed relative abundance: 4–53%) (Whitmore et al., 2018). This indicates an enhanced pelagic primary production leading to shading of the benthic environment. To enhance the assessment of primary production, further research in stocked lakes should include measurements of algal pigments such as chlorophyl a, which were found to be a strong predictor of fish stocking effects on primary production (Schindler et al., 2001).

The reason for the unique sedimentary diatom assemblages may be top-down control, i.e. the predation of planktivorous fish on zooplankton and consequently altered feeding patterns on phytoplankton (Carpenter et al., 1985). In oligotrophic systems, top-down control often suppresses large zooplankton such as Daphnids (Guilizzoni et al., 2006, Post and McQueen, 1987) while it may promote predation-resistant small zooplankton such as rotifers and cyclopid copepodes (Tolotti, 2001, Guilizzoni et al., 2006). The abundance of the zooplankton in turn depends on the trophic state, and a unimodal relationship along the TP gradient was found for Daphnids (Jeppesen et al., 2003). Thus, cascading effects on the phytoplankton are complex and likely to be dependent on the trophic level. While most studies find an effect on phytoplankton species traits and assemblage composition (Post and McQueen, 1987, Gliwicz, 1975) due to the well-documented reduction in size of the zooplankton (Brooks and Dodson, 1965, Post and McQueen, 1987, Sienkiewicz and Gasiorowski, 2016), the response of phytoplankton biomass varies and is dependent on the trophic state of the lakes (Benndorf et al., 2002, Gliwicz, 1990, Jeppesen et al., 2003, Post and McQueen, 1987). The effect on species composition is indicated through the presence of the planktic diatom *Asterionella formosa* Hassall in three of the stocked lakes (relative abundance: 3–16%). This taxon is not edible by small zooplankton due to its large size and formation of colonies (Kissman et al., 2013, Reynolds, 1984). In turn, the most characteristic feature was the high planktic diatom proportion of small centrics (four lakes with > 50% centrics), a pattern documented after the extirpation of large zooplankton (Carpenter et al., 1987). Within our lake set, this may be caused by enhanced nutrient recycling, which in turn may promote small centrics such as *Cyclotella comensis* Grunow*,* coupled with a stable water stratification (Ossyssek et al., 2020). The high share of centrics and *A. formosa* Hassall probably explains the high uniqueness of the stocked lakes as most other lakes had lower abundances of centrics. The only stocked lake with low LCBD values had a low share of centrics (Eng, 3% of centrics). Within this alpine lake, low water temperatures and low lake productivity may lead to low fish-density, enabling the coexistence of large zooplankton with fish (Donald, 1987). Moreover, weaker top-down control may be due to the naturally low density of zooplankton (Benndorf et al., 2002) in ultraoligotrophic lakes, possibly leading to the previously observed feeding of fish on terrestrial insects that settle on the water surface (Pastorino et al., 2020). It remains to be seen whether this possible eutrophication effect will turn the tide for primary producers in this lake, especially since secondary effects through more stable lake stratification at higher water temperatures may come into play (Ossyssek et al., 2020). To conclude, the response of the sedimentary diatom assemblages to fish stocking in our dataset may be triggered by both altered nutrient cycling and top-down effects. The change of nutrient cycling may lead to bottom-up effects that are hypothesized to interact with the top-down control of fish (Benndorf et al., 2002, Gliwicz, 2002).

Unexpectedly, the top-down control in stocked lakes was not reflected by a high LCBD and low RL abundance of planktic samples. This may be due to the more volatile character of the lake plankton: short-term interference to the planktic assemblages through the introduction of benthic diatoms is frequent and depends on the mixing state (Reynolds, 1993, Reynolds et al., 1983). The high rates of benthics in some samples prove a high importance of this process in our dataset. Moreover, the strength of fish-mediated pelagic nutrient recycling also varies during the growing season, with the highest rates occurring during summer, i.e. along with the highest water temperature (Schindler et al., 2001). Our sampling period lasted from June until November, inherently producing temporal variability within the planktic and littoral datasets. Another reason may be that only five true planktic species had a threat status, making inferences based on planktic assemblages more difficult. Thus, the uniqueness of sedimentary diatom samples can be used more reliably to detect effects of fish stocking due to their time integration of environmental conditions (Ossyssek et al., 2022a, Benito et al., 2018). Therefore, littoral diatom samples did not track fish-induced processes in our dataset either. Apart from the temporal variability, this may be due to stronger predation of fish on zooplankton than on zoobenthos. As the predation of zoobenthos increases with fish density (Schindler et al., 2001), the response of littoral diatoms will be more pronounced in eutrophic and low altitude lakes, especially if stocked with bottom-orientated fish.

Overall, the results suggest that introduced fish have a severe impact on mountain lakes in the study region, justifying a halt to further stocking and the eradication of introduced fish, e.g., using gill nets (Knapp and Matthews, 1998). The success of such measures has been seen in the Italian Alps and northern America (Tiberti et al., 2021, Knapp and Matthews, 1998), where the natural trophic structure reappeared only a few years after lakes became fishless, followed by a recolonization with the original species (Parker and Schindler, 2006). Finally, the eradication of fish in naturally fishless lakes will also help to restore associated assemblages outside the aquatic trophic pyramid, such as herpetofauna, which has been impaired or even eradicated in stocked lakes (Knapp, 2005, Knapp et al., 2001, Denoel et al., 2016), and is one of the most threatened groups of animals (Bohm et al., 2013, Cushman, 2006).

Diatom Richness and Conservation Value

Diatom richness was positively correlated with RL richness in all assemblages, and it was additionally negatively correlated with longitude for planktic assemblages. Differences were detected in the impact of the fish-stocked lakes on the respective correlations. For littoral diatoms, the variance of the regression was low, and the stocked lakes were close to the linear regression line. On the other hand, RL richness within sedimentary diatoms of stocked lakes was lower than would be expected by the linear regression model. This suggests that in the regression of RL richness on species richness, the model coefficient, i.e. the slope of the regression line, and the structure within the model residuals are more informative for sedimentary than for littoral assemblages. This may indicate the conservation value of a lake. However, the hypothesized logarithmic correlation was not detected for any of the assemblages, probably because TP was not correlated with total species richness in our dataset. Therefore, the correlation of RL richness and species richness appears to be a rather weak metric of eutrophication of mountain lakes. As for habitat quality, the share of RL taxa was the only metric to track lake eutrophication. Thus, species richness is also unable to exploit the full potential of the diatom Red List, namely detecting rare habitats (Juran and Kastovsky, 2019), as it was not correlated to the share of RL taxa. Preserving a high number of RL species is sometimes used as a stand-alone conservation objective and species richness can be used to assess high numbers of RL species in our dataset. However, this is probably not the most efficient way to sustain assemblages of rare taxa in the long run, as overall species richness was not significantly correlated with the abundance of RL species in sedimentary and littoral assemblages. A species is probably more likely to become extinct with a smaller population size, due to the pronounced effects of ecological drift (Gilbert and Levine, 2017, Fodelianakis et al., 2021). Instead, the combination of species richness and uniqueness is suggested, both of which are complementary components of the assemblages RL status, i.e. RL richness and RL abundance.

5.7 Conclusions

This study substantiates the high conservation value of mountain lakes as documented by a high number, share and abundance of endangered diatom taxa. The ecological vulnerability of the studied lakes in light of eutrophication and fish stocking was demonstrated through decreased shares and abundances of Red List taxa respectively. It is likely that entire lake ecosystems may be altered through the effects of eutrophication, due to external sources and top-down control as well as a change of nutrient cycling through introduced fish. This necessitates restoration measures, such as a stop to fish stocking, lake fencing, a decrease of cattle densities, and mitigation of infrastructure impacts. The results call for the better inclusion of small mountain lakes within legal frameworks such as the European Water Framework Directive. Moreover, our findings suggest the broad applicability of diatoms as bioindicators. Their power to identify endangered freshwater habitats and threats to their biodiversity significantly enhanced by consideration of regional Red Lists of diatoms. It is important to calculate the share of Red List taxa and their abundance per sample as these parameters provide important information on impairments and the conservation value of lakes, compared to the sheer richness of Red List taxa. From a methodical point of view, diatom-based biomonitoring should include sedimentary samples wherever feasible, as the temporal integration of environmental conditions makes them the most robust indicators of eutrophication or fish stocking. Further research may reveal whether multiple sampling of the littoral and pelagic zone leads to converging results between both methods. Finally, diatom α diversity and assemblage uniqueness, i.e. the local contribution to β diversity, were successfully applied to assess the calculated Red List indices. Both components of species diversity contribute complementary information about the conservation value of aquatic ecosystems. At least basic information regarding human disturbance and environmental conditions is necessary for a sound interpretation of assemblage uniqueness.

6 General discussion

This thesis demonstrated the importance of deterministic and stochastic processes for diatom diversity patterns within mountain lakes of the northern European Alps. Stochastic community patterns are due to dispersal (Chapter 4), while deterministic structuring is controlled by environmental variables (Chapter 3 and 4) and species interactions (Chapter 5). Specifically, Chapter 3 demonstrated the dominance of the planktic diatom *Cyclotella comensis* under low turbulence, high water temperature and elevated nitrate level. Total phosphorus, water temperature, and lake depth were identified as drivers of diatom β-diversity in Chapter 4, while diatom α-diversity was constrained by lake size, conductivity and water temperature. Limitation of dispersal was contributing to the explained variance among littoral and planktic assemblages but was less important for sedimentary diatoms. Chapter 5 revealed the suppression of Red List diatom species due to fish stocking and through direct human impacts that lead to eutrophication. This resulted in low uniqueness of diatom assemblages, causing the homogenization of the lake diatom diversity.

Former work has proven that altered lake water temperatures due to climate change impact sedimentary diatoms with varying importance depending on lake depth and elevation (Kuefner, 2021, Hofmann, 2021). This Chapter investigates how climate change impacts on within-lake processes may constrain ecological processes important to diatom diversity. Moreover, the effects of human impacts are elucidated and their inference with assemblage resilience is discussed. Finally, an outlook on future conservation of mountain lakes is provided.

6.1 Within-lake processes under climate change

6.1.1 Mixing regime

Among the most important effects of climate change on mountain lakes is a more stable stratification due to the increase of water temperature. This leads to a higher ratio of planktic to benthic abundance in the sedimentary diatom assemblages (Hofmann, 2021, Kuefner, 2021), a pattern that has also been detected in other climates such as the Ecuadorian Andes (Benito et al., 2019). The results of this thesis provide additional insights by showing that stable lake stratification can lead, at least temporally, to the dominance of a single planktic taxon in the pelagic zone (Chapter 3). However, stratification not only impacts planktic diatoms, but also the interference among planktic, littoral and sedimentary assemblages through dispersal (Reynolds, 1993). In this study, the share of benthic diatoms in the planktic samples varied between 0% and 100%, with a decreasing number of benthic forms under more stable stratification. These differences may have consequences at the regional scale.

The importance of ecological processes for the planktic assemblages varies among lakes with constant mixing, intermittent mixing and stable stratification (Figure 24). Overall, warming water temperatures will increase the frequency of intermittent conditions and stable stratification (Niedrist et al., 2018). Constant mixing (<1/day) during the growing season is dictated by very high dispersal rates of benthic species from littoral habitats to the pelagic zone (Reynolds, 1993), which corresponds to lake internal mass effects (Leibold et al., 2004). Under such conditions, high α-diversity but low within-lake β- and γ-diversity can be expected (Thompson et al., 2020). This was reflected by a diverse planktic community with more than 20 species, but within-lake β-diversity was low due to the homogenization of assemblages (Figure S 18). A stochastic component is inherent because of the important role of dispersal (Hubbell, 2001), but species traits such as small cell size (Reynolds, 1993) or motility (Passy, 2007, Jamoneau et al., 2018) may select for the within-lake dispersal, adding a strong deterministic component to the scenario. In the study lakes, this was reflected by high abundances of small-celled taxa from the genera *Achnanthidum* and *Encyonopsis,* while highly silicified taxa from the genus *Staurosira* were seldom. The projected upward shift of macrophytes due to climate change (Kuefner, 2021) may further constrain the dispersal of diatom species. In turn, the maintenance of diatoms in the water column, i.e. their ability to achieve net growth rates, depends on their reproduction rate ("density-independent response") as well as sinking losses and herbivory ("density-dependent interactions") (Thompson et al., 2020, Huisman et al., 2004). The predation on diatoms under mixing conditions is complex, however, most studies predict a lower rate of predator-prey encounters compared to stable stratification (Kiorboe and Saiz, 1995, Yamazaki, 1996, Botte et al., 2013). Thus, the scenario of polymictic conditions marks the state with a high importance of stochasticity and weak species interactions, while selection is mainly based on species traits.

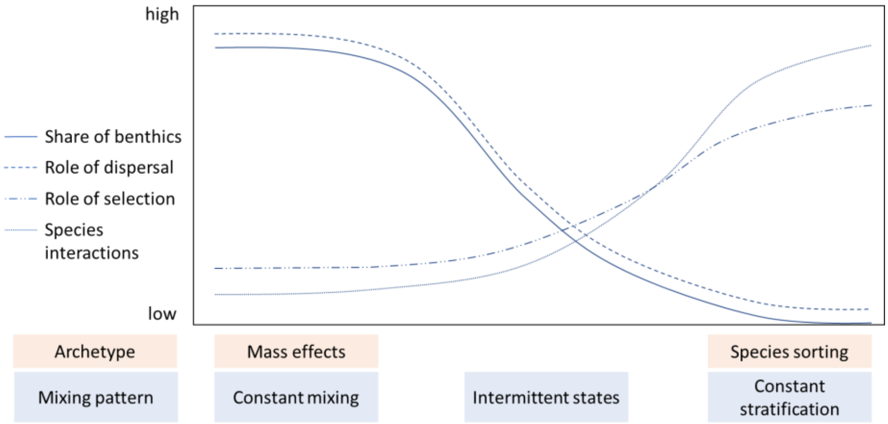

Figure 24: Lake mixing patterns constrains ecological processes and the share of benthic species in the pelagic diatom assemblages, leading to a transition among metacommunity archetypes.

The second scenario describes a state of intermittent phases of stratification and mixing lasting up to several days. Dispersal processes are less important than during polymixis, while the role of species interactions increases due to a higher encounter rate of predator and prey during phases of stratification (Tilman, 1977). This may lead to trade-offs between competition-predator avoidance that can effectuate coexistence of disparate competitors (Sommers and Chesson, 2019). This state can be characterized by a temporary variant mixture of benthic and planktic diatoms. The latter group may overcome adverse environmental conditions through resting stages (Round et al., 1990), corresponding to the concept of storage effects that may strengthen species coexistence patterns (Chesson, 2000). Species coexistence may further be enhanced by the spatial variability of nutrient concentrations (Tilman, 1977). Overall, high pelagic α- and β-diversity of intermittently mixing lakes can be expected due to niche effects and species coexistence. Such a condition is also predicted by the intermediate disturbance hypothesis (IDH) (Shea et al., 2004).

Finally, dimictic lakes with constant stratification during the growing season mark a state of low disturbance and high importance of competitional effects. Coexistence theory predicts that such a state leads to the dominance of one species, if species are stronger interspecific than intraspecific competitors (Chesson, 2000), a single resource is limiting (Tilman, 1977) and competition-predator avoidance is of minor importance (Sommers and Chesson, 2019). Chapter 3 describes how this state is nearly reached through the dominance of *Cyclotella comensis* during stable stratification in phosphate-limited lakes with profound thermoclines and high levels of nitrate and major ions. Coexistence of centric diatoms with long-spined taxa from the genus *Fragilaria* was found in lakes with lower nitrate levels and low temperatures. Overall, this scenario marks low planktic α-diversity but high within-lake β-diversity. Selection processes are important and therefore water properties such as lake trophic level determine within-lake γ-diversity. Further insight into plankton dynamics in mountain lakes will be gained through a high temporal sampling frequency of phyto- and zooplankton, combined with continuous assessment of physical and chemical water properties. Interpretation of observations may be further enhanced by ecological models that include competition, predation and competition-predator avoidance (Leibold et al., 2022, Thompson et al., 2020).

In sum, the interaction of within-lake dispersal and selection processes sustains the diversity of planktic diatom communities in mountain lakes, which has effects on lake diatom assemblages of the whole lake. Even though an equilibrium state is never reached in phytoplankton (Reynolds, 1993, Scheffer et al., 2003) deep, stratified lakes come closest to this state among the investigated lakes. The predicted increase in stable lake stratification may enhance predator-prey dynamics and the effects of fish stocking. Direct human impacts that lead to eutrophication and supress species richness may also be more pronounced under stable stratification due to the higher importance of selection processes in the pelagic zone. Moreover, a strong regional dispersal limitation (Chapter 4) can be assumed for littoral diatoms, as the dispersal of benthic species into the pelagic is weaker, decreasing their dispersal by wind, insects, and birds. In terms of ecological functioning of the lakes, an important question is if ecological tipping points are reached that lead to a fundamental change of biotic interactions. Kuefner

(2021) proposed such a tipping point when pelagic assemblages shift from benthic to planktic dominance. Functionally, benthic and planktic forms may be similar. They compete for resources with other planktic autotrophs and provide prey for zooplankton. Thus, these tychoplanktic assemblages can be considered as an integral and competitive feature within the pelagic zone, as demonstrated within mesocosm experiments (Garstecki and Wickham, 2001). A tipping point may be reached if feeding mechanisms of invertebrates are specific for planktic or benthic forms, leading to concomitant community shifts among higher trophic levels (Moens et al., 2014, Leibold, 1999) or after a fundamental shift among primary producers. Generally, the predicted stronger among-lake dispersal limitation may be relevant for the resilience of diatom communities, i.e. their ability to recover after local extinctions, as has been demonstrated for the soil microbiome (Sorensen and Shade, 2020) (see Chapter 6.2). Climate-driven desiccation events in lakes (Kuefner, 2021) may further reduce diatom metacommunity resilience by increasing dispersal distance (Crespo-Miguel et al., 2022).

6.1.2 Turbidity

Climate change impacts on mountains are an upward shift of the treeline (Gobiet et al., 2014), intensified weathering through more frequent extreme precipitation (Rosbakh et al., 2014), shorter duration of ice cover and snow cover in the catchment (Moser et al., 2019b) and higher water temperatures through climate forcing (Gobiet et al., 2014) and heat waves (Woolway et al., 2021). The consequences are increased weathering rates leading to additional inputs of nutrients and organic matter (Kamenik et al., 2001), causing higher turbidity (Figure 25).

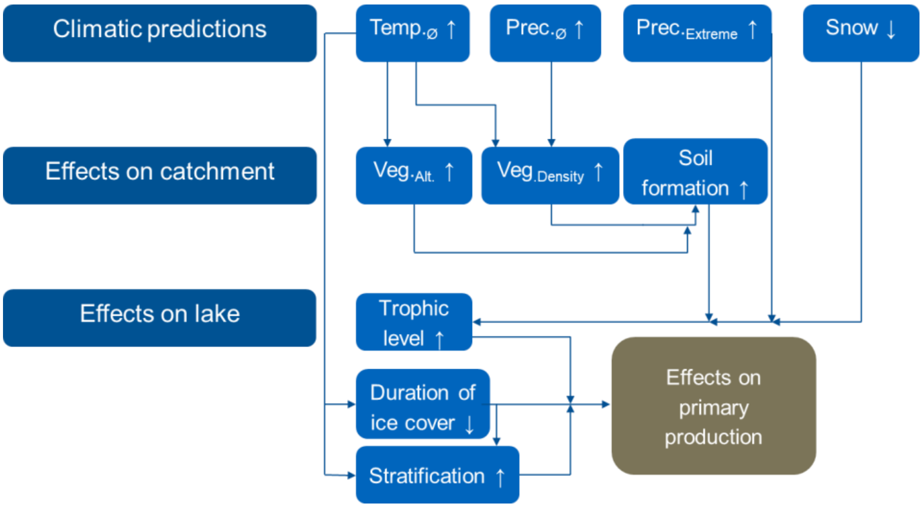

Figure 25: Interplay of Climatic prediction based on future climate change, effects on catchment level and predicted consequences on the aquatic environment in mountain lakes.

Within the study lakes, diatom assemblages were more dissimilar if Secchi depth was less than maximal depth, i.e. if lakes were more turbid (Figure S 19). Thus, future climate change will increase benthic α-diversity of fully illuminated lakes due to stronger species sorting along the lake depth gradient

(Hofmann et al., 2020). This will come along with higher within-lake β-diversities. Even if increased turbidity enhances γ-diversity within the 15 lakes that are still fully illuminated, regional γ-diversity will decrease as lakes become more similar, i.e. fully illuminated lakes are lost. The observed increase of strong light competitors such as *Staurosira* species exemplifies this trend (Hofmann, 2021, Kuefner, 2021). Increasing eutrophication through climate change will further enhance this trend (Chapter 5).

To conclude, stronger and longer-lasting stratification may enhance the separation of the within-lake diatom assemblages (Chapter 6.1.1), while within and among lake dispersal will decrease. Higher turbidity will increase diatom diversity within some lakes but will lead to lower regional diversity. In combination with increasing dispersal limitation this will suppress regional γ-diversity (Thompson et al., 2020).

6.2 Historical legacies and diatom resilience

Communities are considered ecologically resilient if they can tolerate a high degree of disturbance before switching to an alternative stable state (Gunderson, 2000). An example for this is the abrupt shift between phytoplankton and macrophyte dominance in shallow and productive lakes (Scheffer et al., 1993). The role of historical legacies in community response to disturbance can be substantial. Legacies may arise from altered phenotypic plasticity or genetic diversity, as well as adaption and acclimation as a response to previous conditions that either reduce or increase resilience (Hawkes and Keitt, 2015).

Change of species richness

Ecosystem stability is mediated by resistance and resilience. While species diversity differently affects both components (Baert et al., 2016, Isbell et al., 2015) a tendency for higher stability with increasing species richness is observed (Pimm et al., 2014, Hooper et al., 2012). Even though the ecological resilience of mountain lakes is high (Benito et al., 2021), direct human impacts may have supressed local species richness in the study lakes (Chapter 5). Moreover, the decreasing abundance of oligotraphentic taxa due to eutrophication may be associated with lower genetic diversity, possibly increasing the effects of drift that can lead to further species loss (Gilbert and Levine, 2017, Fodelianakis et al., 2021). Altered within-lake processes (Chapter 6.1) may limit recolonization (Hawkes and Keitt, 2015), leading to open niches and consequently lower resource use efficiency. This may allow other groups of primary producers to become established in the lake systems, increasing the probability of their dominance if other factors such as trophic level become suitable. For example, cyanobacteria dominance becomes likely at TP levels among 30-50 µg/l (Salmaso and Tolotti, 2021) and this process may be accelerated through the described human influences on diatoms. Subalpine lakes that experience the strongest climate change effects (Kuefner et al., 2020a), with elevated trophic state and/or fish stocking such as lake Röthensteiner See, Soinsee Süd, Soinsee Nord, Grünsee West and Soiernsee West are especially vulnerable for such a regime shift.

Acclimation effects

Acclimation effects from fish stocking are known for zooplankton species, e.g. through higher growth rates that prevailed after fish eradication and under the simulation of climate change, leading to community shifts (Symons et al., 2021). Similar adaptions may also be found among diatoms as a response to abrupt environmental shifts, possibly explaining some of the observed community patterns in Chapter 5. For example, rapid nutrient enrichment due to fish stocking may trigger the upregulation of genes coding for different P-transporters, as has been observed for marine diatoms (Caceres et al., 2019). A higher k_s (half-saturation constant for nutrient uptake efficiency) can be the consequence, leading to competitive advantages of certain species, followed by community shifts (Tilman et al., 1982). This could also explain the observed reinforcement of climate change effects through direct anthropogenic pressures among the study lakes (Hofmann, 2021, Kuefner, 2021), as climate change leads to higher nutrient inputs that would favour species that are already acclimated to such conditions. More generally, the often observed hysteresis when the same nutrient loading supports higher biomass during oligotrophication than during eutrophication of lakes (Lampert and Sommer, 2007) can also be explained by such acclimation effects. Within the lake set of this thesis, an example of a fish-mediated community shift can possibly be seen in the sediment core of lake Taubensee, where around 1900 *Cyclotella comensis* rapidly progressed*,* possibly leading to the recession of the previously dominant *C. radiosa* and the current dominance of *C. comensis* (Chapter 3 and 5). A similar shift was observed for *C. cf. comensis* around 1900 in lake Engeratsgundsee, marked by an abrupt shift from sub-dominance (c. 20%) to persistent dominance (c. 70%, Chapter 3 and 5) (Kuefner, 2021). Despite the temporal gap between these major community shifts and the onset of climate change around 1970, both processes may be entangled. Besides fish stocking other triggers for the observed shifts could be debris flows after storms, or land use change (e.g., clear cutting). This could be revealed by further in-depth studies of these lakes or historical investigations.

Elevation and resilience

In this thesis, a weak decrease of littoral α-diversity with altitude was detected (Chapter 4), suggesting a lower resilience of diatoms at higher elevation (c.f. Chapter 6.2). If this pattern of species richness in temperate mountain lakes is representative may be revealed by including mountain lakes of the Central and Southern European Alps, expanding the elevational gradient to approximately 3,400 masl (Viani et al., 2022). Diatom assemblage resilience is also mediated by species specific traits such as elevational range size. Rapoport´s rule states that species occurring at higher elevations have larger elevational ranges than species at lower elevations (Stevens, 1992). The few studies that have tested the Rapoport´s rule on eukaryotic algae in temperate freshwater habitats came to different findings. No elevational relationship was found for diatoms in Scandinavian streams (Teittinen et al., 2016), while soil eukaryotic algae in Switzerland conformed to Rapoport´s rule as their geographic and elevational range increased with elevation (Fernandez et al., 2021). Further studies on diatom range sizes will help to elucidate if resilience of diatom assemblages depends on altitude. This will sharpen predictions of their responses to climatic changes.

6.3 Implications for conservation

The results of this thesis and previous work suggest that the diatom assemblages within the study lakes respond strongly to direct human impacts (Chapter 5) and to climate change (Chapter 3, Hofmann, 2021, Kuefner, 2021). Furthermore, species loss due to eutrophication may decrease resilience of the biotic communities (Chapter 6.2). This will be reinforced by the amplification of the already important dispersal limitation among lakes (Chapter 4) resulting from weaker dispersal within lakes due to enhanced stratification (Chapter 6.1). The response of an ecological system to environmental change can be elastic if the disturbance lessens and the system is than stable in its disturbance regime (Davis 2018). This enables the restoration of the original species pool and processes, i.e. ecosystem functioning, if enough time is provided and species from other lakes can disperse. Examples are the reorganization of the original trophic cascade in US mountain lakes after fish eradication and immigration and resettlement by original species (Knapp et al., 2001). The study lakes experienced similar disturbances, thus restoration measures that target the direct human impacts may be effective in re-establishing locally extinct species, restoring trophic cascades and mitigating the effects of climate change. The most important direct human impacts detected in this thesis and previous work are fish stocking, cattle herding, damming and tourism.

Fish stocking

The strongest direct impact on lakes is the introduction of fish, which lowers the abundance of Red List species and dramatically changes species composition, as reflected by sedimentary diatom samples (Chapter 5). It is therefore of paramount importance to preserve the fishless lakes and to prohibit fish stocking. In stocked lakes, a stop of further stocking can lead to a gradual reduction of fish abundance and biomass if cannot reproduce naturally (Schindler et al., 2001). This may be the case for the alpine lake Engeratsgundsee. In lakes with natural fish reproduction, active eradication of fish can lead to fast recovery of the original species assemblages, trophic interactions, and trophic state (Tiberti et al., 2019, Toro et al., 2020, Parker et al., 2001). Among the mechanical removal methods, gill netting provided the best results (Tiberti et al., 2021), especially if applied in several consecutive seasons (Parker et al., 2001). Eradicating alien fish is suggested in EU regulations as a mitigate measure for human impacts and funding is available under the EU "Life" programme (EU, 2022). Based on these legal and financial frameworks, a successful implementation will depend on social factors and public opinion (Estevez et al., 2015). Early stakeholder consultation and public information is essential, especially since mountain lakes are popular recreation areas (Schirpke et al., 2021a). Like in any aquatic conservation measure, prior investigation of conservation object, scope and possible secondary influence (e.g., reintroduction of fish through streams) that may jeopardize the conservation goal is important (Geist, 2015). Moreover, realistic time planning may prevent public disappointment. This can be informed by new modelling approaches to predict the number of seasons necessary for complete eradication of fish in mountain lakes through mechanical methods (Tiberti et al., 2021).

Cattle herding

Intensive cattle herding was the second most important factor for degradation of the study lakes. Among the lakes with the highest impacts TP content was three- to fourfold higher than under natural conditions (Chapter 5). Effective reduction of cattle-generated nutrients in catchments of mountain lakes is pivotal, especially since it is assumed that heavy rain events induced by climate change will increasingly transport cattle dung into the lakes via stormwater run-off.

Currently, the highest TP level among the study lakes was 20.8 µg/l. Total biomass of diatoms sharply decreases at 30-50 µg/l TP and cyanobacteria will become the dominant group (Salmaso and Tolotti, 2021). Corresponding TP levels appear to be realistic for some of the study lakes and increasing water stability (Chapter 6.1) (Reynolds et al., 1987) and historical legacies (Chapter 6.2) may promote cyanobacteria, potentially leading to ecological tipping points and changes of ecosystem functioning. The effect of cattle herding on mountain lake primary production strongly depends on grazing pressure. While low to moderate grazing pressure has been found to have little or no impact on trophic levels, high livestock densities can have disparately strong impacts (Tiberti et al., 2014a). Thus, cattle herding and a low trophic state of mountain lakes are not mutually exclusive, but it is of primary importance to take measure to avoid strong herding pressures. Impacts on lakes has been shown to be large when cattle density is very high, livestock have free access to the lakes and tributaries and nutrients easily reach the lakes from degraded land areas (Tiberti et al., 2014a). Mitigation measures include fencing, keeping livestock away from lake tributaries and reduction of cattle density. Reduced cattle density may additionally help to recover overgrazed pastures and improve nutrient retention in the catchment (Sun et al., 2017).

For montane lakes with low water level fluctuations, the enclosure of cattle may also result in restoration of the riparian vegetation, which contributes to nutrient retention (Nussle et al., 2017) and potentially mitigates the effects of climate-induced warming through shading of the shoreline

(Miranda and Raines, 2019). As the exact nutrient pathways from the cattle excrements to mountain lakes are still unknown (Derlet et al., 2012), a stepwise approach appears appropriate to track the response of the lake systems. The ecological monitoring should include lake trophic state (TP, Chlorophyl a) and the share of diatom Red List species. A stepwise approach also supports assessing impacts on the vegetation structure of the pastures. Too low herding intensity may lead to the reforestation of grasslands in the subalpine region (Schirpke et al., 2017), possibly resulting in the loss of plant diversity (Fontana et al., 2020). A sensitive approach and close cooperation with farmers are necessary to avoid conflicts, especially as cattle herding rights often date back a long time and their implementation is coupled with public subvention (Streifeneder et al., 2018).

Damming

The damming leads to a very rapid change of lake abiotic conditions (Salmaso and Tolotti, 2021). Especially for lakes with inflow, the water level rises quickly, and the lake water is diluted. However, the strongest impact on lake´s biota are expected from the mineralization of the flooded soil and vegetation layer. These mineralization processes will release high amounts of nitrogen compounds, as well as phosphorus stored in plants. This mineralization potential decreases with altitude (Zhang et al., 2012), probably explaining the lower impact of a dam on an alpine lake compared to subalpine lakes (Chapter 5). Due to the potential eutrophication effect, damming of mountain lakes should be prohibited especially for montane to subalpine lakes to prevent progressing degradation of these aquatic ecosystems. To better understand the impacts of dams on high mountain lakes further research should focus on the effects of nutrient inputs resulting from dams and those from other sources such as cattle herding, which often do co-occur.

Tourism

Tourism can have multiple effects on mountain lakes. The correlation of nearby hiking trails and mountain lake degradation suggests strong interactions of tourists with the lakes ecological status (Senetra et al., 2020). Moreover, mountain huts may lead to eutrophication of lakes (Hofmann et al., 2021, Muri and Brancelj, 2003, Muri et al., 2018, Sienkiewicz and Gasiorowski, 2014) and the results in Chapter 5 of this thesis underpin this finding. However, it is not straightforward to disentangle the various possible interactions of infrastructure, people roaming the sites and the lake response. A principal step for the lakes of the data set from this thesis with huts and restaurants directly located on the shoreline would be to check the sewage treatment systems for their efficiency and compile solutions based on previous applied research (BOKU, 2010, Menz, 2008).

7 Conclusions and outlook

Among the 43 lakes the local environment was identified to significantly constrain metacommunity structure of sedimentary, planktic and littoral diatoms, while pure spatial effects on diatom assemblages structure were detected mainly for littoral and planktic diatoms. This suggests that both, environmental filtering and dispersal limitation structure diatom metacommunities. Former paleolimnological works revealed varying temporal beta diversity patterns of subfossil diatom assemblages from a subset of the lakes of this thesis (Hofmann, 2021, Kuefner, 2021). The results show that the different patterns were caused by disparate responses on climate change mediated by the position of the lakes along the elevational gradient, i.e. they were spatially structured. Lake properties that were related to disturbance such as lake mixing and eutrophication were proposed to cause varying stability of the systems (Donohue et al., 2016), i.e. non-linear community responses that may result in tipping points. In this respect, a future challenge will be to assess diatom dispersal rates to quantify colonization-extinction patterns as a basis to understand changes of diatom diversity through space and time. Further collaboration between paleolimnologists, limnologists and modellers are needed to solve this challenging yet stimulating task. Dispersal rates of specific diatom species and the influence of distance may be assessed through mesocosm experiments at the lake sites. Moreover, this approach may reveal the influence of dispersal vectors, for example by using photo traps and insect traps. Thereupon the relative role of wind dispersal and the passive transport by organisms may be studied, a topic that is on of the roots of diatom biogeography.

This work highlights the vulnerability of mountain lake primary producers towards eutrophication and disturbance of the trophic cascade, i.e. fish introduction. A next step will be to study the responses of the zooplankton on such alterations. Restoring the fishless state of high mountain lakes is suggested and should be backed by a long-term monitoring of the lower trophic level organisms. Recently, powerful modelling techniques known as “species distribution modelling” were developed and these may be expanded across several trophic levels. Long-term monitoring programs that capture ecological changes after restoration of lakes will be a source of valuable data to calibrate ecological models and path the way for the much needed unification of theoretical and practical ecological research. Generally, small mountain lakes should be better considered in national and European conservation strategies due to their unique and diverse aquatic communities that are still less well studied than their lower elevation counterparts.

8 Acknowledgements

I would like to thank Prof. Dr. Jürgen Geist for his guidance and dedicated efforts that were a strong motivation to improve and advance this work. I would also like to express my gratitude to my advisor Dr. Uta Raeder for her support and open ear, not just in scientific aspects, and for teaching me the foundations of Limnology during my studies. I highly appreciated to do this PhD at the Limnological Research Station in Iffeldorf, a unique place to study and to work at, hopefully for generations of Limnologists to come. Moreover, I gratefully acknowledge funding for my research through a PhD scholarship by the Deutsche Bundesstiftung Umwelt (DBU).

I would like to thank my mentor Dr. Petra Werner for her critical but motivating view that helped me to improve my work. Special thanks are due to my long year colleague Dr. Andrea Hofmann who introduced me to the miraculous universe of the diatoms during my Master´s thesis.

I am grateful for the time spent with my dear colleague and friend Dr. Wolfgang Küfner who was the most upright companion I could imagine during the intense two year sampling campaign. Shortly after we celebrated his successful PhD defence out in the mountains Wolfi tragically passed away in an alpine accident.

I would like to thank my master, bachelor and project students Lorenz Tschampel, Lena Hofmeister, Diana Neif, Kristina Bichler and Lukas Zwosta. Without their courageous support in the field even under grim conditions and their contributions to laboratory work this thesis would not have been possible and certainly would have been far less fun!

Many thanks go to my co-doctoral students Simon Baier, Dr. Franzi Bauer, Dr. Nico Corti, Dr. Tine Fritz, Dr. Basti Lenz, Dr. Steffi Rüegg and Dr. Pia Scheerer for sharing all the joys and sorrows along this journey. I also want to thank all the staff at the Limnological Station, especially Dr. Markus Hofmann who is the master of the machines and helped me a lot with laboratory work. Finally, I would like to thank all the warm hearted people in Iffeldorf how made this research station such a unique place to work.

I am thankful to my friends and my sister Barbara who always had an open ear when scientific life was trouble, cheered me up and never let me down. You encouraged me to make it until the finish line!

Mein tiefer Dank gebührt meinen Eltern Lieselotte und Joachim für ihre beständige Unterstützung auf meinem Weg, für ihre Liebe und Fürsorge!

9 Publication list and author contributions

Peer-reviewed publications included in this thesis:

OSSYSSEK, S., GEIST, J., WERNER, P. & RAEDER, U. 2020. Identification of the ecological preferences of Cyclotella comensis in mountain lakes of the northern European Alps. Arctic Antarctic and Alpine Research, 52, 512-523.

Author contributions: SO developed the concept and design of this study with input from JG, PW and UR. SO conducted the fieldwork and the microscopic analyses. SO analysed the data, performed the statistical analysis and wrote a first draft of this paper with input by JG, PW and UR. All authors read and approved the final version.

OSSYSSEK, S., HOFMANN, A., GEIST, J. & RAEDER, U. 2022a. Diatom Red List species reveal high conservation value and vulnerability of mountain lakes. Diversity 2022, 14, 389.

Author contributions: SO developed the concept and design of this study with input from JG and UR. SO and AH conducted the fieldwork and the microscopic analyses. SO analysed the data, performed the statistical analysis and wrote a first draft of this paper with input by JG and UR. All authors read and approved the final version.

Currently under review in Hydrobiologia:

OSSYSSEK, S., HOFMANN, A., GEIST, J. & RAEDER, U. 2022b. Sedimentary, planktic and littoral diatom metacommunities in mountain lakes of the northern European Alps show divergent assembly patterns.

Author contributions: SO developed the concept and design of this study with input from JG and UR. SO and AH conducted the fieldwork and the microscopic analyses. SO analysed the data, performed the statistical analysis and wrote a first draft of this paper with input by JG and UR. All authors read and approved the final version.

Oral contributions related to the PhD thesis:

OSSYSSEK, S. Untersuchung der Diatomeengesellschaften montaner bis alpiner Seen der Nordalpen und Entwicklung von Diatomeen-Nährstofftransferfunktionen. DBU Stipendiatenseminar Volkenroda, 2017. Volkenroda, Germany.

OSSYSSEK, S. Bergseen im Klimawandel - Entwicklung von Modellen zur Rekonstruktion der Nährstoffverhältnisse. DBU Stipendiatenseminar Ostritz, 2018a. Ostritz, Germany.

OSSYSSEK, S. A training set for diatom – phosphorus quantitative reconstructions for montane to alpine lakes of the northern Alps. International Diatom Symposium, 2018b. Berlin, Germany.

OSSYSSEK, S. A training set for diatom – phosphorus quantitative reconstructions for montane to alpine lakes of the northern Alps. Unravelling the Past and Future of Lakes - IPA-IAL Joint Meeting, 2018c. Stockholm, Sweden.

OSSYSSEK, S. Untersuchungen der Kieselalgengemeinschaften von Bergseen der Nordalpen. Presentation at the Chair of Aquatic Ecology of the Ludwig-Maximilians-Universität, 2018d. Munich, Germany.

RAEDER, U., KUEFNER, W. & OSSYSSEK, S. Bergseen im Klimawandel - Einfluss und Anpassung. 40 Jahre Nationalpark Berchtesgaden, 2018. Berchtesgaden, Germany.

HOFMANN, A., KUEFNER. W., OSSYSSEK. S. Bergseen im Klimawandel - Verschiebung der Primärproduzenten in Bergseen als Indikator des Klimawandels. Workshop BergSEEN im Klimawandel, 2019. Iffeldorf, Germany.

OSSYSSEK, S. Bergseen im Klimawandel. P Seminar Q 11 Gymnasium Holzkirchen, 2019a. Holzkirchen, Germany.

OSSYSSEK, S. Kieselalgen in Bergseen der Nordalpen als Indikatoren für Umweltveränderungen. DBU Stipendiatenseminar Ohrbeck, 2019b. Ohrbeck, Germany.

Poster presentations related to the PhD thesis:

HOFMANN, A., KUEFNER W., OSSYSSEK S., RAEDER, U. Bergseen im Klimawandel. Jahrestagung der deutschen Gesellschaft für Limnologie (DGL) und der deutschen und österreichischen Sektion der Societas Internationalis Limnologiae (SIL), 2016. Wien, Austria.

OSSYSSEK, S. & RAEDER, U. Kieselalgen in montanen bis alpinen Seen der Nordalpen. Gewässer im Wandel der Landschaft - 33. Jahrestagung der Deutschen Gesellschaft für Limnologie e.V., 2017. Cottbus, Germany.

HOFMANN, A., KUEFNER, W., OSSYSSEK, S., RAEDER, U. Mountain Lakes, and Climate Change. Central European Diatom meeting, 2017. Prague, Czech Republic.

10 References

AKAIKE, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control,* 19**,** 716-723.

ANDERSON, S. E., CLOSS, G. P. & MATTHAEI, C. D. 2020. Agricultural Land-Use Legacy, The Invasive Alga Didymosphenia geminata and Invertebrate Communities in Upland Streams with Natural Flow Regimes. *Environmental Management,* 65**,** 804-817.

ANDERSSON, B., GODHE, A., FILIPSSON, H. L., ZETTERHOLM, L., EDLER, L., BERGLUND, O. & RENGEFORS, K. 2021. Intraspecific variation in metal tolerance modulate competition between two marine diatoms. *Isme Journal*.

ANGELI, N., CANTONATI, M., SPITALE, D. & BERTALOT, H. L. 2010. A comparison between diatom assemblages in two groups of carbonate, low-altitude springs with different levels of anthropogenic disturbances. *Fottea,* 10**,** 115-128.

ANTONIADES, D., DOUGLAS, M. S. V. & SMOL, J. P. 2005. Quantitative estimates of recent environmental changes in the Canadian High Arctic inferred from diatoms in lake and pond sediments. *Journal of Paleolimnology,* 33**,** 349-360.

ARP, C. D., SCHMIDT, J. C., BAKER, M. A. & MYERS, A. K. 2007. Stream geomorphology in a mountain lake district: hydraulic geometry, sediment sources and sinks, and downstream lake effects. *Earth Surface Processes and Landforms,* 32**,** 525-543.

BAATTRUP-PEDERSEN, A., JOHNSEN, T. J., LARSEN, S. E. & RIIS, T. 2022. Alkalinity and diatom assemblages in lowland streams: How to separate alkalinity from inorganic phosphorus in ecological assessments? *Science of the Total Environment,* 823.

BAE, M. J., KWON, Y., HWANG, S. J., CHON, T. S., YANG, H. J., KWAK, I. S., PARK, J. H., HAM, S. A. & PARK, Y. S. 2011. Relationships between three major stream assemblages and their environmental factors in multiple spatial scales. *Annales De Limnologie-International Journal of Limnology,* 47**,** S91-S105.

BAERT, J. M., DE LAENDER, F., SABBE, K. & JANSSEN, C. R. 2016. Biodiversity increases functional and compositional resistance, but decreases resilience in phytoplankton communities. *Ecology,* 97**,** 3433-3440.

BARTOZEK, E. C. R., DA SILVA-LEHMKUHL, A. M., GREGORY-EAVES, I. & BICUDO, D. C. 2019. Environmental and spatial drivers of diatom assemblages in the water column and surface sediment of tropical reservoirs. *Journal of Paleolimnology,* 62**,** 245-257.

BASELGA, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography,* 19**,** 134-143.

BASELGA, A. 2013. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution,* 4**,** 552-557.

BASELGA, A. 2017. Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution,* 8**,** 799-808.

BASELGA, A. & ORME, C. D. L. 2012. betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution,* 3**,** 808-812.

BATTARBEE, R. W. 1984. Diatom analysis and the acidification of lakes. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 305**,** 451-477.

BATTARBEE, R. W., THOMPSON, R., CATALAN, J., GRYTNES, J. A. & BIRKS, H. J. B. 2002. Climate variability and ecosystem dynamics of emote alpine and arctic lakes: the MOLAR project. *Journal of Paleolimnology,* 28**,** 1-6.

BAUMAN, D., DROUET, T., DRAY, S. & VLEMINCKX, J. 2018. Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography,* 41**,** 1638-1649.

BEHRENFELD, M. J., HALSEY, K. H., BOSS, E., KARP-BOSS, L., MILLIGAN, A. J. & PEERS, G. 2021. Thoughts on the evolution and ecological niche of diatoms. *Ecological Monographs,* 91.

BENITO, X., FEITL, M. G., FRITZ, S. C., MOSQUERA, P. V., SCHNEIDER, T., HAMPEL, H., QUEVEDO, L. & STEINITZ-KANNAN, M. 2019. Identifying temporal and spatial patterns of diatom community change in the tropical Andes over the last c. 150 years. *Journal of Biogeography,* 46**,** 1889-1900.

BENITO, X., FRITZ, S. C., STEINITZ-KANNAN, M., VELEZ, M. I. & MCGLUE, M. M. 2018. Lake regionalization and diatom metacommunity structuring in tropical South America. *Ecology and Evolution,* 8**,** 7865-7878.

BENITO, X., LUETHJE, M., SCHNEIDER, T., FRITZ, S. C., BAKER, P. A., PEDERSEN, E. J., GAUZERE, P., NASCIMENTO, M. D., BUSH, M. & RUHI, A. 2021. Ecological resilience in tropical Andean lakes: A paleolimnological perspective. *Limnology and Oceanography*.

BENNDORF, J., BOING, W., KOOP, J. & NEUBAUER, I. 2002. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology,* 47**,** 2282-2295.

BENNION, H., FLUIN, J. & SIMPSON, G. L. 2004. Assessing eutrophication and reference conditions for Scottish freshwater lochs using subfossil diatoms. *Journal of Applied Ecology,* 41**,** 124-138.

BERGSTRÖM, A.-K. 2010. The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. *Aquatic Sciences,* 72**,** 277-281.

BERGSTROM, A. K. 2010. The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. *Aquatic Sciences,* 72**,** 277-281.

BIGGS, J., VON FUMETTI, S. & KELLY-QUINN, M. 2017. The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. *Hydrobiologia,* 793**,** 3-39.

BIVAND, R. S. & WONG, D. W. S. 2018. Comparing implementations of global and local indicators of spatial association. *TEST,* 27**,** 716-748.

BLANCHET, F. G., LEGENDRE, P. & BORCARD, D. 2008. Forward selection of explanatory variables. *Ecology,* 89**,** 2623-2632.

BOHM, M., COLLEN, B., BAILLIE, J. E. M., BOWLES, P., CHANSON, J., COX, N., HAMMERSON, G., HOFFMANN, M., LIVINGSTONE, S. R., RAM, M., RHODIN, A. G. J., STUART, S. N., VAN DIJK, P. P., YOUNG, B. E., AFUANG, L. E., AGHASYAN, A., GARCIA, A., AGUILAR, C., AJTIC, R., AKARSU, F., ALENCAR, L. R. V., ALLISON, A., ANANJEVA, N., ANDERSON, S., ANDREN, C., ARIANO-SANCHEZ, D., ARREDONDO, J. C., AULIYA, M., AUSTIN, C. C., AVCI, A., BAKER, P. J., BARRETO-LIMA, A. F., BARRIO-AMOROS, C. L., BASU, D., BATES, M. F., BATISTELLA, A., BAUER, A., BENNETT, D., BOHME, W., BROADLEY, D., BROWN, R., BURGESS, J., CAPTAIN, A., CARREIRA, S., CASTANEDA, M. D., CASTRO, F., CATENAZZI, A., CEDENO-VAZQUEZ, J. R., CHAPPLE, D. G., CHEYLAN, M., CISNEROS-HEREDIA, D. F., COGALNICEANU, D., COGGER, H., CORTI, C., COSTA, G. C., COUPER, P. J., COURTNEY, T., CRNOBRNJA-ISAILOVIC, J., CROCHET, P. A., CROTHER, B., CRUZ, F., DALTRY, J. C., DANIELS, R. I. R., DAS, I., DE SILVA, A., DIESMOS, A. C., DIRKSEN, L., DOAN, T. M., DODD, C. K., DOODY, J. S., DORCAS, M. E., DE BARROS, J. D., EGAN, V. T., EL MOUDEN, E., EMBERT, D., ESPINOZA, R. E., FALLABRINO, A., FENG, X., FENG, Z. J., FITZGERALD, L., FLORES-VILLELA, O., FRANCA, F. G. R., FROST, D., GADSDEN, H., GAMBLE, T., GANESH, S. R., GARCIA, M. A., GARCIA-PEREZ, J. E., GATUS, J., GAULKE, M., GENIEZ, P., GEORGES, A., GERLACH, J., GOLDBERG, S., GONZALEZ, J. C. T., GOWER, D. J., GRANT, T., GREENBAUM, E., GRIECO, C., GUO, P., et al. 2013. The conservation status of the world's reptiles. *Biological Conservation,* 157**,** 372-385.

BOKU 2010. Integrale Evaluierung der Ver- und Entsorgungssysteme bei Berg- und Schutzhütten. Deutsche Bundesstiftung Umwelt, Deutscher Alpenverein, Lebensministerium Österreich.

BORCARD, D., LEGENDRE, P. & DRAPEAU, P. 1992. PARTIALLING OUT THE SPATIAL COMPONENT OF ECOLOGICAL VARIATION. *Ecology,* 73**,** 1045-1055.

BOTTE, V., D'ALCALA, M. R. & MONTRESOR, M. 2013. Hydrodynamic interactions at low Reynolds number: an overlooked mechanism favouring diatom encounters. *Journal of Plankton Research,* 35**,** 914-918.

BREMBU, T., MUHLROTH, A., ALIPANAH, L. & BONES, A. M. 2017. The effects of phosphorus limitation on carbon metabolism in diatoms. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 372.

BRIED, J. T. & VILMI, A. 2022. Improved detection of mass effect species assembly for applied metacommunity thinking. *Journal of Applied Ecology,* 59**,** 921-926.

BROOKS, J. L. & DODSON, S. I. 1965. Predation Body Size and Composition of Plankton. *Science,* 150**,** 28-&.

BRZEZINSKI, M. A. 1985. The Si:C:N ratio of marine diatoms: Interspecific variability and the effect of some environmental variables. *Journal of Phycology,* 21**,** 347-357.

BUCKEL, J., OTTO, J. C., PRASICEK, G. & KEUSCHNIG, M. 2018. Glacial lakes in Austria - Distribution and formation since the Little Ice Age. *Global and Planetary Change,* 164**,** 39-51.

BULLOCK, A. M. & COUTTS, R. R. 1985. The Impact of Solar Ultraviolett-Radiation upon the Skin of Rainbow-Trout, Salmo-Gairdneri Richardson, Farmed at High-Altitude in Bolivia. *Journal of Fish Diseases,* 8**,** 263-272.

BUSSENI, G., CAPUTI, L., PIREDDA, R., FREMONT, P., MELE, B. H., CAMPESE, L., SCALCO, E., DE VARGAS, C., BOWLER, C., D'OVIDIO, F., ZINGONE, A., D'ALCALA, M. R. & IUDICONE, D. 2020. Large scale patterns of marine diatom richness: Drivers and trends in a changing ocean. *Global Ecology and Biogeography,* 29**,** 1915-1928.

CABRERA, S., LOPEZ, M. & TARTAROTTI, B. 1997. Phytoplankton and zooplankton response to ultraviolet radiation in a high-altitude Andean lake: short- versus long-term effects. *Journal of Plankton Research,* 19**,** 1565-1582.

CACERES, C., SPATHARIS, S., KAISERLI, E., SMETI, E., FLOWERS, H. & BONACHELA, J. A. 2019. Temporal phosphate gradients reveal diverse acclimation responses in phytoplankton phosphate uptake. *Isme Journal,* 13**,** 2834-2845.

CANTIN, A., BEISNER, B. E., GUNN, J. M., PRAIRIE, Y. T. & WINTER, J. G. 2011. Effects of thermocline deepening on lake plankton communities. *Canadian Journal of Fisheries and Aquatic Sciences,* 68**,** 260-276.

CANTONATI, M., BILOUS, O., SPITALE, D., ANGELI, N., SEGADELLI, S., BERNABÈ, D., LICHTENWÖHRER, K., GERECKE, R. & SABER, A. A. 2022a. Diatoms from the Spring Ecosystems Selected for the Long-Term Monitoring of Climate-Change Effects in the Berchtesgaden National Park (Germany). *Water,* 14**,** 381.

CANTONATI, M., FUREDER, L., GERECKE, R., JUTTNER, I. & COX, E. J. 2012. Crenic habitats, hotspots for freshwater biodiversity conservation: toward an understanding of their ecology. *Freshwater Science,* 31**,** 463-480.

CANTONATI, M., HOFMANN, G., SPITALE, D., WERUM, M. & LANGE-BERTALOT, H. 2022b. Diatom Red Lists: important tools to assess and preserve biodiversity and habitats in the face of direct impacts and environmental change. *Biodiversity and Conservation*.

CANTONATI, M., KELLY, M. & LANGE–BERTALOT, H. 2017. Freshwater benthic diatoms of Central Europe: over 800 common species used in ecological assessment.–942 pp. *Schmitten-Oberreifenberg: Koeltz Botanical Books*.

CANTONATI, M. & LANGE-BERTALOT, H. 2006. Achnanthidium dolomiticum sp. nov. (Bacillariophyta) from oligotrophic Mountain Springs and Lakes fed by Dolomite Aquifers. *Journal of Phycology,* 42**,** 1184-1188.

CANTONATI, M. & LANGE-BERTALOT, H. 2010. Diatom biodiversity of springs in the Berchtesgaden National Park (North-Eastern Alps, Germany), with the ecological and morphological characterization of two species new to science. *Diatom Research,* 25**,** 251-280.

CANTONATI, M., LANGE-BERTALOT, H., DECET, F. & GABRIELI, J. 2011. Diatoms in very-shallow pools of the site of community importance Danta di Cadore Mires (south-eastern Alps), and the potential contribution of these habitats to diatom biodiversity conservation. *Nova Hedwigia,* 93**,** 475-507.

CANTONATI, M., SCOLA, S., ANGELI, N., GUELLA, G. & FRASSANITO, R. 2009. Environmental controls of epilithic diatom depth-distribution in an oligotrophic lake characterized by marked water-level fluctuations. *European Journal of Phycology,* 44**,** 15-29.

CANTONATI, M., SEGADELLI, S., SPITALE, D., GABRIELI, J., GERECKE, R., ANGELI, N., DE NARDO, M. T., OGATA, K. & WEHR, J. D. 2020. Geological and hydrochemical prerequisites of unexpectedly high biodiversity in spring ecosystems at the landscape level. *Science of the Total Environment,* 740.

CANTONATI, M. & SPITALE, D. 2009. The role of environmental variables in structuring epiphytic and epilithic diatom assemblages in springs and streams of the Dolomiti Bellunesi National Park (south-eastern Alps). *Fundamental and Applied Limnology,* 174**,** 117-133.

CARPENTER, S. R., COTTINGHAM, K. L. & SCHINDLER, D. E. 1992. Biotic Feedbacks in Lake Phosphorus Cycles. *Trends in Ecology & Evolution,* 7**,** 332-336.

CARPENTER, S. R., KITCHELL, J. F. & HODGSON, J. R. 1985. Cascading Trophic Interactions and Lake Productivity. *Bioscience,* 35**,** 634-639.

CARPENTER, S. R., KITCHELL, J. F., HODGSON, J. R., COCHRAN, P. A., ELSER, J. J., ELSER, M. M., LODGE, D. M., KRETCHMER, D., HE, X. & VONENDE, C. N. 1987. Regulation of Lake Primary Productivity by Food Web Structure. *Ecology,* 68**,** 1863-1876.

CARRERA, G., FERNANDEZ, P., VILANOVA, R. M. & GRIMALT, J. O. 2001. Persistent organic pollutants in snow from European high mountain areas. *Atmospheric Environment,* 35**,** 245-254.

CASAMAYOR, E. O. 2017. Towards a Microbial Conservation Perspective in High Mountain Lakes. *In:* CATALAN, J., NINOT, J. M. & ANIZ, M. M. (eds.) *High Mountain Conservation in a Changing World.* 1. ed. Cham, Switzerland: Springer Nature.

CASTENHOLZ, R. 1961. Effect of Grazing on Marine Littoral Diatom Populations. *Ecology,* 42**,** 783-&.

CASTILLO-ESCRIVA, A., VALLS, L., ROCHERA, C., CAMACHO, A. & MESQUITA-JOANES, F. 2017. Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes. *Hydrobiologia,* 787**,** 61-72.

CATALAN, J., BARBIERI, M. G., BARTUMEUS, F., BITUSIK, P., BOTEV, I., BRANCELJ, A., COGALNICEANU, D., MANCA, M., MARCHETTO, A., OGNJANOVA-RUMENOVA, N., PLA, S., RIERADEVALL, M., SORVARI, S., STEFKOVA, E., STUCHLIK, E. & VENTURA, M. 2009. Ecological thresholds in European alpine lakes. *Freshwater Biology,* 54**,** 2494-2517.

CATALAN, J. & FEE, E. 1994. Interannual variability in limnic ecosystems: origin, patterns, and predictability.

CATALAN, J., PLA-RABES, S., WOLFE, A. P., SMOL, J. P., RUHLAND, K. M., ANDERSON, N. J., KOPACEK, J., STUCHLIK, E., SCHMIDT, R., KOINIG, K. A., CAMARERO, L., FLOWER, R. J., HEIRI, O., KAMENIK, C., KORHOLA, A., LEAVITT, P. R., PSENNER, R. & RENBERG, I. 2013. Global change revealed by palaeolimnological records from remote lakes: a review. *Journal of Paleolimnology,* 49**,** 513-535.

CATALAN, J., PLA, S., RIERADEVALL, M., FELIP, M., VENTURA, M., BUCHACA, T., CAMARERO, L., BRANCELJ, A., APPLEBY, P. G., LAMI, A., GRYTNES, A., AGUSTI-PANAREDA, A. & THOMPSON, R. 2002a. Lake Redo ecosystem response to an increasing warming in the Pyrenees during the twentieth century. *Journal of Paleolimnology,* 28**,** 129-145.

CATALAN, J., VENTURA, M., BRANCELJ, A., GRANADOS, I., THIES, H., NICKUS, U., KORHOLA, A., LOTTER, A. F., BARBIERI, A., STUCHLIK, E., LIEN, L., BITUSIK, P., BUCHACA, T., CAMARERO, L., GOUDSMIT, G. H., KOPACEK, J., LEMCKE, G., LIVINGSTONE, D. M., MULLER, B., RAUTIO, M., SISKO, M., SORVARI, S., SPORKA, F., STRUNECKY, O. & TORO, M. 2002b. Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. *Journal of Paleolimnology,* 28**,** 25-46.

CATALAN, J., VENTURA, M., BRANCELJ, A., GRANADOS, I., THIES, H., NICKUS, U., KORHOLA, A., LOTTER, A. F., BARBIERI, A., STUCHLÍK, E., LIEN, L., BITUŠÍK, P., BUCHACA, T., CAMARERO, L., GOUDSMIT, G. H., KOPÁĆEK, J., LEMCKE, G., LIVINGSTONE, D. M., MÜLLER, B., RAUTIO, M., ŠIŠKO, M., SORVARI, S., ŠPORKA, F., STRUNECKÝ, O. & TORO, M. 2002c. Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. *Journal of Paleolimnology,* 28**,** 25-46.

CEN 2015. Water quality — Guidance on quantitative and qualitative sampling of phytoplankton from inland waters. *NA 119-01-03 AA.* Brussels: European Committee for Standardization.

CHEN, G. J., SAULNIER-TALBOT, E., SELBIE, D. T., BROWN, E., SCHINDLER, D. E., BUNTING, L., LEAVITT, P. R., FINNEY, B. P. & GREGORY-EAVES, I. 2011. Salmon-derived nutrients drive diatom beta-diversity patterns. *Freshwater Biology,* 56**,** 292-301.

CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics,* 31**,** 343-366.

CLEVE, P. T. & MÖLLER, J. D. 1878. *Collection of 324 diatom slides with accompanying analyses of A. Grunow,* Uppsala.

COTTENIE, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters,* 8**,** 1175-1182.

CRAMPTON, J. S., CODY, R. D., LEVY, R., HARWOOD, D., MCKAY, R. & NAISH, T. R. 2016. Southern Ocean phytoplankton turnover in response to stepwise Antarctic cooling over the past 15 million years. *Proceedings of the National Academy of Sciences of the United States of America,* 113**,** 6868-6873.

CRESPO-MIGUEL, R., JARILLO, J. & CAO-GARCIA, F. J. 2022. Scaling of population resilience with dispersal length and habitat size. *Journal of Statistical Mechanics-Theory and Experiment,* 2022.

CUDLIN, P., KLOPCIC, M., TOGNETTI, R., MALIS, F., ALADOS, C. L., BEBI, P., GRUNEWALD, K., ZHIYANSKI, M., ANDONOWSKI, V., LA PORTA, N., BRATANOVA-DONCHEVA, S., KACHAUNOVA, E., EDWARDS-JONASOVA, M., NINOT, J. M., RIGLING, A., HOFGAARD, A., HLASNY, T., SKALAK, P. & WIELGOLASKI, F. E. 2017. Drivers of treeline shift in different European mountains. *Climate Research,* 73**,** 135-150.

CURTIS, C. J., JUGGINS, S., CLARKE, G., BATTARBEE, R. W., KERNAN, M., CATALAN, J., THOMPSON, R. & POSCH, M. 2009. Regional influence of acid deposition and climate change in European mountain lakes assessed using diatom transfer functions. *Freshwater Biology,* 54**,** 2555-2572.

CUSHMAN, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation,* 128**,** 231-240.

DARWALL, W. R. T., HOLLAND, R. A., SMITH, K. G., ALLEN, D., BROOKS, E. G. E., KATARYA, V., POLLOCK, C. M., SHI, Y. C., CLAUSNITZER, V., CUMBERLIDGE, N., CUTTELOD, A., DIJKSTRA, K. D. B., DIOP, M. D., GARCIA, N., SEDDON, M. B., SKELTON, P. H., SNOEKS, J., TWEDDLE, D. & VIE, J. C. 2011. Implications of bias in conservation research and investment for freshwater species. *Conservation Letters,* 4**,** 474-482.

DARWALL, W. R. T. & VIE, J. C. 2005. Identifying important sites for conservation of freshwater biodiversity: extending the species-based approach. *Fisheries Management and Ecology,* 12**,** 287-293.

DAVIDSON, T. A., BENNION, H., REID, M., SAYER, C. D. & WHITMORE, T. J. 2018. Towards better integration of ecology in palaeoecology: from proxies to indicators, from inference to understanding. *Journal of Paleolimnology,* 60**,** 109-116.

DE OLIVEIRA, P. H. F., MACHADO, K. B., TERESA, F. B., HEINO, J. & NABOUT, J. C. 2020. Spatial processes determine planktonic diatom metacommunity structure of headwater streams. *Limnologica,* 84.

DENOEL, M., SCIME, P. & ZAMBELLI, N. 2016. Newt life after fish introduction: extirpation of paedomorphosis in a mountain fish lake and newt use of satellite pools. *Current Zoology,* 62**,** 61-69.

DENYS, L. & OOSTERLYNCK, P. 2015. Diatom assemblages of non-living substrates in petrifying Cratoneurion springs from lower Belgium. *Fottea,* 15**,** 123-138.

DERLET, R. W., RICHARDS, J. R. & GOLDMAN, C. R. 2012. Does Above-Normal Precipitation Reduce the Impact of Mountain Cattle Grazing on Watershed Algae and Bacteria? *Water Quality Exposure and Health,* 4**,** 105-112.

DETMER, T. & LEWIS, W. M. 2019. Influences of fish on food web structure and function in mountain lakes. *Freshwater Biology,* 64**,** 1572-1583.

DETMER, T., MCCUTCHAN, J. H. & LEWIS, W. M. 2017. Trophic interactions across lake-stream boundaries in mountain lakes. *Inland Waters,* 7**,** 440-448.

DIN 1983. Deutsche Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung; Kationen (Gruppe E); Bestimmung des Ammonium-Stickstoffs (E 5). Berlin: Beuth Verlag GmbH.

DIN 2014. Water quality - Guidance for the routine sampling and preparation of benthic diatoms from rivers and lakes. *EN 13946:2014.* Berlin: Beuth Verlag GmbH.

DIN 2015a. Water quality - Guidance on quantitative and qualitative sampling of phytoplankton from inland waters. *In:* TECHNICAL COMMITTEE WATER ANALYSIS (ed.). Beuth.

DIN 2015b. Water quality - Guidance on quantitative and qualitative sampling of phytoplankton from inland waters. Beuth Verlag GmbH.

DIXIT, S. S., SMOL, J. P., KINGSTON, J. C. & CHARLES, D. F. 1992. DIATOMS - POWERFUL INDICATORS OF ENVIRONMENTAL-CHANGE. *Environmental Science & Technology,* 26**,** 22-33.

DONALD, D. B. 1987. Assessment of the Outcome of Eight Decades of Trout Stocking in the Mountain National Parks, Canada. *North American Journal of Fisheries Management,* 7**,** 545-553.

DONOHUE, I., HILLEBRAND, H., MONTOYA, J. M., PETCHEY, O. L., PIMM, S. L., FOWLER, M. S., HEALY, K., JACKSON, A. L., LURGI, M., MCCLEAN, D., O'CONNOR, N. E., O'GORMAN, E. J. & YANG, Q. 2016. Navigating the complexity of ecological stability. *Ecology Letters,* 19**,** 1172-1185.

DRAY, S., LEGENDRE, P. & PERES-NETO, P. R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling,* 196**,** 483-493.

DRAY, S. B., D.; BLANCHET, G.; BORCARD, D.; CLAPPE, S.; GUENARD, G.;JOMBART, T.; LAROCQUE, G.;, LEGENDRE, P.; MADI, N.; WAGNER, H. 2020. R package adespatial: Tools for the multiscale spatial analysis of multivariate data.

DRINAN, T. J., FOSTER, G. N., NELSON, B. H., O'HALLORAN, J. & HARRISON, S. S. C. 2013. Macroinvertebrate assemblages of peatland lakes: Assessment of conservation value with respect to anthropogenic land-cover change. *Biological Conservation,* 158**,** 175-187.

DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z. I., KNOWLER, D. J., LEVEQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A. H., SOTO, D., STIASSNY, M. L. J. & SULLIVAN, C. A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews,* 81**,** 163-182.

DYNOWSKI, P., SENETRA, A., ZROBEK-SOKOLNIK, A. & KOZLOWSKI, J. 2019. The Impact of Recreational Activities on Aquatic Vegetation in Alpine Lakes. *Water,* 11.

EBNER, M., FONTANA, V., SCHIRPKE, U. & TAPPEINER, U. 2022. Stakeholder perspectives on ecosystem services of mountain lakes in the European Alps. *Ecosystem Services,* 53.

EEA 1994. *European Rivers and Lakes - Assessment of their Environmental State,* Copenhagen, European Environmental Agency.

EEA 2018. *European waters — assessment of status and pressures,* Copenhagen, European Environmental Agency.

EEA. 2021. Introduction to the EU Water Framework Directive Available: https://ec.europa.eu/environment/water/water-framework/info/intro_en.htm [Accessed 16.3.2022].

EHRENBERG, C. G. 1843. *Verbreitung und Einfluß des mikroskopischen Lebens in Süd- und Nord-Amerika,* Berlin.

ELLENBERG, H. 1948. Unkrautgesellschaften als Mass für den Säuregrad, die Verdichtung und andere Eigenschaften des Ackerbodens. *Ber. Landtech***,** 130-146.

ESTEVEZ, R. A., ANDERSON, C. B., PIZARRO, J. C. & BURGMAN, M. A. 2015. Clarifying values, risk perceptions, and attitudes to resolve or avoid social conflicts in invasive species management. *Conservation Biology,* 29**,** 19-30.

EU. 2022. Invasive Alien Species. Available: https://ec.europa.eu/environment/nature/invasivealien/index_en.htm.

EVANS, K. M., CHEPURNOV, V. A., SLUIMAN, H. J., THOMAS, S. J., SPEARS, B. M. & MANN, D. G. 2009. Highly Differentiated Populations of the Freshwater Diatom Sellaphora capitata Suggest Limited Dispersal and Opportunities for Allopatric Speciation. *Protist,* 160**,** 386-396.

FALASCO, E., PIANO, E. & BONA, F. 2016. Diatom flora in Mediterranean streams: flow intermittency threatens endangered species. *Biodiversity and Conservation,* 25**,** 2965-2986.

FALASCO, E., PIANO, E., DORETTO, A., FENOGLIO, S. & BONA, F. 2019. Resilience of benthic diatom communities in Mediterranean streams: role of endangered species. *Marine and Freshwater Research,* 70**,** 212-224.

FALKOWSKI, P. G., BARBER, R. T. & SMETACEK, V. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science,* 281**,** 200-206.

FERNANDEZ, L. D., HERNANDEZ, C. E., SCHIAFFINO, M. R., IZAGUIRRE, I. & LARA, E. 2017. Geographical distance and local environmental conditions drive the genetic population structure of a freshwater microalga (Bathycoccaceae; Chlorophyta) in Patagonian lakes. *Fems Microbiology Ecology,* 93.

FERNANDEZ, L. D., SEPPEY, C. V. W., SINGER, D., FOURNIER, B., TATTI, D., MITCHELL, E. A. D. & LARA, E. 2021. Niche Conservatism Drives the Elevational Diversity Gradient in Major Groups of Free-Living Soil Unicellular Eukaryotes. *Microbial Ecology*.

FINLAY, B. J. 2002. Global dispersal of free-living microbial eukaryote species. *Science,* 296**,** 1061-1063.

FLAIM, G., ANDREIS, D., PICCOLROAZ, S. & OBERTEGGER, U. 2020. Ice Cover and Extreme Events Determine Dissolved Oxygen in a Placid Mountain Lake. *Water Resources Research,* 56.

FLOWER, R. J. & BATTARBEE, R. W. 1983. Diatom evidence for recent acidification of 2 Scottish Lochs. *Nature,* 305**,** 130-133.

FODELIANAKIS, S., VALENZUELA-CUEVAS, A., BAROZZI, A. & DAFFONCHIO, D. 2021. Direct quantification of ecological drift at the population level in synthetic bacterial communities. *Isme Journal,* 15**,** 55-66.

FONTANA, V., GUARIENTO, E., HILPOLD, A., NIEDRIST, G., STEINWANDTER, M., SPITALE, D., NASCIMBENE, J., TAPPEINER, U. & SEEBER, J. 2020. Species richness and beta diversity patterns of multiple taxa along an elevational gradient in pastured grasslands in the European Alps. *Scientific Reports,* 10.

FRANCE, R. 1997. Land-water linkages: influences of riparian deforestation on lake thermocline depth and possible consequences for cold stenotherms. *Canadian Journal of Fisheries and Aquatic Sciences,* 54**,** 1299-1305.

FRANKOVA, M., BOJKOVA, J., POULICKOVA, A. & HAJEK, M. 2009. The structure and species richness of the diatom assemblages of the Western Carpathian spring fens along the gradient of mineral richness. *Fottea,* 9**,** 355-368.

GARCIA-GIRON, J., LINDHOLM, M., HEINO, J., TOIVONEN, H. & ALAHUHTA, J. 2021. Historical contingency via priority effects counteracts environmental change on metacommunity dynamics across decades. *Limnology and Oceanography*.

GARSTECKI, T. & WICKHAM, S. A. 2001. Effects of resuspension and mixing on population dynamics and trophic interactions in a model benthic microbial food web. *Aquatic Microbial Ecology,* 25**,** 281-292.

GAUCH, H. G. 1982. *Multivariate Analysis in Community Ecology,* Cambridge, Cambridge University Press.

GEIST, J. 2011. Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators,* 11**,** 1507-1516.

GEIST, J. 2015. Seven steps towards improving freshwater conservation. *Aquatic Conservation-Marine and Freshwater Ecosystems,* 25**,** 447-453.

GILBERT, B. & LEVINE, J. M. 2017. Ecological drift and the distribution of species diversity. *Proceedings of the Royal Society B-Biological Sciences,* 284.

GLIWICZ, Z. 1975. Effect of zooplankton grazing on photosynthetic activity and composition of phytoplankton. *Int. Ver. Theor. Angew. Limnol. Verh.,* 19**,** 1490-1497.

GLIWICZ, Z. M. 1990. Why do Cladocerans fail to control Algal Blooms? *Hydrobiologia,* 200**,** 83-97.

GLIWICZ, Z. M. 2002. On the different nature of top-down and bottom-up effects in pelagic food webs. *Freshwater Biology,* 47**,** 2296-2312.

GOBIET, A., KOTLARSKI, S., BENISTON, M., HEINRICH, G., RAJCZAK, J. & STOFFEL, M. 2014. 21st century climate change in the European Alps—A review. *Science of The Total Environment,* 493**,** 1138-1151.

GODHE, A. & RYNEARSON, T. 2017. The role of intraspecific variation in the ecological and evolutionary success of diatoms in changing environments. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 372.

GONZALEZ-PAZ, L., COMESANA, M., PARDO, I., BARQUIN, J., GOLDENBERG-VILAR, A. & DELGADO, C. 2021. Variability of diatom community composition and structure in mountain streams. *Hydrobiologia*.

GONZALEZ-TRUJILLO, J. D., SAITO, V. S., PETSCH, D. K., MUNOZ, I. & SABATER, S. 2021. Historical legacies and contemporary processes shape beta diversity in Neotropical montane streams. *Journal of Biogeography,* 48**,** 101-117.

GOODMAN, K. J., BAKER, M. A. & WURTSBAUGH, W. A. 2010. Mountain lakes increase organic matter decomposition rates in streams. *Journal of the North American Benthological Society,* 29**,** 521-529.

GROOM, M., MEFFE, G. & CARROLL, C. 2012. *Principles of Conservation Biology,* Sunderland, Massachusetts, Sinauer Associates.

GUILIZZONI, P., LAMI, A., MANCA, M., MUSAZZI, S. & MARCHETTO, A. 2006. Palaeoenvironmental changes inferred from biological remains in short lake sediment cores from the Central Alps and Dolomites. *Hydrobiologia,* 562**,** 167-191.

GUIRY, M. D. 2012. How many Species of Algae are there? *Journal of Phycology,* 48**,** 1057-1063.

GUNDERSON, L. H. 2000. Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics,* 31**,** 425-439.

GUNKEL, G. & CASALLAS, J. 2002. Limnology of an equatorial high mountain lake - Lago San Pablo, Ecuador: The significance of deep diurnal mixing for lake productivity. *Limnologica,* 32**,** 33-43.

HAIRSTON, N. G. 1959. Species Abundance and Community Organization. *Ecology,* 40**,** 404-416.

HALL, R. & SMOL, J. P. 1992. A weighted—averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. *Freshwater Biology,* 27**,** 417-434.

HAMILTON, A. J. 2005. Species diversity or biodiversity? *Journal of Environmental Management,* 75**,** 89-92.

HASTIE, T. 2019. Generalized Additive Models.

HAWKES, C. V. & KEITT, T. H. 2015. Resilience vs. historical contingency in microbial responses to environmental change. *Ecology Letters,* 18**,** 612-625.

HAYNES, W. 2013. Bonferroni Correction. *In:* DUBITZKY, W., WOLKENHAUER, O., CHO, K.-H. & YOKOTA, H. (eds.) *Encyclopedia of Systems Biology.* New York, NY: Springer New York.

HEIKKINEN, J. M., AALTO, J., RANTAMAKI, O., RUIKKALA, T., SOININEN, J. & PAJUNEN, V. 2022. Observing diatom diversity and community composition along environmental gradients in subarctic mountain ponds. *Freshwater Biology,* 67**,** 731-741.

HEINO, J., MELO, A. S., SIQUEIRA, T., SOININEN, J., VALANKO, S. & BINI, L. M. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology,* 60**,** 845-869.

HEINO, J. & SOININEN, J. 2005. Assembly rules and community models for unicellular organisms: patterns in diatoms of boreal streams. *Freshwater Biology,* 50**,** 567-577.

HILL, M. O. & GAUCH, H. G. 1980. Detrended correspondence analysis: An improved ordination technique. *Vegetatio,* 42**,** 47-58.

HOBBS, J. M. R., HOBBS, W. O., EDLUND, M. B., ZIMMER, K. D., THEISSEN, K. M., HOIDAL, N., DOMINE, L. M., HANSON, M. A., HERWIG, B. R. & COTNER, J. B. 2016. The legacy of large regime shifts in shallow lakes. *Ecological Applications,* 26**,** 2660-2674.

HOFMANN, A. 2021. *The response of Alpine aquatic ecosystems to climate change: a combined limnological and paleolimnological approach based on diatom, pigment and stable isotope analyses.* PhD Dissertation, Technical University Munich.

HOFMANN, A. M., GEIST, J., NOWOTNY, L. & RAEDER, U. 2020. Depth-distribution of lake benthic diatom assemblages in relation to light availability and substrate: implications for paleolimnological studies. *Journal of Paleolimnology,* 64**,** 315-334.

HOFMANN, A. M., KUEFNER, W., MAYR, C., DUBOIS, N., GEIST, J. & RAEDER, U. 2021. Unravelling climate change impacts from other anthropogenic influences in a subalpine lake: a multi-proxy sediment study from Oberer Soiernsee (Northern Alps, Germany). *Hydrobiologia,* 848**,** 4285-4309.

HOFMANN, G., LANGE-BERTALOT, H., WERUM, M. & KLEE, R. 2018. Rote Liste und Gesamtartenliste der limnischen Kieselalgen (Bacillariophyta) Deutschlands. *In:* METZING, D. H., N.; LUDWIG, G. & MATZKE-HAJEK, G (ed.) *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 7: Pflanzen.* Münster: Landwirtschaftsverlag.

HOOPER, D. U., ADAIR, E. C., CARDINALE, B. J., BYRNES, J. E. K., HUNGATE, B. A., MATULICH, K. L., GONZALEZ, A., DUFFY, J. E., GAMFELDT, L. & O'CONNOR, M. I. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature,* 486**,** 105-U129.

HUBBELL, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*, Princeton University Press.

HUGONI, M., VELLET, A. & DEBROAS, D. 2017. Unique and highly variable bacterial communities inhabiting the surface microlayer of an oligotrophic lake. *Aquatic Microbial Ecology,* 79**,** 115-125.

HUISMAN, J., SHARPLES, J., STROOM, J. M., VISSER, P. M., KARDINAAL, W. E. A., VERSPAGEN, J. M. H. & SOMMEIJER, B. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology,* 85**,** 2960-2970.

HUISMAN, J., VAN OOSTVEEN, P. & WEISSING, F. J. 1999. Critical depth and critical turbulence: Two different mechanisms for the development of phytoplankton blooms. *Limnology and Oceanography,* 44**,** 1781-1787.

HUISMAN, J. & WEISSING, F. J. 1995. COMPETITION FOR NUTRIENTS AND LIGHT IN A MIXED WATER COLUMN - A THEORETICAL-ANALYSIS. *American Naturalist,* 146**,** 536-564.

HUSTEDT, F. 1927-1966. *Die Kieselalgen Deutschlands, Oesterreichs und der Schweiz. Mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete*, Akademische Verlagsgesellschaft Geest & Portig K.-G.

HUSTEDT, F. 1930. Die Kieselalgen Deutschlands, Osterreichs und der Schweiz mit Berucksichtigung der ubrigen Lander Europas sowie der angrenzenden Meersgebiete. *In:* RABENHORST, L. & GRUNOW, C. (eds.) *Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Osterreich und der Schweiz.* Leipzig: Akademische Verlagsgesellschaft Geest und Portig K.-G.

ISBELL, F., CRAVEN, D., CONNOLLY, J., LOREAU, M., SCHMID, B., BEIERKUHNLEIN, C., BEZEMER, T. M., BONIN, C., BRUELHEIDE, H., DE LUCA, E., EBELING, A., GRIFFIN, J. N., GUO, Q. F., HAUTIER, Y., HECTOR, A., JENTSCH, A., KREYLING, J., LANTA, V., MANNING, P., MEYER, S. T., MORI, A. S., NAEEM, S., NIKLAUS, P. A., POLLEY, H. W., REICH, P. B., ROSCHER, C., SEABLOOM, E. W., SMITH, M. D., THAKUR, M. P., TILMAN, D., TRACY, B. F., VAN DER PUTTEN, W. H., VAN RUIJVEN, J., WEIGELT, A., WEISSER, W. W., WILSEY, B. & EISENHAUER, N. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature,* 526**,** 574-U263.

JAGER, C. G., DIEHL, S. & EMANS, M. 2010. Physical Determinants of Phytoplankton Production, Algal Stoichiometry, and Vertical Nutrient Fluxes. *American Naturalist,* 175**,** E91-E104.

JÄGER, C. G., DIEHL, S. & SCHMIDT, G. M. 2008. Influence of water-column depth and mixing on phytoplankton biomass, community composition, and nutrients. *Limnology and Oceanography,* 53**,** 2361-2373.

JAMONEAU, A., PASSY, S. I., SOININEN, J., LEBOUCHER, T. & TISON-ROSEBERY, J. 2018. Beta diversity of diatom species and ecological guilds: Response to environmental and spatial mechanisms along the stream watercourse. *Freshwater Biology,* 63**,** 62-73.

JARVINEN, M., DRAKARE, S., FREE, G., LYCHE-SOLHEIM, A., PHILLIPS, G., SKJELBRED, B., MISCHKE, U., OTT, I., POIKANE, S., SONDERGAARD, M., PASZTALENIEC, A., VAN WICHELEN, J. & PORTIELJE,

R. 2013. Phytoplankton indicator taxa for reference conditions in Northern and Central European lowland lakes. *Hydrobiologia,* 704**,** 97-113.

JAVAHERI, N., DRIES, R., BURSON, A., STAL, L. J., SLOOT, P. M. A. & KAANDORP, J. A. 2015. Temperature affects the silicate morphology in a diatom. *Scientific Reports,* 5.

JEPPESEN, E., JENSEN, J. P., JENSEN, C., FAAFENG, B., HESSEN, D. O., SONDERGAARD, M., LAURIDSEN, T., BRETTUM, P. & CHRISTOFFERSEN, K. 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: A study of 466 lakes from the temperate zone to the arctic. *Ecosystems,* 6**,** 313-325.

JEPPESEN, E., JENSEN, J. P., SONDERGAARD, M., LAURIDSEN, T. & LANDKILDEHUS, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology,* 45**,** 201-218.

JUGGINS, S. 2013. Quantitative reconstructions in palaeolimnology: new paradigm or sick science? *Quaternary Science Reviews,* 64**,** 20-32.

JURAN, J. & KASTOVSKY, J. 2019. The procedure of compiling the Red List of microscopic algae of the Czech Republic. *Biodiversity and Conservation,* 28**,** 2499-2529.

KACZMARSKA, I., MATHER, L., LUDDINGTON, I. A., MUISE, F. & EHRMAN, J. M. 2014. Cryptic Diversity in a Cosmopolitan Diatom known as Asterionellopsis Glacialis (Fragilariaceae): Implications for Ecology, Biogeography, and Taxonomy. *American Journal of Botany,* 101**,** 267-286.

KAGAMI, M., DE BRUIN, A., IBELINGS, B. W. & VAN DONK, E. 2007. Parasitic chytrids: their effects on phytoplankton communities and food-web dynamics. *Hydrobiologia,* 578**,** 113-129.

KAMENIK, C., SCHMIDT, R., KUM, G. & PSENNER, R. 2001. The influence of catchment characteristics on the water chemistry of mountain lakes. *Arctic Antarctic and Alpine Research,* 33**,** 404-409.

KARNA, O. M., HEINO, J., LAAMANEN, T., JYRKANKALLIO-MIKKOLA, J., PAJUNEN, V., SOININEN, J., TOLONEN, K. T., TUKIAINEN, H. & HJORT, J. 2019. Does catchment geodiversity foster stream biodiversity? *Landscape Ecology,* 34**,** 2469-2485.

KERNAN, M., VENTURA, M., BITUSIK, P., BRANCELJ, A., CLARKE, G., VELLE, G., RADDUM, G. G., STUCHLIK, E. & CATALAN, J. 2009. Regionalisation of remote European mountain lake ecosystems according to their biota: environmental versus geographical patterns. *Freshwater Biology,* 54**,** 2470-2493.

KIORBOE, T. & SAIZ, E. 1995. Planktivorous Feeding in Calm and Turbulent Environments, with Emphasis on Copepods. *Marine Ecology Progress Series,* 122**,** 135-145.

KIRILLIN, G., LEPPARANTA, M., TERZHEVIK, A., GRANIN, N., BERNHARDT, J., ENGELHARDT, C., EFREMOVA, T., GOLOSOV, S., PALSHIN, N., SHERSTYANKIN, P., ZDOROVENNOVA, G. & ZDOROVENNOV, R. 2012. Physics of seasonally ice-covered lakes: a review. *Aquatic Sciences,* 74**,** 659-682.

KISSMAN, C. E. H., WILLIAMSON, C. E., ROSE, K. C. & SAROS, J. E. 2013. Response of phytoplankton in an alpine lake to inputs of dissolved organic matter through nutrient enrichment and trophic forcing. *Limnology and Oceanography,* 58**,** 867-880.

KLAUSMEIER, C. A., LITCHMAN, E., DAUFRESNE, T. & LEVIN, S. A. 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature,* 429**,** 171-174.

KNAPP, R. A. 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. *Biological Conservation,* 121**,** 265-279.

KNAPP, R. A. & MATTHEWS, K. R. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restoration Ecology,* 6**,** 207-213.

KNAPP, R. A., MATTHEWS, K. R. & SARNELLE, O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs,* 71**,** 401-421.

KNIGHT, A. T., COWLING, R. M., ROUGET, M., BALMFORD, A., LOMBARD, A. T. & CAMPBELL, B. M. 2008. Knowing but not doing: Selecting priority conservation areas and the research-implementation gap. *Conservation Biology,* 22**,** 610-617.

KOINIG, K. A., KAMENIK, C., SCHMIDT, R., AGUSTÍ-PANAREDA, A., APPLEBY, P., LAMI, A., PRAZAKOVA, M., ROSE, N., SCHNELL, Ø. A., TESSADRI, R., THOMPSON, R. & PSENNER, R. 2002. Environmental changes in an alpine lake (Gossenköllesee, austria) over the last two centuries

– the influence of air temperature on biological parameters. *Journal of Paleolimnology,* 28**,** 147-160.

KOLZAU, S., WIEDNER, C., RÜCKER, J., KÖHLER, J., KÖHLER, A. & DOLMAN, A. M. 2014. Seasonal Patterns of Nitrogen and Phosphorus Limitation in Four German Lakes and the Predictability of Limitation Status from Ambient Nutrient Concentrations. *PLOS ONE,* 9**,** e96065.

KORNER, C. 2004. Mountain biodiversity, its causes and function. *Ambio***,** 11-17.

KORNER, C. 2021. The cold range limit of trees. *Trends in Ecology & Evolution,* 36**,** 979-989.

KRAEMER, B. M., ANNEVILLE, O., CHANDRA, S., DIX, M., KUUSISTO, E., LIVINGSTONE, D. M., RIMMER, A., SCHLADOW, S. G., SILOW, E., SITOKI, L. M., TAMATAMAH, R., VADEBONCOEUR, Y. & MCINTYRE, P. B. 2015. Morphometry and average temperature affect lake stratification responses to climate change. *Geophysical Research Letters,* 42**,** 4981-4988.

KRAMMER, K. 2000. *Diatoms of the european inland waters and comparable habitats: The genus Pinnularia,* Rugell, A.R.G. Gartner Verlag K.G.

KRAMMER, K. 2002. *Diatoms of the european inland waters and comparable habitats: Cymbella,* Rugell, A.R.G. Gartner Verlag K.G.

KRAMMER, K. & LANGE-BERTALOT, H. 1981-1996. *Bacillariophyceae,* Stuttgart/Jena, Fischer.

KRAMMER, K. & LANGE-BERTALOT, H. 1991a. *Bacillariophyceae, 3. Teil: Centrales, Fragilariaceae, Eunotiaceae,* Stuttgart, Jena, Gustav Fischer Verlag.

KRAMMER, K. & LANGE-BERTALOT, H. 1991b. *Bacillariophyceae, 4. Teil: Achnanthaceae, kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema,* Stuttgart, Jena, Gustav Fischer Verlag.

KRAMMER, K. & LANGE-BERTALOT, H. 1997a. *Bacillariophyceae, 1. Teil: Naviculaceae,* Stuttgart, Jena, Gustav Fischer Verlag.

KRAMMER, K. & LANGE-BERTALOT, H. 1997b. *Bacillariophyceae, 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae,* Stuttgart, Jena, Gustav Fischer Verlag.

KRISTENSEN, P. & GLOBEVNIK, L. 2014. European Small Waterbodies. *Biology and Environment-Proceedings of the Royal Irish Academy,* 114B**,** 281-287.

KUEFMANN, C. 2003. Soil types and eolian dust in high-mountainous karst of the Northern Calcareous Alps (Zugspitzplatt, Wetterstein Mountains, Germany). *Catena,* 53**,** 211-227.

KUEFNER, W. 2021. *Response of diatoms to climate change in mountain lakes in the Northern calcareous Alps with indications for the future development of the lake biota.* PhD Dissertation, Technical University Munich.

KUEFNER, W., HOFMANN, A., OSSYSSEK, S., DUBOIS, N., GEIST, J. & RAEDER, U. 2020a. Composition of highly diverse diatom community shifts as response to climate change: A down-core study of 23 central European mountain lakes. *Ecological Indicators,* 117**,** 106590.

KUEFNER, W., HOFMANN, A. M., GEIST, J. & RAEDER, U. 2020b. Evaluating climate change impacts on mountain lakes by applying the new silicification value to paleolimnological samples. *Science of the Total Environment,* 715**,** 12.

KUEFNER, W., HOFMANN, A. M., GEIST, J. & RAEDER, U. 2020c. Evaluating climate change impacts on mountain lakes by applying the new silicification value to paleolimnological samples. *Science of the Total Environment,* 715.

KUEFNER, W., OSSYSSEK, S., GEIST, J. & RAEDER, U. 2020d. The silicification value: a novel diatom-based indicator to assess climate change in freshwater habitats. *Diatom Research,* 35**,** 1-16.

KÜTZING, F. 1844. *Die kieselschaligen Bacillarien oder Diatomeen,* Nordhausen.

LAMPERT, W. & SOMMER, U. 2007. *Limnoecology - The Ecology of Lakes and Streams,* Oxford, Oxford University Press.

LANGE-BERTALOT, H. 2001. *Diatoms of the european inland waters and comparable habitats: Navicula sensu stricto, 10 genera separated from Navicula sensu stricto, Frustulia,* Rugell, A.R.G. Gartner Verlag K.G.

LANGE-BERTALOT, H., HOFMANN, G., WERUM, M. & CANTONATI, M. 2017. *Freshwater benthic diatoms of Central Europe. Over 800 common species used in ecological assessment,* Oberreifenberg, Koeltz Botanical Books.

LEBOUCHER, T., MIGNIEN, L., WACH, M., BOUTRY, S., JAMONEAU, A., PASSY, S. I. & TISON-ROSEBERY, J. 2021. Consideration of mass effect processes in bioindication allows more accurate bioassessment of water quality. *Ecological Indicators,* 127.

LEBOUCHER, T., TISON-ROSEBERY, J., BUDNICK, W., JAMONEAU, A., VYVERMAN, W., SOININEN, J., BOUTRY, S. & PASSY, S. I. 2020. A metacommunity approach for detecting species influenced by mass effect. *Journal of Applied Ecology,* 57**,** 2031-2040.

LEGENDRE, P. & DE CACERES, M. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters,* 16**,** 951-963.

LEGENDRE, P. & GALLAGHER, E. D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia,* 129**,** 271-280.

LEIBOLD, M. A. 1999. Biodiversity and nutrient enrichment in pond plankton communities. *Evolutionary Ecology Research,* 1**,** 73-95.

LEIBOLD, M. A. & CHASE, J. M. 2018. *Metacommunity Ecology, Volume 59,* Princeton, United States Princeton University Press.

LEIBOLD, M. A., ECONOMO, E. P. & PERES-NETO, P. 2010. Metacommunity phylogenetics: separating the roles of environmental filters and historical biogeography. *Ecology Letters,* 13**,** 1290-1299.

LEIBOLD, M. A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPES, M. F., HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D., LOREAU, M. & GONZALEZ, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters,* 7**,** 601-613.

LEIBOLD, M. A., RUDOLPH, F. J., BLANCHET, F. G., DE MEESTER, L., GRAVEL, D., HARTIG, F., PERES-NETO, P., SHOEMAKER, L. & CHASE, J. M. 2022. The internal structure of metacommunities. *Oikos,* 2022.

LEIRA, M., CHEN, G., DALTON, C., IRVINE, K. & TAYLOR, D. 2009. Patterns in freshwater diatom taxonomic distinctness along an eutrophication gradient. *Freshwater Biology,* 54**,** 1-14.

LITCHMAN, E. 2003. Competition and coexistence of phytoplankton under fluctuating light: experiments with two cyanobacteria. *Aquatic Microbial Ecology,* 31**,** 241-248.

LIVINGSTONE, D. M. & DOKULIL, M. T. 2001. Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. *Limnology and Oceanography,* 46**,** 1220-1227.

LIVINGSTONE, D. M., LOTTER, A. F. & WALKER, I. R. 1999. The decrease in summer surf are water temperature with altitude in Swiss Alpine lakes: A comparison with air temperature lapse rates. *Arctic Antarctic and Alpine Research,* 31**,** 341-352.

LOTTER, A. F. & BIGLER, C. 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquatic Sciences,* 62**,** 125-141.

LOTTER, A. F., BIRKS, H. J. B., HOFMANN, W. & MARCHETTO, A. 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps .1. Climate. *Journal of Paleolimnology,* 18**,** 395-420.

LOTTER, A. F., BIRKS, H. J. B., HOFMANN, W. & MARCHETTO, A. 1998. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology,* 19**,** 443-463.

LUKACS, B. A., SRAMKO, G. & MOLNAR, V. A. 2013. Plant diversity and conservation value of continental temporary pools. *Biological Conservation,* 158**,** 393-400.

LUND, J. W. G. 1954. The Seasonal Cycle of the Plankton Diatom, Melosira-Italica (Ehr) Kutz subsp Subarctica o Mull. *Journal of Ecology,* 42**,** 151-&.

MACARTHUR, R. H. 1965. Patterns of Species Diversity. *Biological Reviews,* 40**,** 510-+.

MALIK, H. I., NORTHINGTON, R. M. & SAROS, J. E. 2017. Nutrient limitation status of Arctic lakes affects the responses of Cyclotella sensu lato diatom species to light: implications for distribution patterns. *Polar Biology,* 40**,** 2445-2456.

MANN, D. G. 1999. The species concept in diatoms. *Phycologia,* 38**,** 437-495.

MANN, D. G. & DROOP, S. J. M. 1996. Biodiversity, biogeography and conservation of diatoms. *Hydrobiologia,* 336**,** 19-32.

MANN, D. G. & VANORMELINGEN, P. 2013. An Inordinate Fondness? The Number, Distributions, and Origins of Diatom Species. *Journal of Eukaryotic Microbiology,* 60**,** 414-420.

MANOYLOV, K. M. 2009. Intra- and Interspecific Competition for Nutrients and Light in Diatom Cultures. *Journal of Freshwater Ecology,* 24**,** 145-157.

MARTIN, S. L., HAYES, D. B., KENDALL, A. D. & HYNDMAN, D. W. 2017. The land-use legacy effect: Towards a mechanistic understanding of time-lagged water quality responses to land use/cover. *Science of the Total Environment,* 579**,** 1794-1803.

MARTINEZ-SANZ, C., CENZANO, C. S. S., FERNANDEZ-ALAEZ, M. & GARCIA-CRIADO, F. 2012. Relative contribution of small mountain ponds to regional richness of littoral macroinvertebrates and the implications for conservation. *Aquatic Conservation-Marine and Freshwater Ecosystems,* 22**,** 155-164.

MCDONALD, B. A. & LINDE, C. 2002. Pathogen population genetics, evolutionary potential, and durable resistance. *Annual Review of Phytopathology,* 40**,** 349-+.

MCINTIRE, C. D. & OVERTON, W. S. 1971. Distributional Patterns in Assemblages of Attached Diatoms from Yaquina Estuary, Oregon. *Ecology,* 52**,** 758-+.

MEDINA-SANCHEZ, J. M., VILLAR-ARGAIZ, M. & CARRILLO, P. 2004. Neither with nor without you: A complex algal control on bacterioplankton in a high mountain lake. *Limnology and Oceanography,* 49**,** 1722-1733.

MEDLIN, L. K. 2016. Evolution of the diatoms: major steps in their evolution and a review of the supporting molecular and morphological evidence. *Phycologia,* 55**,** 79-103.

MEDLIN, L. K., KOOISTRA, W., GERSONDE, R. & WELLBROCK, U. 1996. Evolution of the diatoms (Bacillariophyta) .2. Nuclear-encoded small-subunit rRNA sequence comparisons confirm a paraphyletic origin for the centric diatoms. *Molecular Biology and Evolution,* 13**,** 67-75.

MENZ, V. 2008. *Umwelttechnik für alpine Berg- und Schutzhütten,* Munich, Bergverlag Rother.

MERGEAY, J., DE MEESTER, L., EGGERMONT, H. & VERSCHUREN, D. 2011. Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. *Ecology,* 92**,** 2267-2275.

MICHELS, E., COTTENIE, K., NEYS, L. & DE MEESTER, L. 2001. Zooplankton on the move: first results on the quantification of dispersal of zooplankton in a set of interconnected ponds. *Hydrobiologia,* 442**,** 117-126.

MIRANDA, L. E. & RAINES, C. D. 2019. Reservoir Diel Water Quality Patterns Relative to Riparian Shade. *Lake and Reservoir Management,* 35**,** 148-155.

MITTERMEIER, R. A., MYERS, N., THOMSEN, J. B., DA FONSECA, G. A. B. & OLIVIERI, S. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. *Conservation Biology,* 12**,** 516-520.

MOENS, T., VAFEIADOU, A. M., DE GEYTER, E., VANORMELINGEN, P., SABBE, K. & DE TROCH, M. 2014. Diatom feeding across trophic guilds in tidal flat nematodes, and the importance of diatom cell size. *Journal of Sea Research,* 92**,** 125-133.

MOGNA, M., CANTONATI, M., ANDREUCCI, F., ANGELI, N., BERTA, G. & MISERERE, L. 2015. Diatom communities and vegetation of springs in the south-western Alps. *Acta Botanica Croatica,* 74**,** 265-285.

MOISEN, G. G. & FRESCINO, T. S. 2002. Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling,* 157**,** 209-225.

MORLON, H., SCHWILK, D. W., BRYANT, J. A., MARQUET, P. A., REBELO, A. G., TAUSS, C., BOHANNAN, B. J. M. & GREEN, J. L. 2011. Spatial patterns of phylogenetic diversity. *Ecology Letters,* 14**,** 141-149.

MOSER, K. A., BARON, J. S., BRAHNEY, J., OLEKSY, I. A., SAROS, J. E., HUNDEY, E. J., SADRO, S. A., KOPACEK, J., SOMMARUGA, R., KAINZ, M. J., STRECKER, A. L., CHANDRA, S., WALTERS, D. M., PRESTON, D. L., MICHELUTTI, N., LEPORI, F., SPAULDING, S. A., CHRISTIANSON, K. R., MELACK,

J. M. & SMOL, J. P. 2019a. Mountain lakes: Eyes on global environmental change. *Global and Planetary Change,* 178**,** 77-95.

MOSER, K. A., BARON, J. S., BRAHNEY, J., OLEKSY, I. A., SAROS, J. E., HUNDEY, E. J., SADRO, S. A., KOPÁČEK, J., SOMMARUGA, R., KAINZ, M. J., STRECKER, A. L., CHANDRA, S., WALTERS, D. M., PRESTON, D. L., MICHELUTTI, N., LEPORI, F., SPAULDING, S. A., CHRISTIANSON, K. R., MELACK, J. M. & SMOL, J. P. 2019b. Mountain lakes: Eyes on global environmental change. *Global and Planetary Change*.

MÜLLER, O. F. 1783. Strand-Parlebandet och Armbandet, tvanne microscopiska Strandvaxter. *Kongl Vetenskaps Academiens, Nya Handlingar,* 4**,** 80-85.

MURI, G. & BRANCELJ, A. 2003. Seasonal water chemistry variations in three Slovenian mountain lakes. *Acta Chimica Slovenica,* 50**,** 137-+.

MURI, G., CERMELJ, B., JACIMOVIC, R., RAVNIKAR, T., SMUC, A., TURSIC, J. & VRECA, P. 2018. Factors that contributed to recent eutrophication of two Slovenian mountain lakes. *Journal of Paleolimnology,* 59**,** 411-426.

MURI, G., CERMELJ, B., JACIMOVIC, R., SKABERNE, D., SMUC, A., BURNIK STURM, M., TURSIC, J. & VRECA, P. 2013. Consequences of anthropogenic activity for two remote alpine lakes in NW Slovenia as tracked by sediment geochemistry. *Journal of Paleolimnology,* 50**,** 457-470.

MURPHY, J. & RILEY, J. P. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta,* 27**,** 31-36.

MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature,* 403**,** 853-858.

NAIMI, B. 2017. Package 'usdm'. 1.1-18 ed.

NAIMI, B., HAMM, N., GROEN, T. A., SKIDMORE, A. K. & TOXOPEUS, A. G. 2014. Where is positional uncertainty a problem for species distribution modelling. *Ecography,* 37**,** 191-203.

NAKOV, T., BEAULIEU, J. M. & ALVERSON, A. J. 2019. Diatoms diversify and turn over faster in freshwater than marine environments. *Evolution,* 73**,** 2497-2511.

NAVONE, R. 1964. Proposed method for nitrate in potable waters. *American Water Works Association,* 56**,** 781-783.

NIEDRIST, G. H., PSENNER, R. & SOMMARUGA, R. 2018. Climate warming increases vertical and seasonal water temperature differences and inter-annual variability in a mountain lake. *Climatic Change,* 151**,** 473-490.

NING, D. L., DENG, Y., TIEDJE, J. M. & ZHOU, J. Z. 2019. A general framework for quantitatively assessing ecological stochasticity. *Proceedings of the National Academy of Sciences of the United States of America,* 116**,** 16892-16898.

NIXDORF, B., HOEHN, E., RIEDMÜLLER, U., MISCHKE, U. & SCHÖNFELDER, I. 2014a. Probenahme und Analyse des Phytoplanktons in Seen und Flüssen zur Ökologischen Bewertung gemäß der EU-WRRL. *In:* HUPFER, M. & FISCHER, H. (eds.) *Handbuch Angewandte Limnologie: Grundlagen - Gewässerbelastung - Restaurierung - Aquatische Ökotoxikologie - Bewertung - Gewässerschutz.* Weinheim: Wiley-VCH Verlag GmbH & Co. KGaA.

NIXDORF, B., HOEHN, E., RIEDMÜLLER, U., MISCHKE, U. & SCHÖNFELDER, I. 2014b. Probenahme und Analyse des Phytoplanktonsin Seen und Flüssen zur ökologischen Bewertunggemäß der EU-WRRL. *In:* HUPFER, M., CALMANO, W. & KLAPPER, H. (eds.) *Handbuch Angewandte Limnologie.*

NUSSLE, S., MATTHEWS, K. R. & CARLSON, S. M. 2017. Patterns and dynamics of vegetation recovery following grazing cessation in the California golden trout habitat. *Ecosphere,* 8.

OKSANEN, J., BLANCHET, G. F., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., HENRY, M., STEVENS, H., SZOECS, E. & WAGNER, H. 2018. vegan: Community Ecology Package. R package version 2.5-2 ed.

OKSANEN, J., KINDT, R., LEGENDRE, P., O'HARA, B., HENRY, M. & STEVENS, S. 2007. The vegan package. The R Foundation.

OLEKSY, I. A., BARON, J. S., LEAVITT, P. R. & SPAULDING, S. A. 2020. Nutrients and warming interact to force mountain lakes into unprecedented ecological states. *Proceedings of the Royal Society B-Biological Sciences,* 287.

ORMEROD, S. J., RUNDLE, S. D., WILKINSON, S. M., DALY, G. P., DALE, K. M. & JUTTNER, I. 1994. Altitudinal Trends in the Diatoms, Bryophytes, Macroinvertebrates and Fish of a Nepalese River System. *Freshwater Biology,* 32**,** 309-322.

ORTIZ-ALVAREZ, R., TRIADO-MARGARIT, X., CAMARERO, L., CASAMAYOR, E. O. & CATALAN, J. 2018. High planktonic diversity in mountain lakes contains similar contributions of autotrophic, heterotrophic and parasitic eukaryotic life forms. *Scientific Reports,* 8.

OSSYSSEK, S., GEIST, J., WERNER, P. & RAEDER, U. 2020. Identification of the ecological preferences of Cyclotella comensis in mountain lakes of the northern European Alps. *Arctic Antarctic and Alpine Research,* 52**,** 512-523.

OSSYSSEK, S., HOFMANN, A., GEIST, J. & RAEDER, U. 2022a. Sedimentary, planktic and littoral diatom metacommunities in mountain lakes of the northern European Alps show divergent assembly patterns. *submitted to Hydrobiologia*.

OSSYSSEK, S., HOFMANN, A. M., GEIST, J. & RAEDER, U. 2022b. Diatom Red List Species Reveal High Conservation Value and Vulnerability of Mountain Lakes. *Diversity,* 14**,** 389.

OWEN, R. B., RENAUT, R. W. & JONES, B. 2008. Geothermal diatoms: a comparative study of floras in hot spring systems of Iceland, New Zealand, and Kenya. *Hydrobiologia,* 610**,** 175-192.

PARADIS, E., CLAUDE, J. & STRIMMER, K. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics,* 20**,** 289-290.

PARKER, B. R. & SCHINDLER, D. W. 2006. Cascading trophic interactions in an oligotrophic species-poor alpine lake. *Ecosystems,* 9**,** 157-166.

PARKER, B. R., SCHINDLER, D. W., DONALD, D. B. & ANDERSON, R. S. 2001. The effects of stocking and removal of a nonnative salmonid on the plankton of an alpine lake. *Ecosystems,* 4**,** 334-345.

PASSY, S. I. 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. *Aquatic Botany,* 86**,** 171-178.

PASTORINO, P., PREARO, M., BERTOLI, M., MENCONI, V., ESPOSITO, G., RIGHETTI, M., MUGETTI, D., PEDERIVA, S., ABETE, M. C. & PIZZUL, E. 2020. Assessment of Biological and Sanitary Condition of Alien Fish from a High-Mountain Lake (Cottian Alps). *Water,* 12.

PATRICK, R. 1948. Factors Effecting the Distribution of Diatoms. *Botanical Review,* 14**,** 473-524.

PIENITZ, R., SMOL, J. P. & BIRKS, H. J. B. 1995. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology,* 13**,** 21-49.

PIMM, S. L., JENKINS, C. N., ABELL, R., BROOKS, T. M., GITTLEMAN, J. L., JOPPA, L. N., RAVEN, P. H., ROBERTS, C. M. & SEXTON, J. O. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science,* 344**,** 987-+.

PINI, R., RAVAZZI, C., RAITERI, L., GUERRESCHI, A., CASTELLANO, L. & COMOLLI, R. 2017. From pristine forests to high-altitude pastures: an ecological approach to prehistoric human impact on vegetation and landscapes in the western Italian Alps. *Journal of Ecology,* 105**,** 1580-1597.

PINSEEL, E., JANSSENS, S. B., VERLEYEN, E., VANORMELINGEN, P., KOHLER, T. J., BIERSMA, E. M., SABBE, K., VAN DE VIJVER, B. & VYVERMAN, W. 2020. Global radiation in a rare biosphere soil diatom. *Nature Communications,* 11.

PITHER, J. & AARSSEN, L. W. 2005. The evolutionary species pool hypothesis and patterns of freshwater diatom diversity along a pH gradient. *Journal of Biogeography,* 32**,** 503-513.

PLA-RABES, S. & CATALAN, J. 2018. Diatom species variation between lake habitats: implications for interpretation of paleolimnological records. *Journal of Paleolimnology,* 60**,** 169-187.

POST, J. R. & MCQUEEN, D. J. 1987. The Impact of planktivorous Fish on the Structure of a Plankton Community. *Freshwater Biology,* 17**,** 79-89.

POTAPOVA, M. G. & CHARLES, D. F. 2002. Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. *Journal of Biogeography,* 29**,** 167-187.

POULICKOVA, A., VESELA, J., NEUSTUPA, J. & SKALOUD, P. 2010. Pseudocryptic Diversity versus Cosmopolitanism in Diatoms: a Case Study on Navicula cryptocephala Kutz. (Bacillariophyceae) and Morphologically Similar Taxa. *Protist,* 161**,** 353-369.

PRENTICE, I. C. 1980. Multidimensional scaling as a research tool in quaternary palynology: A review of theory and methods. *Review of Palaeobotany and Palynology,* 31**,** 71-104.

R CORE TEAM 2013. R: A language and environment for statistical computing. 3.4.3 ed. Vienna: R Foundation for Statistical Computing.

RAMOS-JILIBERTO, R., OYANEDEL, J. P., VEGA-RETTER, C. & VALDOVINOS, F. S. 2009. Nested structure of plankton communities from Chilean freshwaters. *Limnologica,* 39**,** 319-324.

RAMSTACK, J. M., FRITZ, S. C., ENGSTROM, D. R. & HEISKARY, S. A. 2003. The Application of a Diatom-based Transfer Function to Evaluate Regional Water-Quality Trends in Minnessota Since 1970. *Journal of Paleolimnology,* 29**,** 79-94.

RAPOPORT, E. H. 1982. Ecological Areography. *In:* RAPOPORT, E. H. (ed.) *Areography.* Pergamon.

READ, J. S., HAMILTON, D. P., JONES, I. D., MURAOKA, K., WINSLOW, L. A., KROISS, R., WU, C. H. & GAISER, E. 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling & Software,* 26**,** 1325-1336.

REAVIE, E. D., SGRO, G. V., ESTEPP, L. R., BRAMBURGER, A. J., SHAW CHRAÏBI, V. L., PILLSBURY, R. W., CAI, M., STOW, C. A. & DOVE, A. 2017. Climate warming and changes in Cyclotella sensu lato in the Laurentian Great Lakes. *Limnology and Oceanography,* 62**,** 768-783.

REMMER, C. R., ROBICHAUD, C. D., POLOWYK, H. & ROONEY, R. 2019. The role of ecological drift in structuring periphytic diatom communities. *Journal of Freshwater Ecology,* 34**,** 363-377.

REYNOLDS, C. S. 1984. *The ecology of freshwater phytoplankton,* CambridgeLondon, Cambridge University Press.

REYNOLDS, C. S. 1993. Scales of Disturbance and their Role in Plankton Ecology. *Hydrobiologia,* 249**,** 157-171.

REYNOLDS, C. S., OLIVER, R. L. & WALSBY, A. E. 1987. CYANOBACTERIAL DOMINANCE - THE ROLE OF BUOYANCY REGULATION IN DYNAMIC LAKE ENVIRONMENTS. *New Zealand Journal of Marine and Freshwater Research,* 21**,** 379-390.

REYNOLDS, C. S., WISEMAN, S. W., GODFREY, B. M. & BUTTERWICK, C. 1983. Some Effects of Artificial Mixing on the Dynamics of Phytoplankton Populations in Large Limnetic Enclosures. *Journal of Plankton Research,* 5**,** 203-234.

RIMET, F., BOUCHEZ, A. & TAPOLCZAI, K. 2016. Spatial heterogeneity of littoral benthic diatoms in a large lake: monitoring implications. *Hydrobiologia,* 771**,** 179-193.

RODHE, W., HOBBIE, J. E. & WRIGHT, R. T. 1966. Phototrophy and heterotrophy in high mountain lakes. *SIL Proceedings, 1922-2010,* 16**,** 302-313.

RODRIGUEZ-ALCALA, O., BLANCO, S., GARCIA-GIRON, J., JEPPESEN, E., IRVINE, K., NOGES, P., NOGES, T., GROSS, E. M. & BECARES, E. 2020. Large-scale geographical and environmental drivers of shallow lake diatom metacommunities across Europe. *Science of the Total Environment,* 707.

ROGORA, M., ARISCI, S. & MARCHETTO, A. 2012. The role of nitrogen deposition in the recent nitrate decline in lakes and rivers in Northern Italy. *Science of the Total Environment,* 417**,** 214-223.

ROGORA, M., BUZZI, F., DRESTI, C., LEONI, B., LEPORI, F., MOSELLO, R., PATELLI, M. & SALMASO, N. 2018a. Climatic effects on vertical mixing and deep-water oxygen content in the subalpine lakes in Italy. *Hydrobiologia,* 824**,** 33-50.

ROGORA, M., FRATE, L., CARRANZA, M. L., FREPPAZ, M., STANISCI, A., BERTANI, I., BOTTARIN, R., BRAMBILLA, A., CANULLO, R., CARBOGNANI, M., CERRATO, C., CHELLI, S., CREMONESE, E., CUTINI, M., DI MUSCIANO, M., ERSCHBAMER, B., GODONE, D., IOCCHI, M., ISABELLON, M., MAGNANI, A., MAZZOLA, L., DI CELLA, U. M., PAULI, H., PETEY, M., PETRICCIONE, B., PORRO, F., PSENNER, R., ROSSETTI, G., SCOTTI, A., SOMMARUGA, R., TAPPEINER, U., THEURILLAT, J. P., TOMASELLI, M., VIGLIETTI, D., VITERBI, R., VITTOZ, P., WINKLER, M. & MATTEUCCI, G. 2018b. Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines. *Science of the Total Environment,* 624**,** 1429-1442.

ROGORA, M., MASSAFERRO, J., MARCHETTO, A., TARTARI, G. & MOSELLO, R. 2008. The water chemistry of some shallow lakes in Northern Patagonia and their nitrogen status in comparison with remote lakes in different regions of the globe. *Journal of Limnology,* 67**,** 75-86.

ROGORA, M., SOMASCHINI, L., MARCHETTO, A., MOSELLO, R., TARTARI, G. A. & PARO, L. 2020. Decadal trends in water chemistry of Alpine lakes in calcareous catchments driven by climate change. *Science of the Total Environment,* 708.

ROSBAKH, S., BERNHARDT-ROMERMANN, M. & POSCHLOD, P. 2014. Elevation matters: contrasting effects of climate change on the vegetation development at different elevations in the Bavarian Alps. *Alpine Botany,* 124**,** 143-154.

ROUND, F. E., CRAWFORD, R. M. & MANN, D. G. 1990. The diatoms: biology and morphology of the genera. *Journal of the Marine Biological Association of the United Kingdom,* 1.

RÜHLAND, K., PATERSON, A. M. & SMOL, J. P. 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. *Global Change Biology,* 14**,** 2740-2754.

RÜHLAND, K. M., PATERSON, A. M. & SMOL, J. P. 2015. Lake diatom responses to warming: reviewing the evidence. *Journal of Paleolimnology,* 54**,** 1-35.

RYSANEK, D., HOLZINGER, A. & SKALOUD, P. 2016. Influence of substrate and pH on the diversity of the aeroterrestrial alga Klebsormidium (Klebsormidiales, Streptophyta): a potentially important factor for sympatric speciation. *Phycologia,* 55**,** 347-358.

SADRO, S. & MELACK, J. M. 2012. The Effect of an Extreme Rain Event on the Biogeochemistry and Ecosystem Metabolism of an Oligotrophic High-Elevation Lake. *Arctic Antarctic and Alpine Research,* 44**,** 222-231.

SALMASO, N. & TOLOTTI, M. 2021. Phytoplankton and anthropogenic changes in pelagic environments. *Hydrobiologia,* 848**,** 251-284.

SAROS, J. E. & ANDERSON, N. J. 2015. The ecology of the planktonic diatom Cyclotella and its implications for global environmental change studies. *Biological Reviews,* 90**,** 522-541.

SAROS, J. E., NORTHINGTON, R. M., ANDERSON, D. S. & ANDERSON, N. J. 2016. A whole-lake experiment confirms a small centric diatom species as an indicator of changing lake thermal structure. *Limnology and Oceanography Letters,* 1**,** 27-35.

SAROS, J. E., STONE, J. R., PEDERSON, G. T., SLEMMONS, K. E. H., SPANBAUER, T., SCHLIEP, A., CAHL, D., WILLIAMSON, C. E. & ENGSTROM, D. R. 2012. Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleoecological approaches. *Ecology,* 93**,** 2155-2164.

SCHEFFER, M., HOSPER, S. H., MEIJER, M. L., MOSS, B. & JEPPESEN, E. 1993. ALTERNATIVE EQUILIBRIA IN SHALLOW LAKES. *Trends in Ecology & Evolution,* 8**,** 275-279.

SCHEFFER, M., RINALDI, S., HUISMAN, J. & WEISSING, F. J. 2003. Why plankton communities have no equilibrium: solutions to the paradox. *Hydrobiologia,* 491**,** 9-18.

SCHEFFLER, W., NICKLISCH, A. & SCHONFELDER, I. 2005. Articles on the morphology, ecology and ontogenesis of the planktonic diatom Cyclotella comensis grunow. Studies on the historic and recently sampled material. *Diatom Research,* 20**,** 171-200.

SCHERER, R. 2002. The diatoms: applications for the environmental and earth sciences E. F. Stoermer and J. P. Smol Cambridge University Press, Cambridge 1999 (469 pp) £70/US$115 ISBN 0 521 58281 4. *Journal of Quaternary Science,* 17**,** 283-284.

SCHINDLER, D. E. & EBY, L. A. 1997. Stoichiometry of fishes and their prey: Implications for nutrient recycling. *Ecology,* 78**,** 1816-1831.

SCHINDLER, D. E., KITCHELL, J. F., HE, X., CARPENTER, S. R., HODGSON, J. R. & COTTINGHAM, K. L. 1993. Food-Web Structure and Phosphorus Cycling in Lakes. *Transactions of the American Fisheries Society,* 122**,** 756-772.

SCHINDLER, D. E., KNAPP, R. A. & LEAVITT, P. R. 2001. Alteration of Nutrient Cycles and Algal Production Resulting from Fish Introductions into Mountain Lakes. *Ecosystems,* 4**,** 308-321.

SCHINDLER, D. W. 2009. Lakes as sentinels and integrators for the effects of climate change on watersheds, airsheds, and landscapes. *Limnology and Oceanography,* 54**,** 2349-2358.

SCHIRPKE, U., EBNER, M., PRITSCH, H., FONTANA, V. & KURMAYER, R. 2021a. Quantifying Ecosystem Services of High Mountain Lakes across Different Socio-Ecological Contexts. *Sustainability,* 13.

SCHIRPKE, U., KOHLER, M., LEITINGER, G., FONTANA, V., TASSER, E. & TAPPEINER, U. 2017. Future impacts of changing land-use and climate on ecosystem services of mountain grassland and their resilience. *Ecosystem Services,* 26**,** 79-94.

SCHIRPKE, U., SCOLOZZI, R., KIESSLING, A. & TAPPEINER, U. 2021b. Recreational ecosystem services of mountain lakes in the European Alps: Preferences, visitor groups and management implications. *Journal of Outdoor Recreation and Tourism-Research Planning and Management,* 35.

SCHMELLER, D. S., MIHOUB, J. B., BOWSER, A., ARVANITIDIS, C., COSTELLO, M. J., FERNANDEZ, M., GELLER, G. N., HOBERN, D., KISSLING, W. D., REGAN, E., SAARENMAA, H., TURAK, E. & ISAAC, N. J. B. 2017. An operational definition of essential biodiversity variables. *Biodiversity and Conservation,* 26**,** 2967-2972.

SCHMIDT, R., KAMENIK, C., LANGE-BERTALOT, H. & KLEE, R. 2004. *Fragilaria and Staurosira (Bacillariophyceae) from sediment surfaces of 40 lakes in the Austrian Alps in relation to environmental variables, and their potential for palaeoclimatology*.

SCHÖNFELDER, I., GELBRECHT, J., SCHÖNFELDER, J. & STEINBERG, C. E. W. 2002. Relationships between littoral diatoms and their chemical environment in northeastern German lakes and rivers. *Journal of Phycology,* 38**,** 66-82.

SCHWEFEL, R., MULLER, B., BOISGONTIER, H. & WUEST, A. 2019. Global warming affects nutrient upwelling in deep lakes. *Aquatic Sciences,* 81**,** 11.

SEGURADO, P. & ARAUJO, M. B. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography,* 31**,** 1555-1568.

SELENE, P., PAOLO, P., MARCO, B., SALVI, G., FRANZ, F., MARINO, P. & PIZZUL, E. 2020. Changes in midge assemblages (Diptera Chironomidae) in an alpine lake from the Italian Western Alps: the role and importance of fish introduction. *Hydrobiologia,* 847**,** 2393-2415.

SENETRA, A., DYNOWSKI, P., CIESLAK, I. & ZROBEK-SOKOLNIK, A. 2020. An Evaluation of the Impact of Hiking Tourism on the Ecological Status of Alpine Lakes-A Case Study of the Valley of Dolina Pieciu Stawow Polskich in the Tatra Mountains. *Sustainability,* 12.

SHANNON, C. E. 1948. A Mathematical Theory of Communication. *Bell System Technical Journal,* 27**,** 379-423.

SHEA, K., ROXBURGH, S. H. & RAUSCHERT, E. S. J. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters,* 7**,** 491-508.

SHURIN, J. B., COTTENIE, K. & HILLEBRAND, H. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia,* 159**,** 151-159.

SIENKIEWICZ, E. & GASIOROWSKI, M. 2014. Changes in the Trophic Status of Three Mountain Lakes - Natural or Anthropogenic Process? *Polish Journal of Environmental Studies,* 23**,** 875-892.

SIENKIEWICZ, E. & GASIOROWSKI, M. 2016. The effect of fish stocking on mountain lake plankton communities identified using palaeobiological analyses of bottom sediment cores. *Journal of Paleolimnology,* 55**,** 129-150.

SIMPSON, E. H. 1949. Measurement of Diversity. *Nature,* 163**,** 688-688.

SIMS, P. A., MANN, D. G. & MEDLIN, L. K. 2006. Evolution of the diatoms: insights from fossil, biological and molecular data. *Phycologia,* 45**,** 361-402.

SMALL, J. 1950. Quantitative Evolution - Increase of Species-Number in Diatoms. *Annals of Botany,* 14**,** 91-113.

SMOL, J. P., BIRKS, H. J. & LAST, W. M. 2002. *Tracking environmental change using lake sediments: Terrestrial, algal, and siliceous indicators,* Dordrecht, Springer.

SMOL, J. P., BIRKS, H. J. B., LAST, W. M., BRADLEY, R. S. & ALVERSON, K. 2001. *Tracking Environmental Change Using Lake Sediments*, Springer, Dordrecht.

SMUCKER, N. J. & VIS, M. L. 2011. Contributions of habitat sampling and alkalinity to diatom diversity and distributional patterns in streams: implications for conservation. *Biodiversity and Conservation,* 20**,** 643-661.

SOCOLAR, J. B., GILROY, J. J., KUNIN, W. E. & EDWARDS, D. P. 2016. How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology & Evolution,* 31**,** 67-80.

SOININEN, J., MCDONALD, R. & HILLEBRAND, H. 2007. The distance decay of similarity in ecological communities. *Ecography,* 30**,** 3-12.

SOININEN, J. & TEITTINEN, A. 2019. Fifteen important questions in the spatial ecology of diatoms. *Freshwater Biology,* 64**,** 2071-2083.

SOININEN, J., TUPOLA, V., VOUTILAINEN, I., CANTONATI, M. & TEITTINEN, A. 2021. Diatom biogeography in freshwaters - new insights from between-region comparisons and the role of unmeasured environmental factors. *Diatom Research*.

SOININEN, J. & WECKSTROM, J. 2009. Diatom community structure along environmental and spatial gradients in lakes and streams. *Fundamental and Applied Limnology,* 174**,** 205-213.

SOMMARUGA, R. 2001. The role of solar UV radiation in the ecology of alpine lakes. *Journal of Photochemistry and Photobiology B: Biology,* 62**,** 35-42.

SOMMERS, P. & CHESSON, P. 2019. Effects of Predator Avoidance Behavior on the Coexistence of Competing Prey. *American Naturalist,* 193**,** E132-E148.

SONNLEITNER, R., REDL, B. & SCHINNER, F. 2011. Microbial Mobilization of Major and Trace Elements from Catchment Rock Samples of a High Mountain Lake in the European Alps. *Arctic Antarctic and Alpine Research,* 43**,** 465-473.

SORENSEN, J. W. & SHADE, A. 2020. Dormancy dynamics and dispersal contribute to soil microbiome resilience. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 375.

SORHANNUS, U. 2007. A nuclear-encoded small-subunit ribosomal RNA timescale for diatom evolution. *Marine Micropaleontology,* 65**,** 1-12.

SOUFFREAU, C., VANORMELINGEN, P., VAN DE VIJVER, B., ISHEVA, T., VERLEYEN, E., SABBE, K. & VYVERMAN, W. 2013. Molecular Evidence for Distinct Antarctic Lineages in the Cosmopolitan Terrestrial Diatoms Pinnularia borealis and Hantzschia amphioxys. *Protist,* 164**,** 101-115.

SPAULDING, S. A., VAN DE VIJVER, B., HODGSON, D. A., MCKNIGHT, D. M., VERLEYEN, E. & STANISH, L. 2010. Diatoms as indicators of environmental change in Antarctic and subantarctic freshwaters. *In:* STOERMER, E. F. & SMOL, J. P. (eds.) *The Diatoms: Applications for the Environmental and Earth Sciences.* 2 ed. Cambridge: Cambridge University Press.

SPELLERBERG, I. F. & FEDOR, P. J. 2003. A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. *Global Ecology and Biogeography,* 12**,** 177-179.

STARKWEATHER, P. L. 1990. Zooplankton Community Structure of High Elevation Lakes - Biogeographic and Predator-Prey Interactions. Congress of the International Assoc of Theoretical and Applied Limnology, 1989 1990 Munich, Fed Rep Ger. 513-517.

STEVENS, G. C. 1992. THE ELEVATIONAL GRADIENT IN ALTITUDINAL RANGE - AN EXTENSION OF RAPOPORT LATITUDINAL RULE TO ALTITUDE. *American Naturalist,* 140**,** 893-911.

STIRLING, G. & WILSEY, B. 2001. Empirical relationships between species richness, evenness, and proportional diversity. *American Naturalist,* 158**,** 286-299.

STOCKWELL, J. D., DOUBEK, J. P., ADRIAN, R., ANNEVILLE, O., CAREY, C. C., CARVALHO, L., DOMIS, L. N. D., DUR, G., FRASSL, M. A., GROSSART, H. P., IBELINGS, B. W., LAJEUNESSE, M. J., LEWANDOWSKA, A. M., LLAMES, M. E., MATSUZAKI, S. I. S., NODINE, E. R., NOGES, P., PATIL, V. P., POMATI, F., RINKE, K., RUDSTAM, L. G., RUSAK, J. A., SALMASO, N., SELTMANN, C. T., STRAILE, D., THACKERAY, S. J., THIERY, W., URRUTIA-CORDERO, P., VENAIL, P., VERBURG, P., WOOLWAY, R. I., ZOHARY, T., ANDERSEN, M. R., BHATTACHARYA, R., HEJZLAR, J., JANATIAN, N., KPODONU, A., WILLIAMSON, T. J. & WILSON, H. L. 2020. Storm impacts on phytoplankton community dynamics in lakes. *Global Change Biology,* 26**,** 2756-2784.

STOMP, M., HUISMAN, J., MITTELBACH, G. G., LITCHMAN, E. & KLAUSMEIER, C. A. 2011. Large-scale biodiversity patterns in freshwater phytoplankton. *Ecology,* 92**,** 2096-2107.

STREIFENEDER, T., GIULIANI, C. & HOFFMANN, C. 2018. Eine grenzüberschreitende Analyse der Politiken für die Almwirtschaft in den Alpen. *In:* CHILLA, T. & SIELKER, F. (eds.) *Grenzüberschreitende Raumentwicklung Bayerns - Dynamik in der Kooperation – Potenziale der Verflechtung.* Hannover: Akademie für Raumforschung und Landesentwicklung.

STROCK, K. E., THEODORE, N., GAWLEY, W. G., ELLSWORTH, A. C. & SAROS, J. E. 2017. Increasing dissolved organic carbon concentrations in northern boreal lakes: Implications for lake water transparency and thermal structure. *Journal of Geophysical Research-Biogeosciences,* 122**,** 1022-1035.

SUN, G., ZHU-BARKER, X., CHEN, D. M., LIU, L., ZHANG, N. N., SHI, C. G., HE, L. P. & LEI, Y. B. 2017. Responses of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine meadow: An implication for pasture management. *Plant and Soil,* 416**,** 515-525.

SYMONS, C. C., SCHULHOF, M. A., CAVALHERI, H. B. & SHURIN, J. B. 2021. Legacy effects of fish but not elevation influence lake ecosystem response to environmental change. *Journal of Animal Ecology,* 90**,** 662-672.

SZABO, B., LENGYEL, E., PADISAK, J. & STENGER-KOVACS, C. 2019. Benthic diatom metacommunity across small freshwater lakes: driving mechanisms, β-diversity and ecological uniqueness. *Hydrobiologia,* 828**,** 183-198.

SZABO, B., LENGYEL, E., PADISAK, J., VASS, M. & STENGER-KOVACS, C. 2018. Structuring forces and β-diversity of benthic diatom metacommunities in soda pans of the Carpathian Basin. *European Journal of Phycology,* 53**,** 219-229.

TAXBOCK, L., KARGER, D. N., KESSLER, M., SPITALE, D. & CANTONATI, M. 2020. Diatom Species Richness in Swiss Springs Increases with Habitat Complexity and Elevation. *Water,* 12.

TEITTINEN, A., KALLAJOKI, L., MEIER, S., STIGZELIUS, T. & SOININEN, J. 2016. The roles of elevation and local environmental factors as drivers of diatom diversity in subarctic streams. *Freshwater Biology,* 61**,** 1509-1521.

TEITTINEN, A., WANG, J. J., STROMGARD, S. & SOININEN, J. 2017. Local and geographical factors jointly drive elevational patterns in three microbial groups across subarctic ponds. *Global Ecology and Biogeography,* 26**,** 973-982.

TERBRAAK, C. J. F. & PRENTICE, I. C. 1988. A theory of gradient analysis. *Advances in Ecological Research,* 18**,** 271-317.

TERBRAAK, C. J. F. & VERDONSCHOT, P. F. M. 1995. Canonical Correspondence-Analysis and Related Multivariate Methods in Aquatic Ecology. *Aquatic Sciences,* 57**,** 255-289.

THOMPSON, P. L., GUZMAN, L. M., DE MEESTER, L., HORVATH, Z., PTACNIK, R., VANSCHOENWINKEL, B., VIANA, D. S. & CHASE, J. M. 2020. A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters,* 23**,** 1314-1329.

THOMPSON, R., KAMENIK, C. & SCHMIDT, R. 2005. Ultra-sensitive Alpine lakes and climate change. *Journal of Limnology,* 64.

THRELKELD, S. T. 1988. Planktivory and planktivore Biomass Effects on Zooplankton, Phytoplankton, and the Trophic Cascade. *Limnology and Oceanography,* 33**,** 1362-1375.

THRONDSEN, J. 1978a. Preservation and Storage. *In:* SOURNIA, A. (ed.) *Phytoplankton Manual.* Paris: Muséum Nationale d´Histoire Naturelle

THRONDSEN, R. 1978b. Preservation and storage. *In:* SOURNIA, A. (ed.) *Phytoplankton Manual Monographs on Oceanographic Methodology.* Paris: UNESCO.

TIBERTI, R., BOGLIANI, G., BRIGHENTI, S., IACOBUZIO, R., LIAUTAUD, K., ROLLA, M., VON HARDENBERG, A. & BASSANO, B. 2019. Recovery of high mountain Alpine lakes after the eradication of introduced brook trout Salvelinus fontinalis using non-chemical methods. *Biological Invasions,* 21**,** 875-894.

TIBERTI, R., BUCHACA, T., BOIANO, D., KNAPP, R. A., ROVIRA, Q. P., TAVECCHIA, G., VENTURA, M. & TENAN, S. 2021. Alien fish eradication from high mountain lakes by multiple removal methods: Estimating residual abundance and eradication probability in open populations. *Journal of Applied Ecology,* 58**,** 1055-1068.

TIBERTI, R., ROGORA, M., TARTARI, G. & CALLIERI, C. 2014a. Ecological impact of transhumance on the trophic state of alpine lakes in Gran Paradiso National Park. *Knowledge and Management of Aquatic Ecosystems*.

TIBERTI, R., VON HARDENBERG, A. & BOGLIANI, G. 2014b. Ecological impact of introduced fish in high altitude lakes: a case of study from the European Alps. *Hydrobiologia,* 724**,** 1-19.

TILMAN, D. 1977. Resource Competition between Plankton Algae: An Experimental and Theoretical Approach. *Ecology,* 58**,** 338-348.

TILMAN, D., KILHAM, S. S. & KILHAM, P. 1982. Phytoplankton Community Ecology - The Role of Limiting Nutrients. *Annual Review of Ecology and Systematics,* 13**,** 349-372.

TOLOTTI, M. 2001. Phytoplankton and littoral epilithic diatoms in high mountain lakes of the Adamello-Brenta Regional Park (Trentino, Italy) and their relation to trophic status and …. *J. Limnol,* 60**,** 171-188.

TOLOTTI, M., CORRADINI, F., BOSCAINI, A. & CALLIARI, D. 2007. Weather-driven ecology of planktonic diatoms in Lake Tovel (Trentino, Italy). *Hydrobiologia,* 578**,** 147-156.

TOLOTTI, M., THIES, H., NICKUS, U. & PSENNER, R. 2012. Temperature modulated effects of nutrients on phytoplankton changes in a mountain lake. *Hydrobiologia,* 698**,** 61-75.

TONKIN, J. D., HEINO, J., SUNDERMANN, A., HAASE, P. & JAHNIG, S. C. 2016. Context dependency in biodiversity patterns of central German stream metacommunities. *Freshwater Biology,* 61**,** 607-620.

TORO, M., GRANADOS, I., RUBIO, A., CAMACHO, A., SABAS, I., VENTURA, M. & MONTES, C. 2020. Response of the aquatic invertebrate community to the eradication of an exotic invasive fish 30 years after its introduction into an Iberian alpine lake. *Aquatic Sciences,* 82.

TYLER, P. A. 1996. Endemism in freshwater algae. *Hydrobiologia,* 336**,** 127-135.

VALLETTA, J. J., TORNEY, C., KINGS, M., THORNTON, A. & MADDEN, J. 2017. Applications of machine learning in animal behaviour studies. *Animal Behaviour,* 124**,** 203-220.

VAN DEN WYNGAERT, S., MOST, M., FREIMANN, R., IBELINGS, B. W. & SPAAK, P. 2015. Hidden diversity in the freshwater planktonic diatom Asterionella formosa. *Molecular Ecology,* 24**,** 2955-2972.

VAN DER WERFF, A. & MACAN, T. T. 1955. A new method of concentrating and cleaning diatoms and other organisms. *Proceedings of the International Association of Theoretical and Applied Limnology (SIL),* 12**,** 276-277

VANORMELINGEN, P., EVANS, K. M., CHEPURNOV, V. A., VYVERMAN, W. & MANN, D. G. 2013. Molecular species discovery in the diatom Sellaphora and its congruence with mating trials. *Fottea,* 13**,** 133-148.

VANORMELINGEN, P., VERLEYEN, E. & VYVERMAN, W. 2008. The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism. *Biodiversity and Conservation,* 17**,** 393-405.

VASS, M. & LANGENHEDER, S. 2017. The legacy of the past: effects of historical processes on microbial metacommunities. *Aquatic Microbial Ecology,* 79**,** 13-19.

VELGHE, K., VERMAIRE, J. C. & GREGORY-EAVES, I. 2012. Declines in littoral species richness across both spatial and temporal nutrient gradients: a palaeolimnological study of two taxonomic groups. *Freshwater Biology,* 57**,** 2378-2389.

VENTURA, M., TIBERTI, R., BUCHACA, T., BUNAY, D., SABAS, I. & MIRO, A. 2017. Why Should We Preserve Fishless High Mountain Lakes? *In:* CATALAN, J., NINOT, J. M. & ANIZ, M. M. (eds.) *High Mountain Conservation in a Changing World.*

VIANI, C., COLOMBO, N., BOLLATI, I. M., MORTARA, G., PEROTTI, L. & GIARDINO, M. 2022. Socio-environmental value of glacier lakes: assessment in the Aosta Valley (Western Italian Alps). *Regional Environmental Change,* 22.

VILMI, A., KARJALAINEN, S. M. & HEINO, J. 2017. Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. *Diversity and Distributions,* 23**,** 1042-1053.

VILMI, A., KARJALAINEN, S. M., HELLSTEN, S. & HEINO, J. 2016. Bioassessment in a metacommunity context: Are diatom communities structured solely by species sorting? *Ecological Indicators,* 62**,** 86-94.

VINEBROOKE, R. D. & LEAVITT, P. R. 1999. Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. *Journal of the North American Benthological Society,* 18**,** 15-33.

VOLLENWEIDER, R. A. 1968. *Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication: Technical* *report (DAS/CSI/68.27)*, Organisation for Economic Co-operation and Development Directorate for Scientific Affairs.

VYVERMAN, W., VERLEYEN, E., SABBE, K., VANHOUTTE, K., STERKEN, M., HODGSON, D. A., MANN, D. G., JUGGINS, S., VAN DE VIJVER, B., JONES, V., FLOWER, R., ROBERTS, D., CHEPURNOV, V. A., KILROY, C., VANORMELINGEN, P. & DE WEVER, A. 2007. Historical processes constrain patterns in global diatom diversity. *Ecology,* 88**,** 1924-1931.

WANG, J. J., LEGENDRE, P., SOININEN, J., YEH, C. F., GRAHAM, E., STEGEN, J., CASAMAYOR, E. O., ZHOU, J. Z., SHEN, J. & PAN, F. Y. 2020a. Temperature drives local contributions to beta diversity in mountain streams: Stochastic and deterministic processes. *Global Ecology and Biogeography,* 29**,** 420-432.

WANG, J. J., SOININEN, J., ZHANG, Y., WANG, B. X., YANG, X. D. & SHEN, J. 2011. Contrasting patterns in elevational diversity between microorganisms and macroorganisms. *Journal of Biogeography,* 38**,** 595-603.

WANG, R., HU, Z. J., WANG, Q., XU, M., ZHENG, W. X., ZHANG, K. & YANG, X. D. 2020b. Discrepancy in the responses of diatom diversity to indirect and direct human activities in lakes of the southeastern Tibetan Plateau, China. *Anthropocene,* 30.

WECKSTROM, J., KORHOLA, A. & BLOM, T. 1997. Diatoms as quantitative indicators of pH and water temperature in subarctic Fennoscandian lakes. *Hydrobiologia,* 347**,** 171-184.

WEI, T. & SIMKO, V. 2017a. R package "corrplot": Visualization of a Correlation Matrix.

WEI, T. & SIMKO, V. R. 2017b. Package “corrplot”: Visualization of a Correlation Matrix.

WEIDMAN, P. R., SCHINDLER, D. W., THOMPSON, P. L. & VINEBROOKE, R. D. 2014. Interactive effects of higher temperature and dissolved organic carbon on planktonic communities in fishless mountain lakes. *Freshwater Biology,* 59**,** 889-904.

WERNER, P. & SMOL, J. P. 2006. The distribution of the diatom Cyclotella comensis in Ontario (Canada) lakes. *Nova Hedwigia***,** 373-391.

WHITEHEAD, P. G., WILBY, R. L., BATTARBEE, R. W., KERNAN, M. & WADE, A. J. 2009. A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal-Journal Des Sciences Hydrologiques,* 54**,** 101-123.

WHITMORE, T. J., RIEDINGER-WHITMORE, M. A., LAUTERMAN, F. M. & CURTIS, J. H. 2018. Cyanobacterial influence on diatom community lifeform dynamics in shallow subtropical lakes of Florida USA. *Journal of Paleolimnology,* 60**,** 223-246.

WHITTAKER, R. H. 1965. Dominance and Diversity in Land Plant Communities. *Science,* 147.

WHITTAKER, R. H. 1972. Evolution and Measurement of Species Diversity. *Taxon,* 21**,** 213-251.

WICKHAM, H. & FRANÇOIS, R. 2014. *dplyr: A Grammar of Data Manipulation*.

WIGDAHL-PERRY, C. R., SAROS, J. E., FRITZ, S. C. & HESS, C. T. 2017. Investigating potential effects of zooplankton grazing on diatom-inferred drought reconstructions. *Hydrobiologia,* 786**,** 149-165.

WILCOXON, F. 1945. Individual comparisons by ranking methods. *Biometrics Bulletin,* 1**,** 80-83.

WILLIAMS, L. G. 1964. Possible Relationships Between Plankton-Diaotm Species Numbers + Water-Quality Estimates. *Ecology,* 45**,** 809-&.

WILLIAMSON, C. E., SALM, C., COOKE, S. L. & SAROS, J. E. 2010a. How do UV radiation, temperature, and zooplankton influence the dynamics of alpine phytoplankton communities? *Hydrobiologia,* 648**,** 73-81.

WILLIAMSON, C. E., SALM, C., COOKE, S. L. & SAROS, J. E. 2010b. How do UV radiation, temperature, and zooplankton influence the dynamics of alpine phytoplankton communities? (vol 648, pg 73, 2010). *Hydrobiologia,* 652**,** 395-396.

WILSON, S. E. & GAJEWSKI, K. 2002. Surface-sediment diatom assemblages and water chemistry from 42 subarctic lakes in the southwestern Yukon and northern British Columbia, Canada. *Ecoscience,* 9**,** 256-270.

WINDER, M., REUTER, J. E. & SCHLADOW, S. G. 2009. Lake warming favours small-sized planktonic diatom species. *Proceedings of the Royal Society B-Biological Sciences,* 276**,** 427-435.

WINEGARDNER, A. K., BEISNER, B. E., LEGENDRE, P. & GREGORY-EAVES, I. 2015. Are the landscape-level drivers of water column and surface sediment diatoms different? *Freshwater Biology,* 60**,** 267-281.

WINSLOW, L., READ, R., WOOLWAY, R., BRENTRUP, J., LEACH, T., ZWART, J., ALBERS, S. & COLLINGE, D. 2019. rLakeAnalyzer: Lake Physics Tools. . R package version 1.11.4.1 ed.

WINTER, M., DEVICTOR, V. & SCHWEIGER, O. 2013. Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution,* 28**,** 199-204.

WOLF, K. K. E., ROMANELLI, E., ROST, B., JOHN, U., COLLINS, S., WEIGAND, H. & HOPPE, C. J. M. 2019. Company matters: The presence of other genotypes alters traits and intraspecific selection in an Arctic diatom under climate change. *Global Change Biology,* 25**,** 2869-2884.

WOOD, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B-Statistical Methodology,* 73**,** 3-36.

WOOLWAY, R. I., JENNINGS, E., SHATWELL, T., GOLUB, M., PIERSON, D. C. & MABERLY, S. C. 2021. Lake heatwaves under climate change. *Nature,* 589**,** 402-+.

WUNSAM, S., SCHMIDT, R. & KLEE, R. 1995. Cyclotella-taxa (Bacillariophyceae) in lakes of the Alpine region and their relationship to environmental variables. *Aquatic Sciences,* 57**,** 360-386.

YAMAZAKI, H. 1996. Turbulence problems for planktonic organisms. *Marine Ecology Progress Series,* 139**,** 304-305.

YOOL, A. & TYRRELL, T. 2003. Role of diatoms in regulating the ocean's silicon cycle. *Global Biogeochemical Cycles,* 17.

ZHANG, S. H., CHEN, D. D., SUN, D. S., WANG, X. T., SMITH, J. L. & DU, G. Z. 2012. Impacts of altitude and position on the rates of soil nitrogen mineralization and nitrification in alpine meadows on the eastern Qinghai-Tibetan Plateau, China. *Biology and Fertility of Soils,* 48**,** 393-400.

ZORZAL-ALMEIDA, S., SOININEN, J., BINI, L. M. & BICUDO, D. C. 2017. Local environment and connectivity are the main drivers of diatom species composition and trait variation in a set of tropical reservoirs. *Freshwater Biology,* 62**,** 1551-1563.

11 Supplementary

List of Figures in the Supplementary

List of Tables in the Supplementary

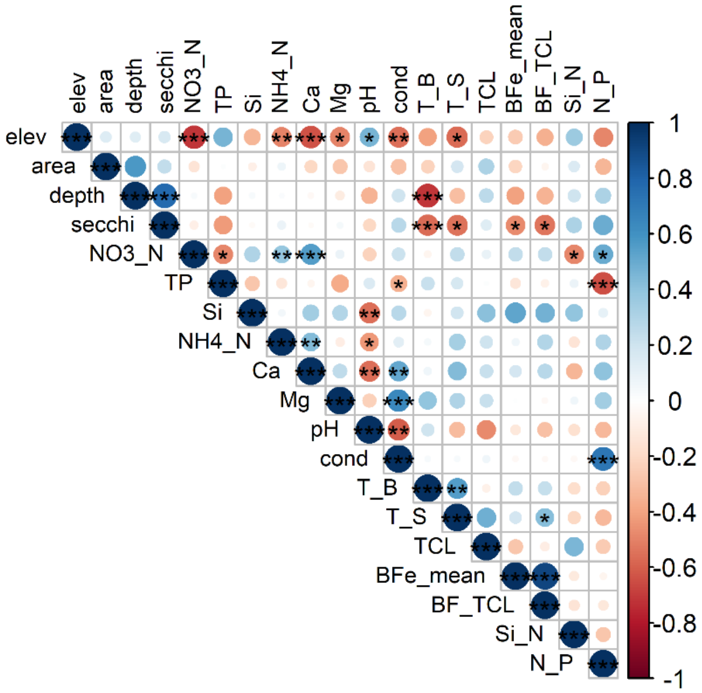

Figure S 1: Correlation plot for 19 environmental variables. Size and color of the dots indicate R^2 correlation values between variables, Bonferroni-adjusted significance levels are indicated by stars: *** ≙ $p < 0.001$; ** ≙ $p < 0.01$; *≙ $p < 0.05$. For variable abbreviations see Table 1.

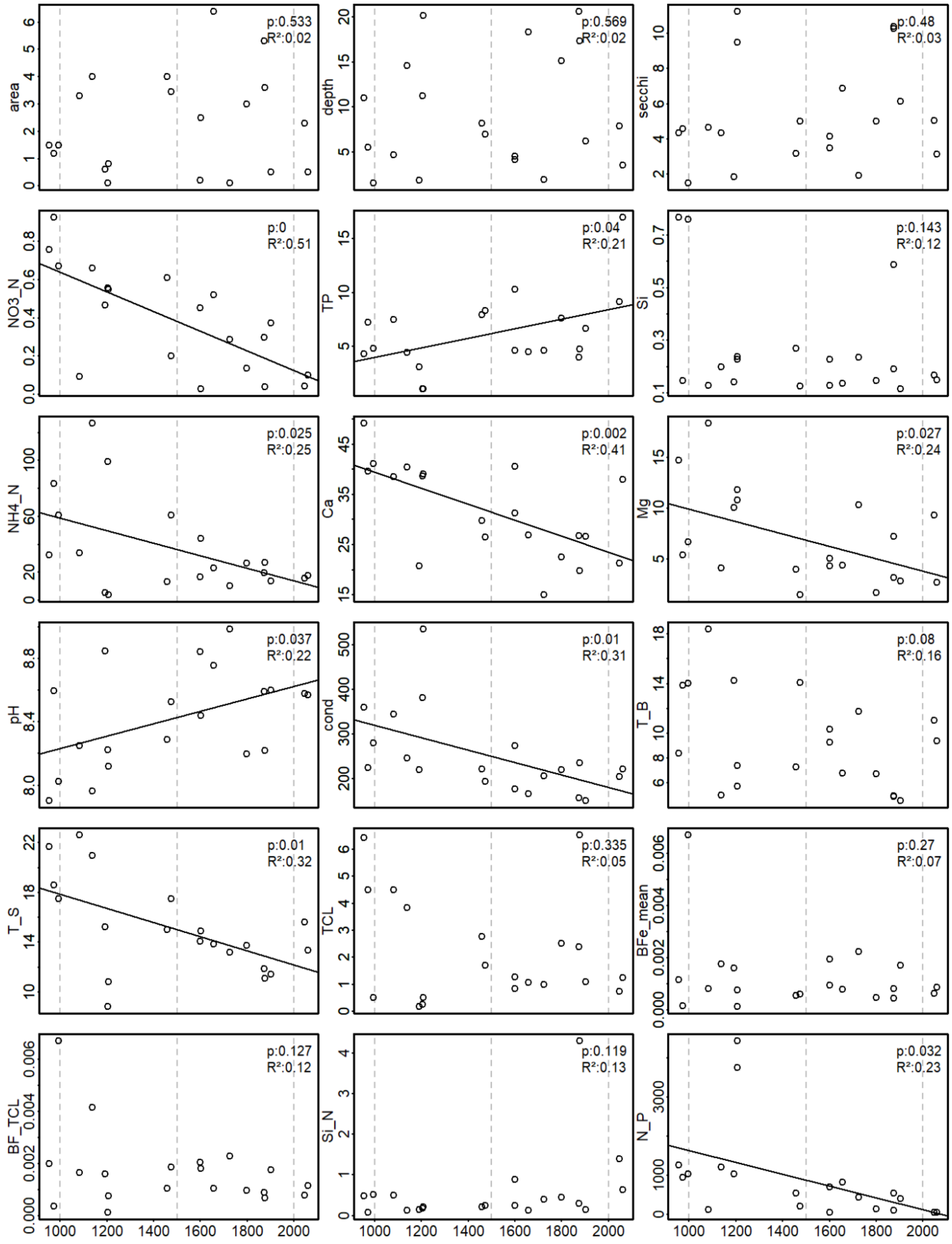

Figure S 2: 18 environmental parameters plotted against elevation. R² values and p values are given for linear regression models, significant models are plotted. For variable abbreviations and units see Table 1.

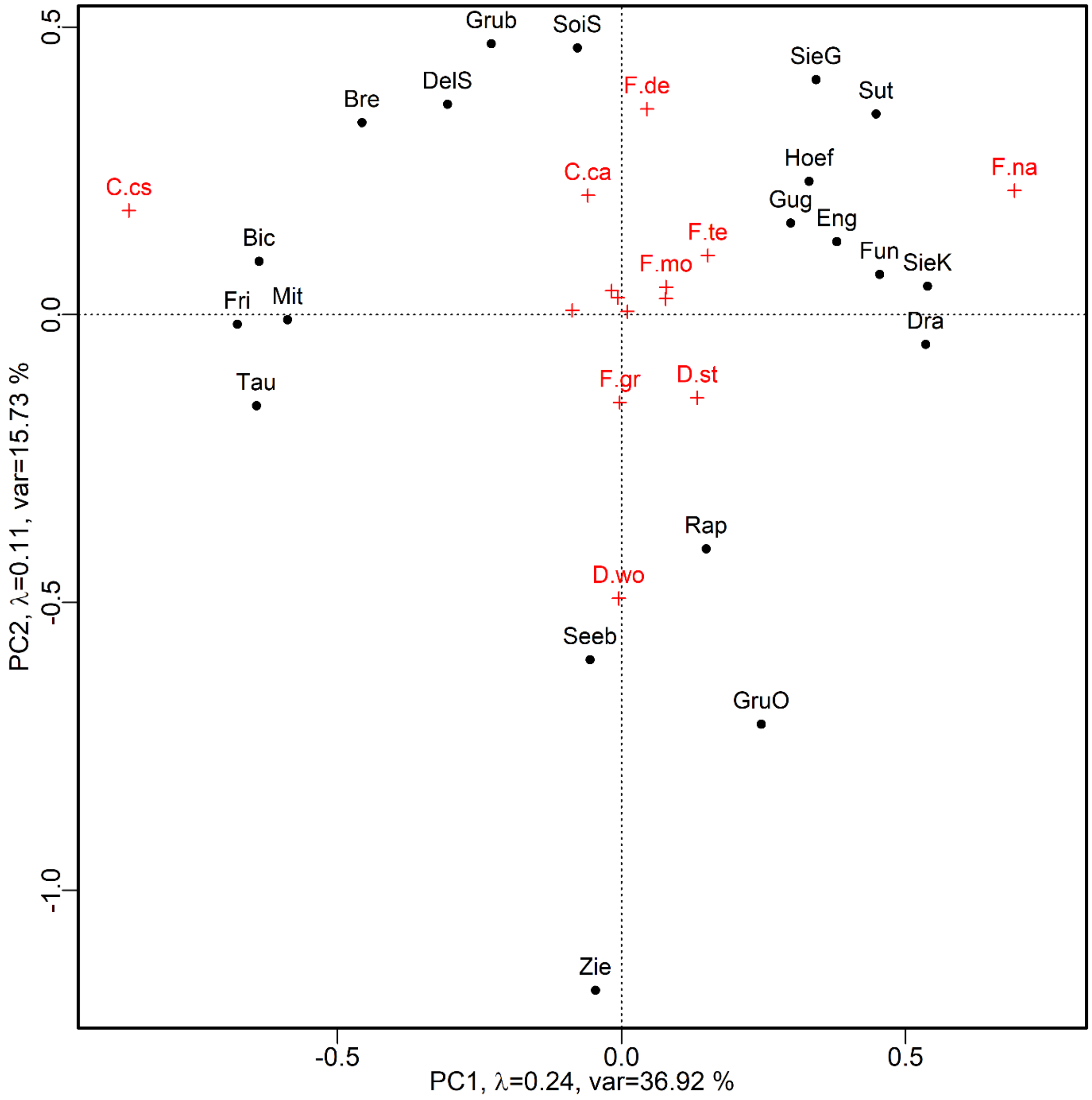

Figure S 3: PCA correlation biplot on 14 planktic diatom taxa for 20 mountain lakes of the northern European Alps. Principal component 1 and 2 (PC1, PC2) are plotted. λ indicates eigenvalues, var indicates percentage of explained variance. For lake and species abbreviations see Table S1 and Table S2, respectively.

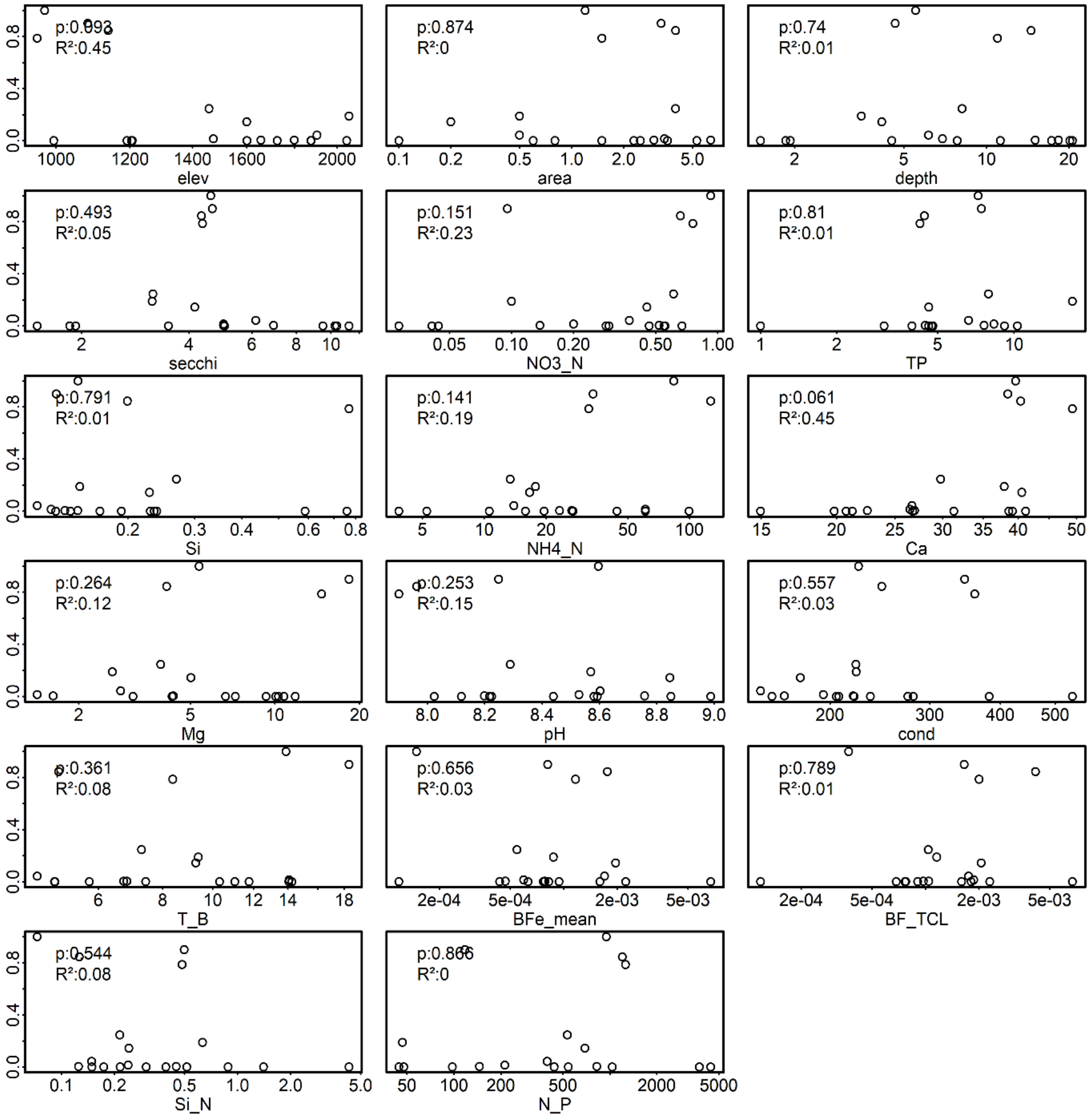

Figure S 4: Relative abundance of *C. comensis* in relation to the assessed environmental parameters.

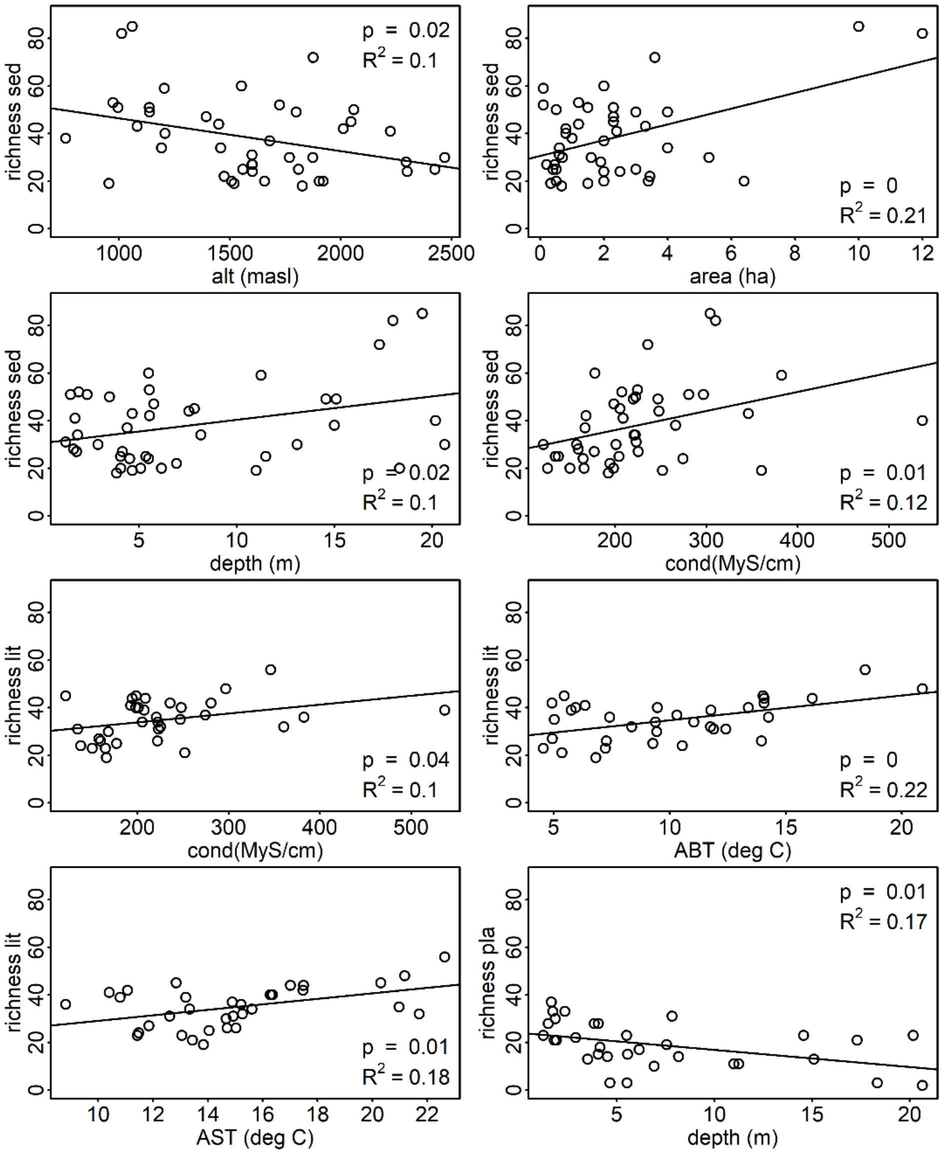

Figure S 5: Linear regression models for sedimentary (n=43), littoral (n=34) and planktic (n=32) Shannon diversity along environmental gradients. “p” indicates p-values of linear regression models, and “R²” gives the multiple R²-value of these models. For abbreviations, see Table S3.

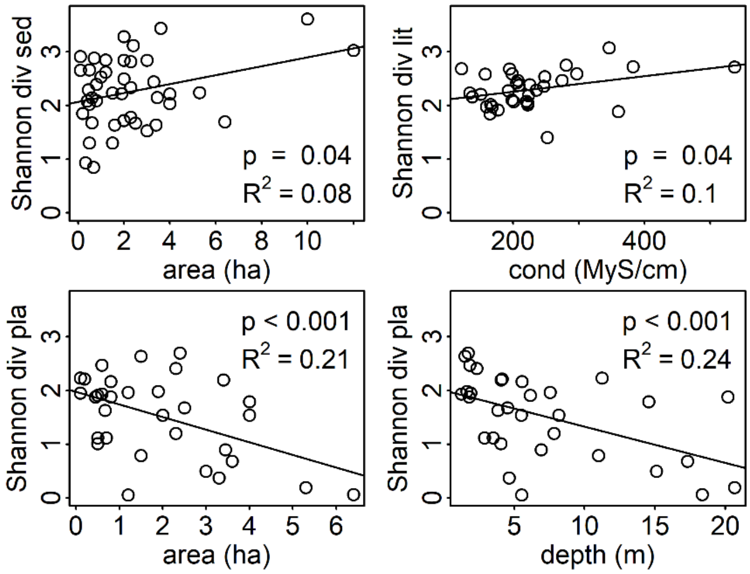

Figure S 6: Linear regression models for sedimentary (n=43), littoral (n=34) and planktic (n=32) species richness along environmental gradients. "p" indicates p-values of linear regression models, and "R^2" gives the multiple R^2-value of these models. For abbreviations, see Table S3.

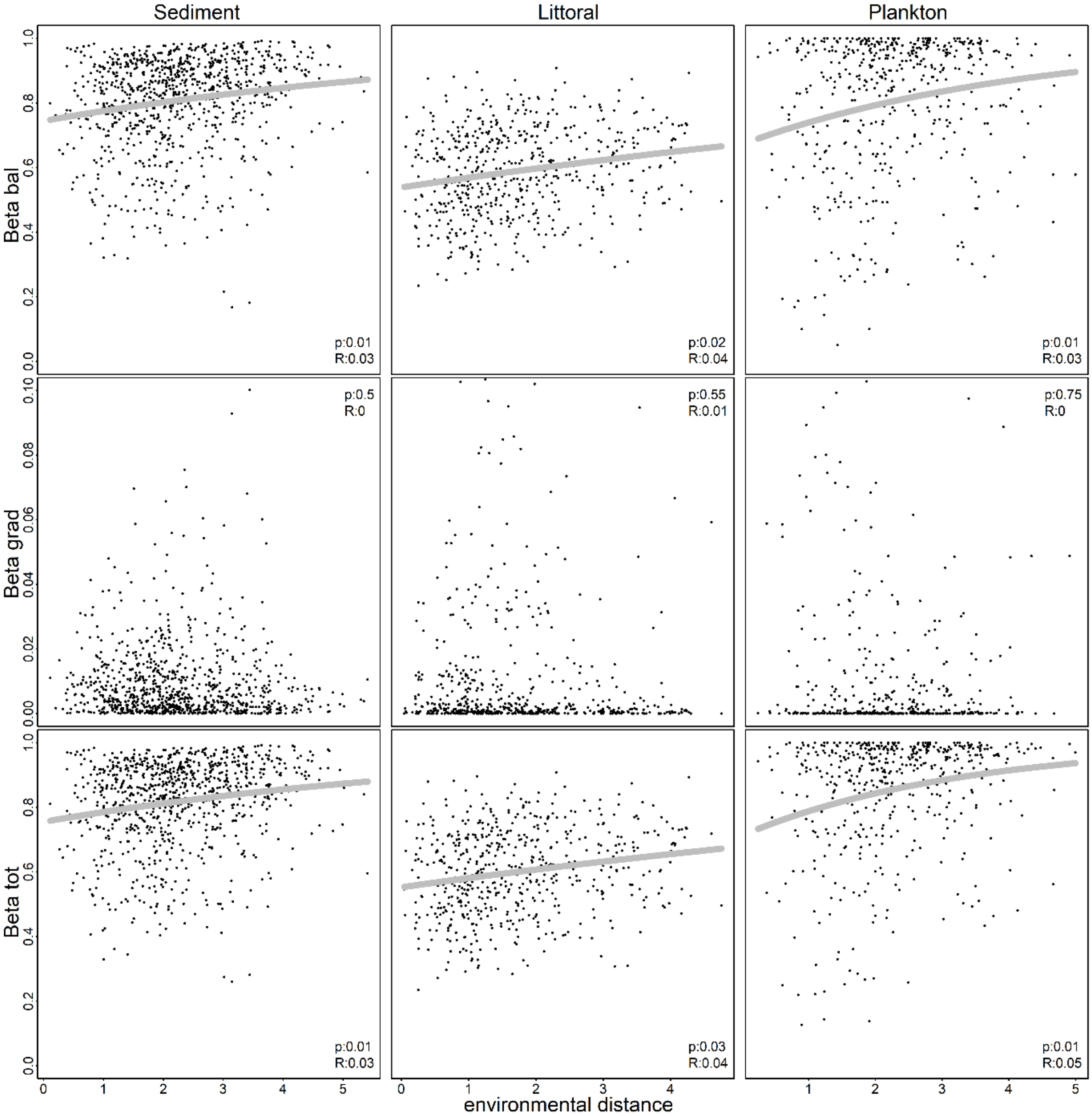

Figure S 7: Decay of pairwise β-diversity (β_{sor}) and its components for turnover and nestedness (β_{sim}, β_{sne}) for incidence data for sedimentary, littoral and planktic diatom assemblages along with increasing environmental distance (represented by the significant parameters identified in RDA backward selection for each assemblage). For combinations with significant Mantel statistics ($p < 0.05$), regression lines are drawn for exponential regression models; model statistics of regression models are given for all combinations.

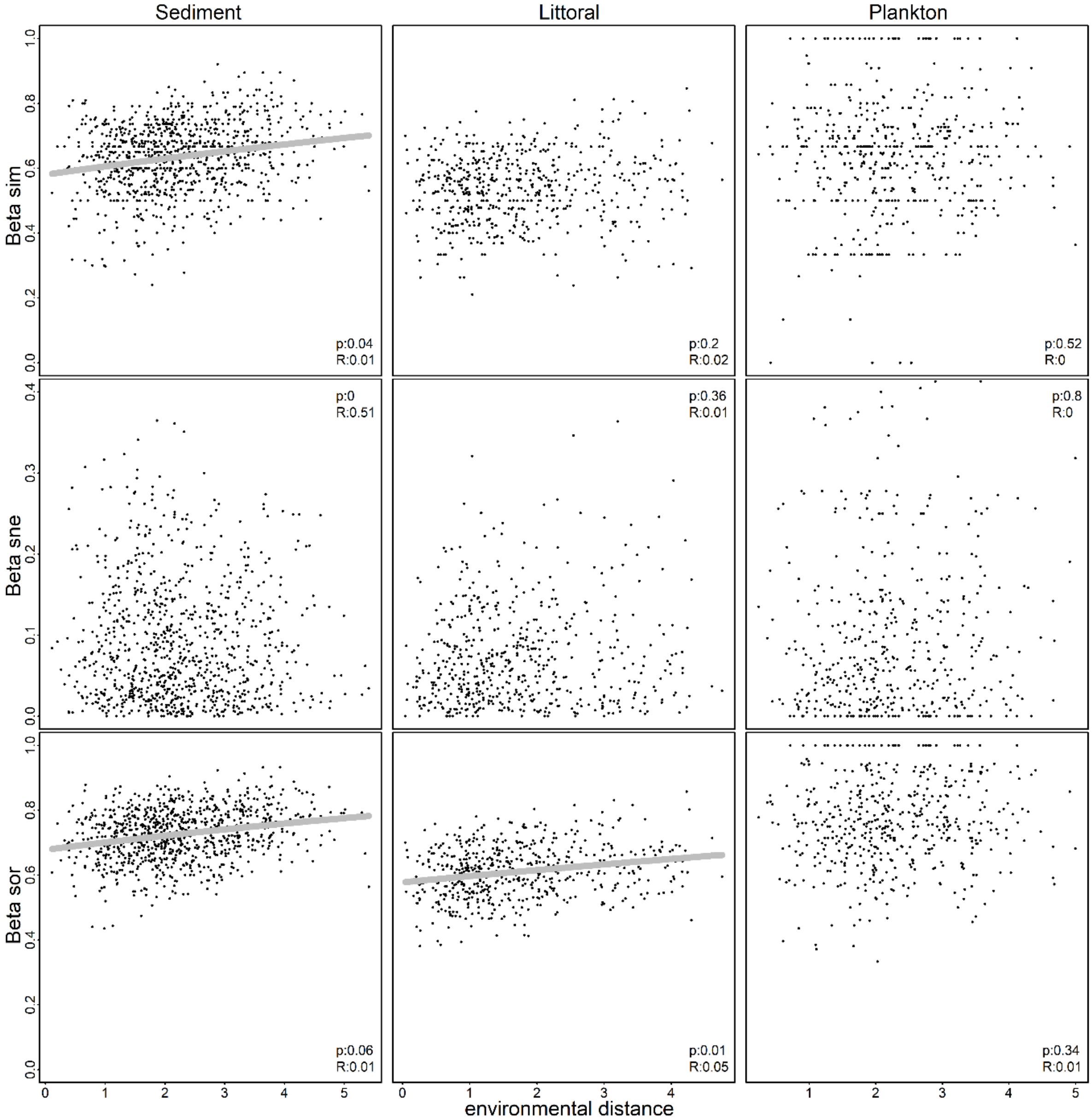

Figure S 8: Decay of pairwise β-diversity (β_{tot}) and its components for balanced variation and abundance gradients (β_{bal}, β_{grad}) for abundance data for sedimentary, littoral and planktic diatom assemblages along with increasing environmental distance. For combinations with significant Mantel statistics ($p < 0.05$), regression lines are drawn for exponential regression models; model statistics of regression models are given for all combinations.

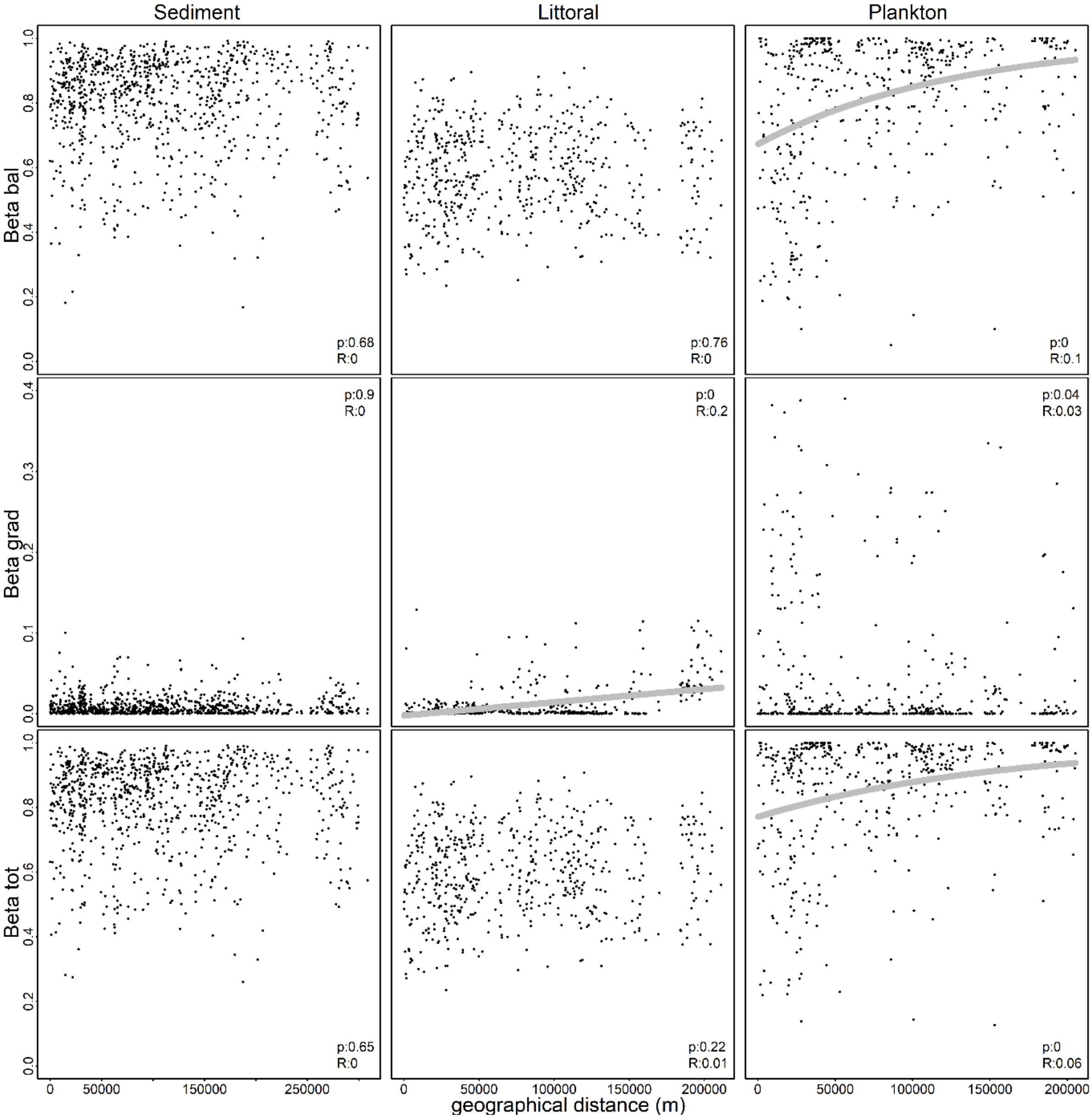

Figure S 9: Decay of pairwise β-diversity (β_{sor}) and its components for turnover and nestedness (β_{sim}, β_{sne}) for incidence data for sedimentary, littoral and planktic diatom assemblages along with increasing geographical distance. For combinations with significant Mantel statistics ($p < 0.05$), regression lines are drawn for exponential regression models; model statistics of regression models are given for all combinations.

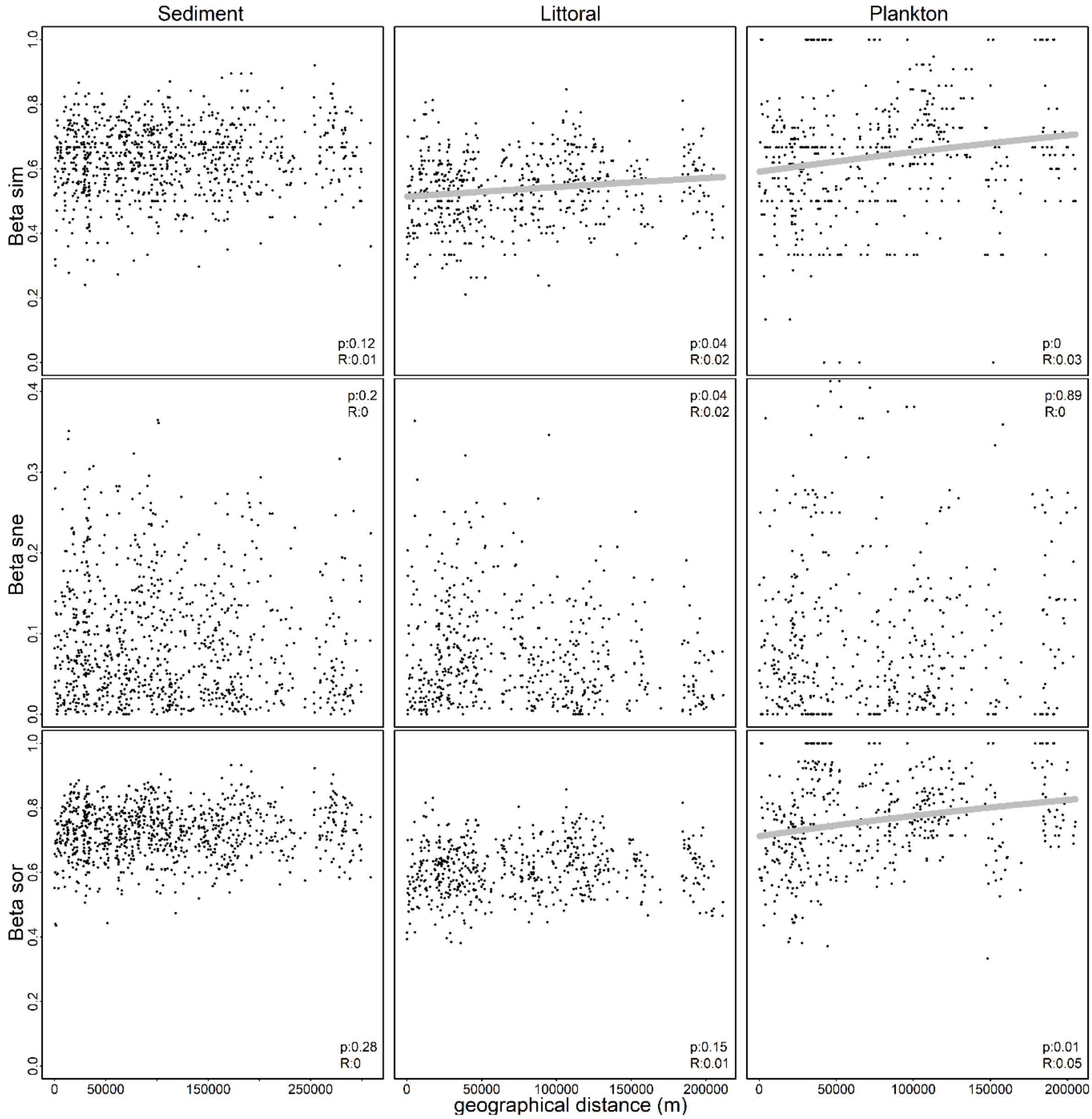

Figure S 10: Decay of pairwise β-diversity (β_{tot}) and its components for balanced variation and abundance gradients (β_{bal}, β_{grad}) for abundance data for sedimentary, littoral and planktic diatom assemblages along with increasing geographical distance. For combinations with significant Mantel statistics ($p < 0.05$), regression lines are drawn for exponential regression models; model statistics of regression models are given for all combinations.

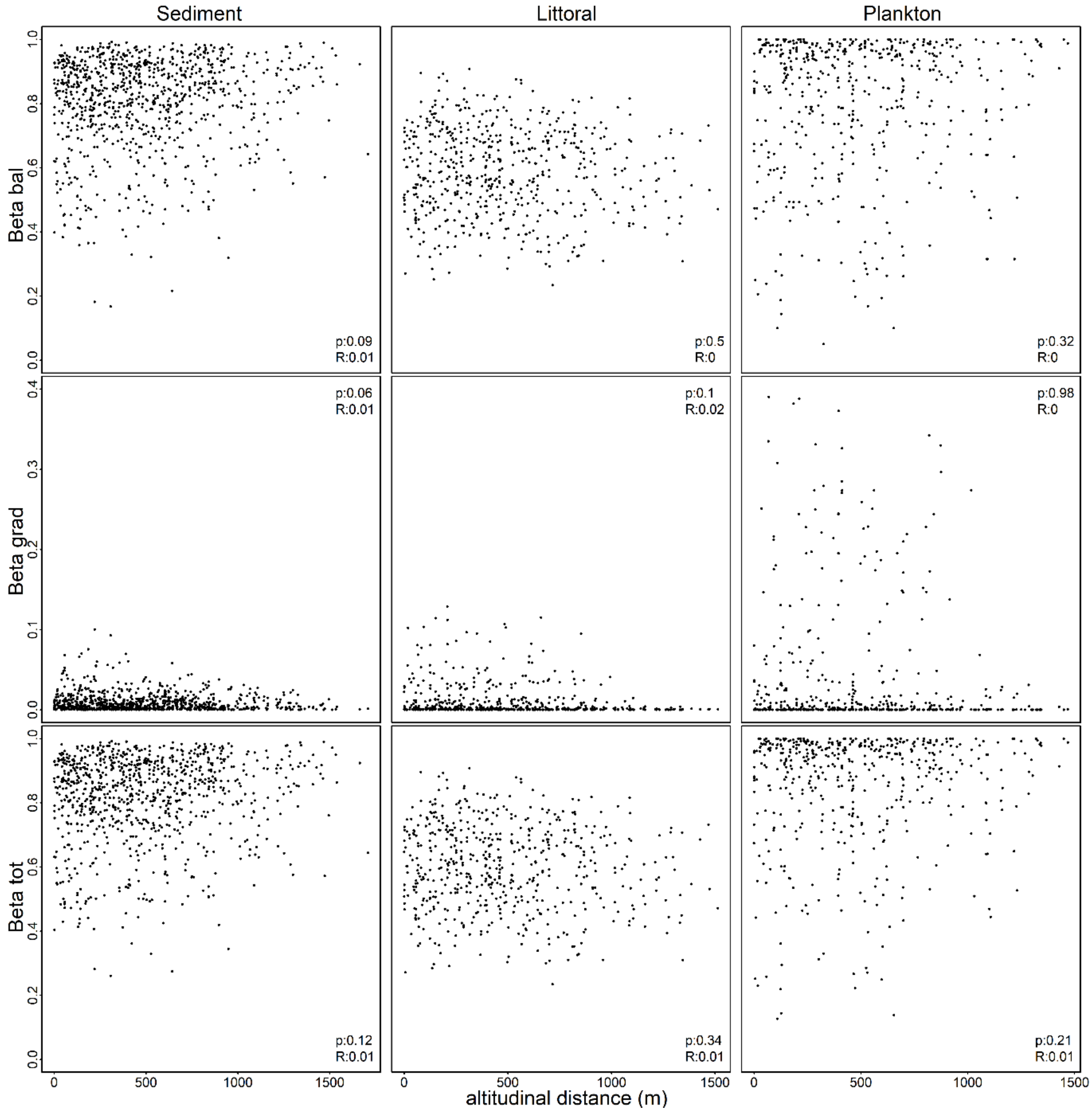

Figure S 11: Decay of pairwise β-diversity (β_{sor}) and its components for turnover and nestedness (β_{sim}, β_{sne}) for incidence data for sedimentary, littoral and planktic diatom assemblages along with increasing altitudinal distance. For combinations with significant Mantel statistics ($p < 0.05$), regression lines are drawn for exponential regression models; model statistics of regression models are given for all combinations.

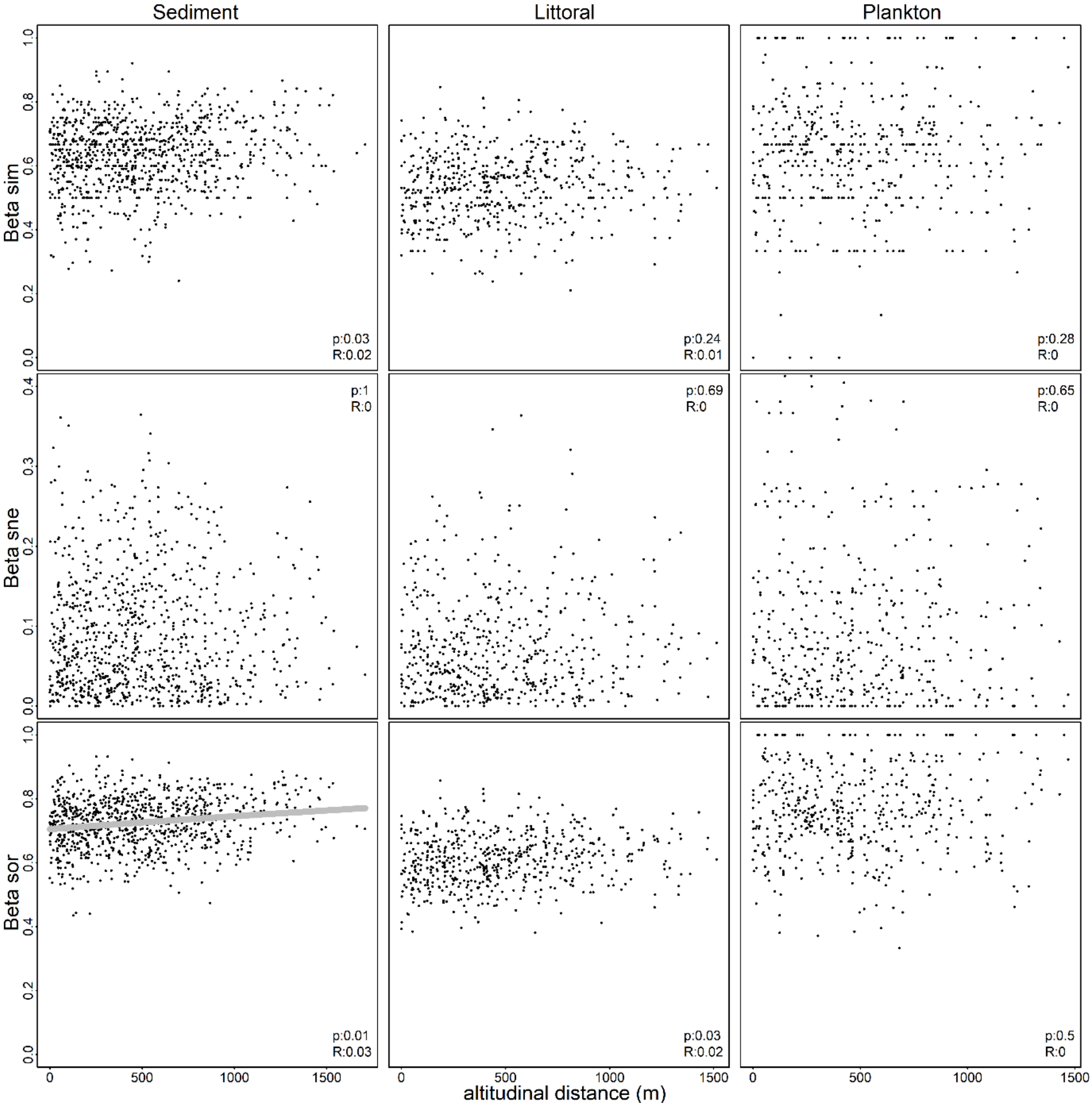

Figure S 12: Decay of pairwise β-diversity (β_{tot}) and its components for balanced variation and abundance gradients (β_{bal}, β_{grad}) for abundance data for sedimentary, littoral and planktic diatom assemblages along with increasing altitudinal distance. For combinations with significant Mantel statistics ($p < 0.05$), regression lines are drawn for exponential regression models; model statistics of regression models are given for all combinations.

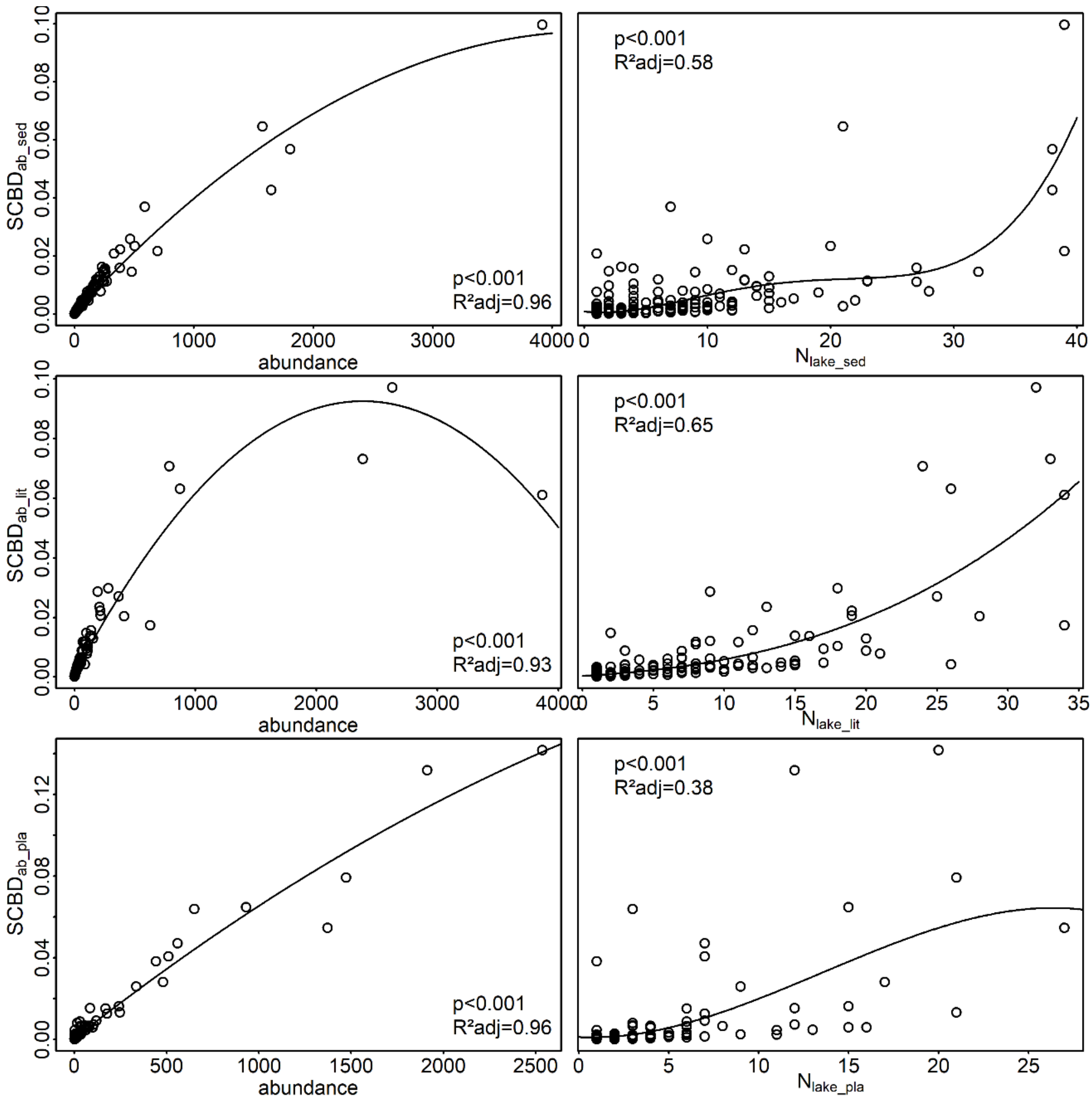

Figure S 13: Influence on the values of species contributions to β-diversity (“SCBD”) investigated for species total abundance (“abundance”) and number of occupied sites (“$N_{\_lake}$”) for abundance data. Model statistics for linear models with polynomial terms: k = number of polynomial terms, p = p-value, R^2_{adj} = adjusted R^2-value.

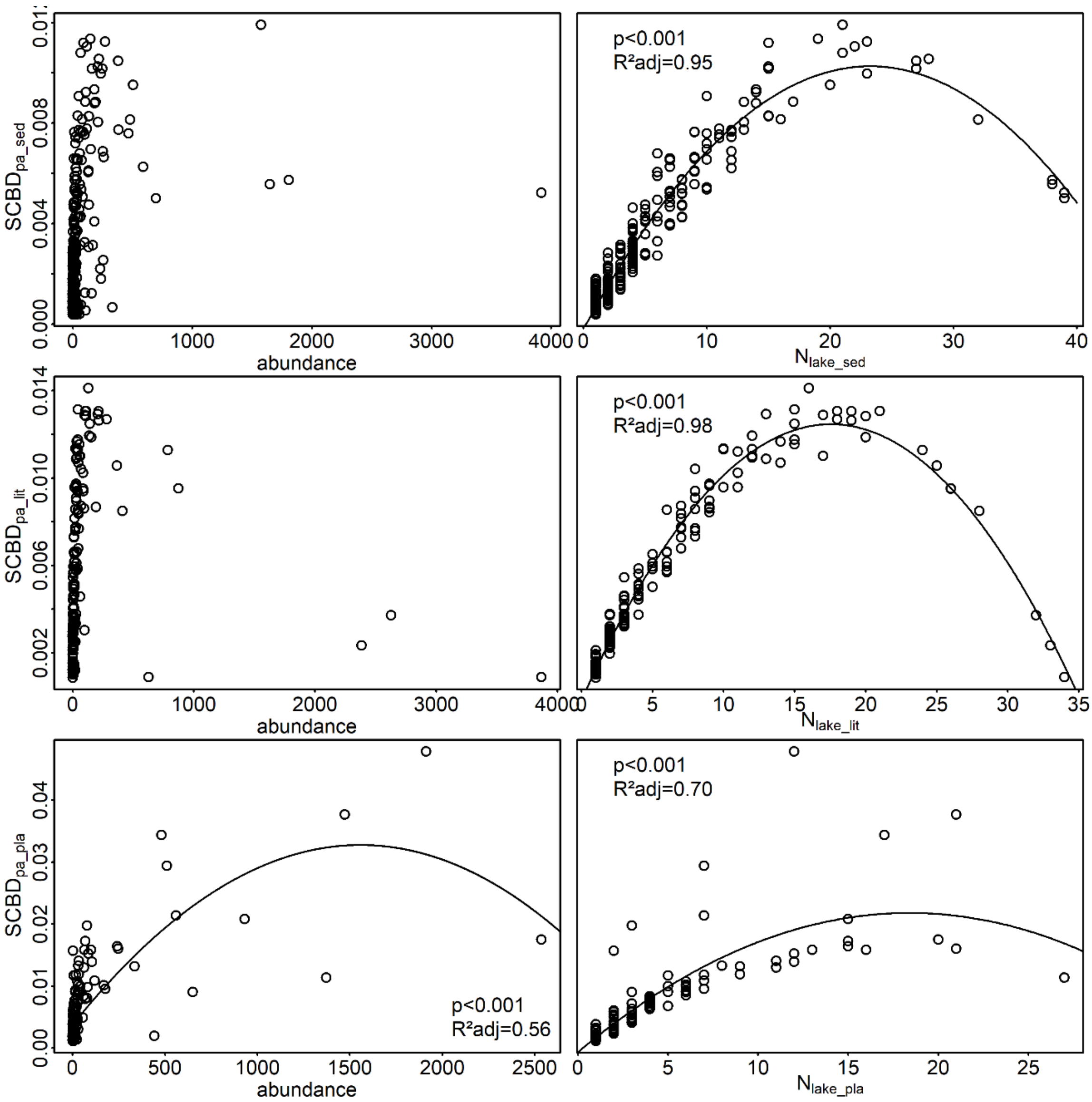

Figure S 14: Influence on the values of species contributions to β-diversity ("SCBD") investigated for species total abundance ("abundance") and number of occupied sites ("$N_{\_lake}$") for incidence data. Model statistics for linear models with polynomial terms: k = number of polynomial terms, p = p-value, R^2_{adj} = adjusted R^2-value.

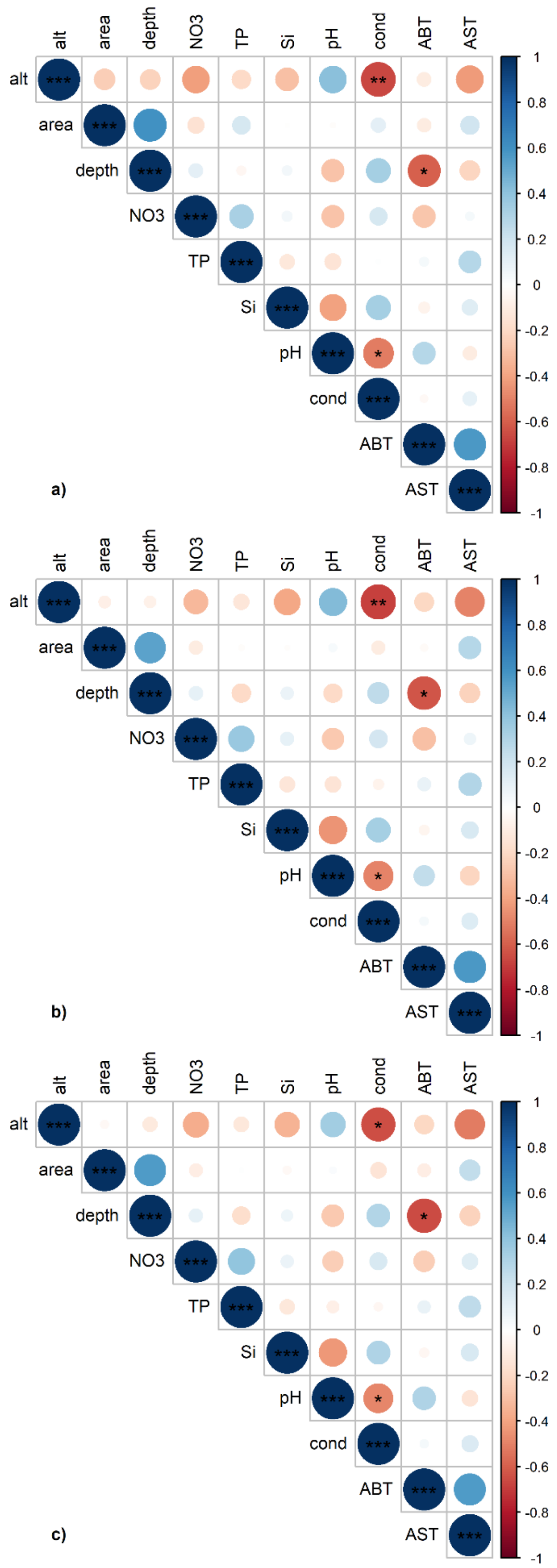

Figure S 15: Correlation plot of variables with VIF´s < 5 for sedimentary (a), littoral (b) and planktic (c) assemblages. Colour range indicates the correlation coefficient, asterisks indicate p-value: *** ≙ p-value < 0.001; ** ≙ p-value < 0.01; * ≙ p-value < 0.05.

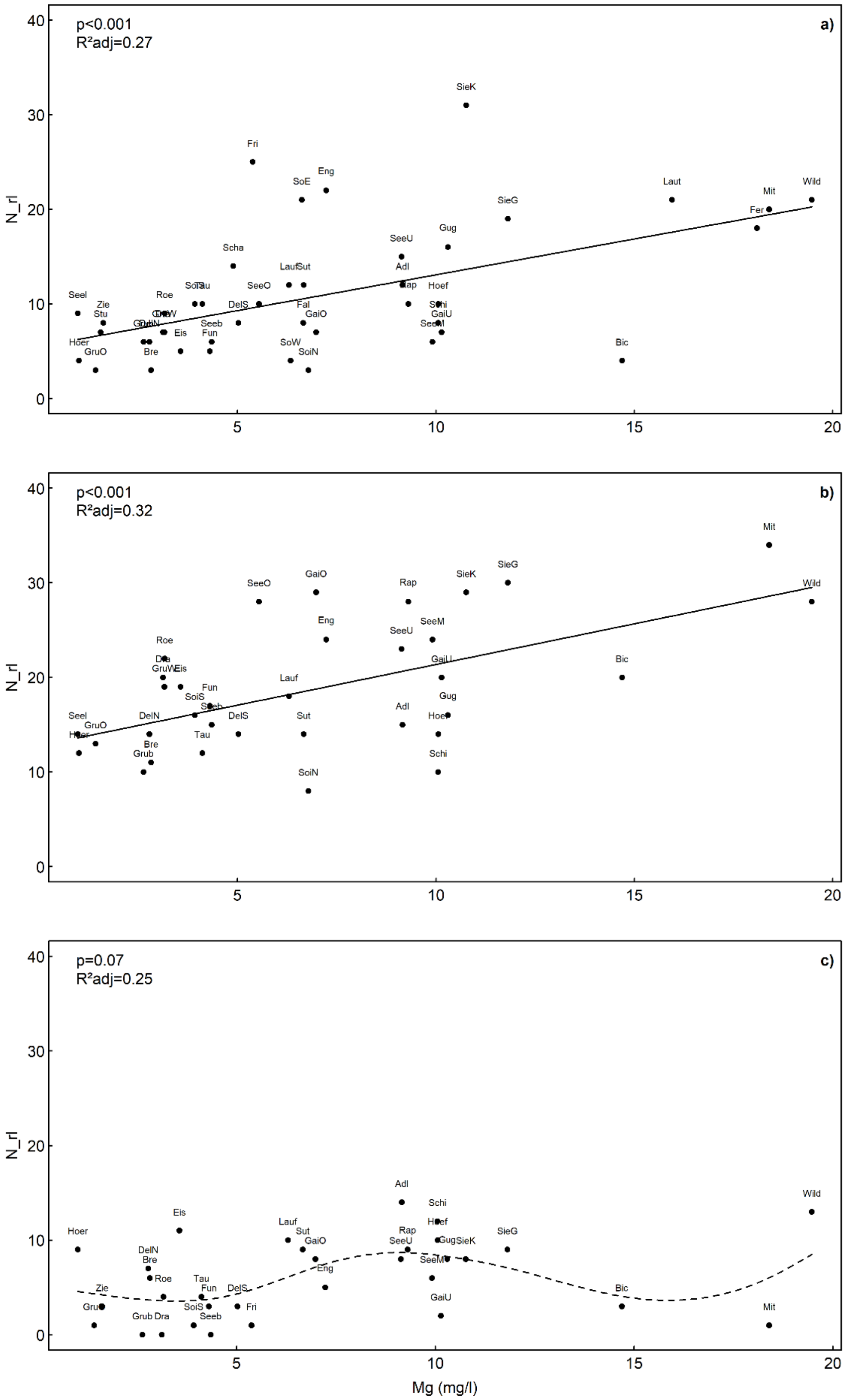

Figure S 16: The number of RL species (N_rl) increases along the magnesium (Mg) gradient for sedimentary (a) and (b) littoral assemblages; no significant relationship was found for planktic assemblages (c). Model parameters are given for GAMs.

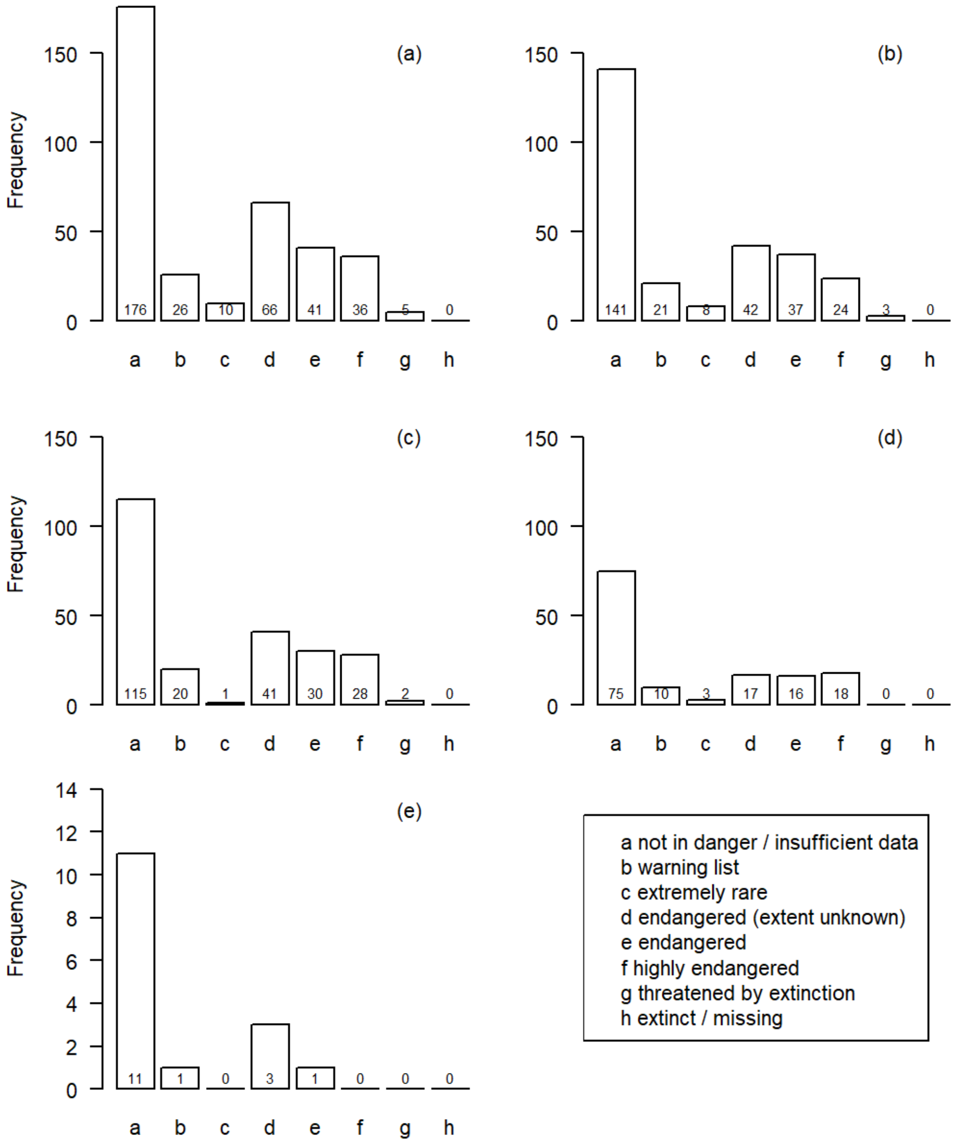

Figure S 17: The number of diatom taxa according to their threat status within the German Red List (2018) is given for (a) the complete data set, (b) sedimentary assemblages, (c) littoral assemblages, (d) planktic assemblages and (e) true planktic assemblages.

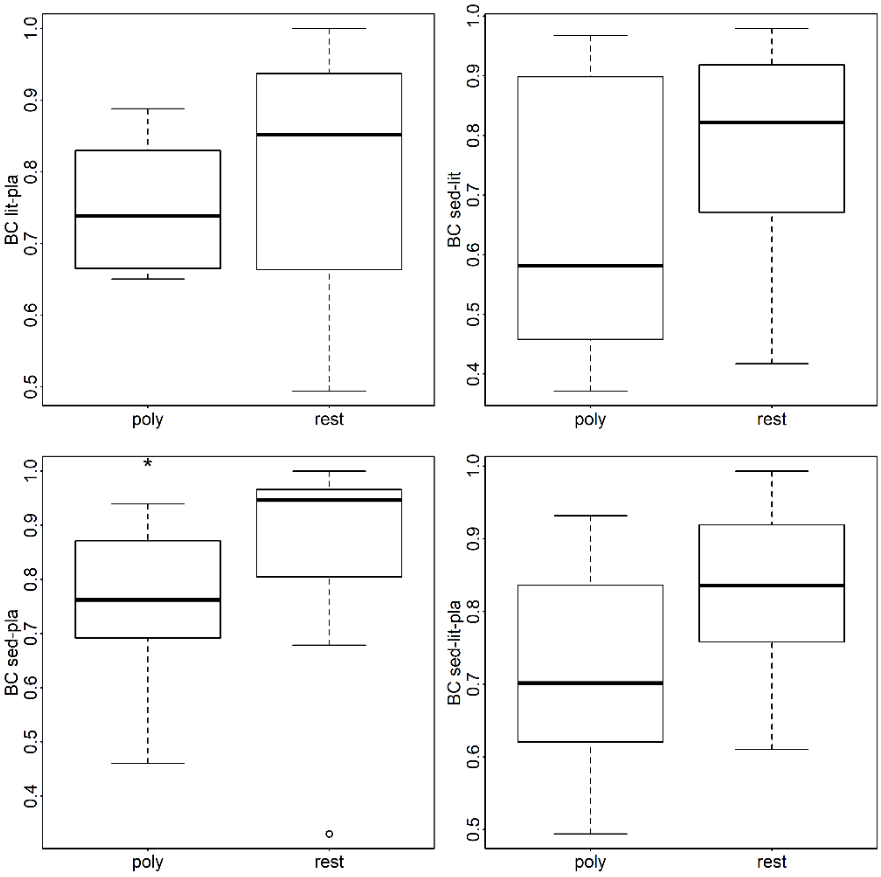

Figure S 18: Boxplots for the pairwise Bray-Curtis dissimilarity (BC) among within-lake diatom assemblages in relation to lake mixing state (NBC lit-pla=32, NBC sed-lit=34, NBC sed-pla=32, NBC sed-lit-pla=32; Asterisks: *: $p < 0.05$.

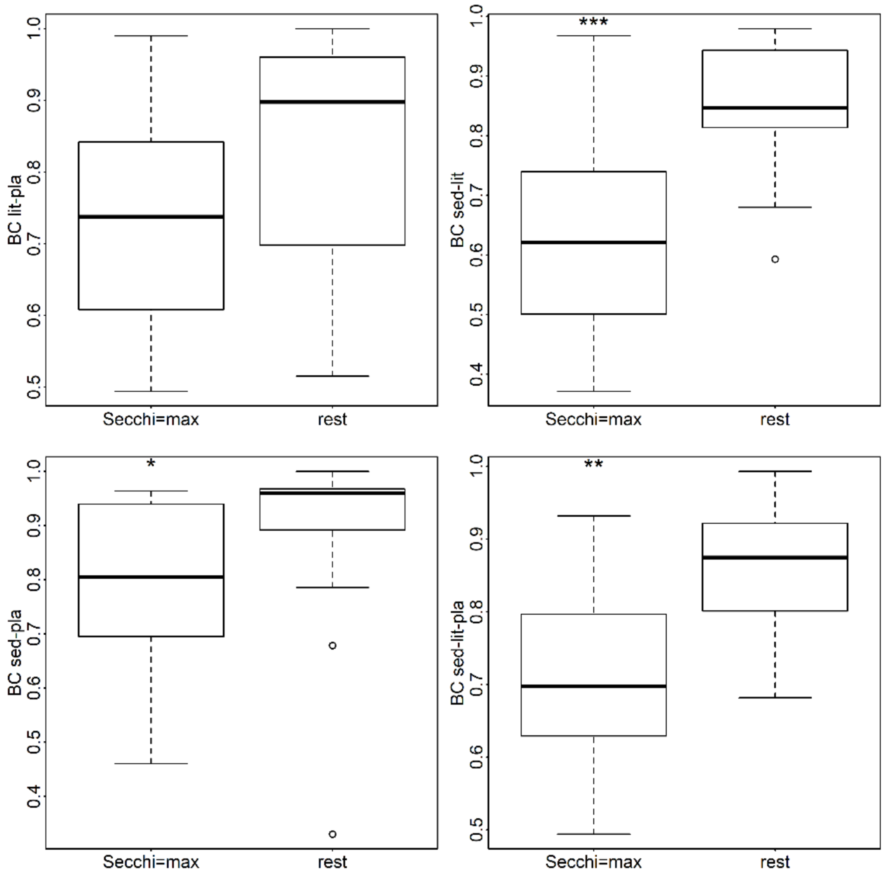

Figure S 19: Bray-Curtis dissimilarity (BC) of within-lake diatom assemblages in relation to lake mixing state (N=43). Asterisks: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

.

Table S 1: Measured and calculated environmental variables for the 20 lake set. Lakes with names written in italics are karstic. Asterisks (*) denote the outlier lake which was excluded. Explanation: Area = Lake area, Depth = Maximum lake depth, Secchi = Secchi depth, TP = Total phosphorus, Si = Silica, NO3_N = Nitrate-nitrogen, NH4_N = Ammonia-nitrogen, Ca = Calcium, Mg = Magnesium, pH = pH-Value, cond = conductivity, T_B = Mean August bottom temperature, T_S = Mean August surface temperature, TCL= Thermocline depth, BFe_mean = Epilimnetic mean buoancy frequency, BF_TCL = Buoancy freqeuncy at the thermocline, SI_N=Ratio of silica to nitrate-N + ammonia-N, N_TP= Ratio of nitrate-N + ammonia-N to total phosphorus.

Lake Name	**Abbreviation**	**Eleva-tion (masl)**	**Area (ha)**	**Depth (m)**	**Secchi (m)**	**Z_euph (m)**	**TP (µg/l)**	**Si (mg/l)**	**NO_3_N (mg/l)**	**NH_4_N (µg/l)**	**Ca (mg/l)**	**Mg (mg/l)**	**pH**	**cond (µS/cm)**	**T_B (°C)**	**T_S (°C)**	**TCL (m)**	**BFe_ Mean (s^{-1})**	**BF_TCL (s^{-1})**	**Si_N**	**N_TP**
Bichlersee	Bic	955	1.5	11.0	4.4	10.5	< 5	0.77	0.76	32.3	49.24	14.70	7.90	360.3	8.37	21.71	6.4	0.0012	0.0020	0.5	1259.1
Brendlsee	Bre	1,903	0.5	6.2	> 6.2	> 12.4	6.6	0.12	0.37	14.0	26.67	2.82	8.60	150.6	4.56	11.44	1.1	0.0017	0.0017	0.1	396.3
Delpssee süd	DelS	1,600	0.2	4.2	> 4.2	> 10.2	< 5	0.23	0.45	16.7	40.55	5.02	8.85	177.2	9.28	14.05	0.8	0.0020	0.0021	0.2	691.0
Drachensee	Dra	1,874	5.3	20.7	10.3	16.0	< 5	0.19	0.30	19.6	26.75	3.12	8.59	157.7	4.94	11.85	2.3	0.0008	0.0009	0.3	541.5
Engeratsgundsee	Eng	1,876	3.6	17.3	10.4	16.1	< 5	0.59	0.04	27.0	19.82	7.23	8.22	235.6	4.93	11.07	6.5	0.0004	0.0007	4.3	97.7
Frillensee	Fri	973	1.2	5.5	4.6	10.7	7.2	0.15	0.93	83.7	39.62	5.38	8.60	224.3	13.88	18.59	4.5	0.0001	0.0004	0.1	949.7
Funtensee	Fun	1,601	2.5	4.5	3.5	9.4	10.3	0.13	0.03	44.3	31.30	4.31	8.44	274.4	10.31	14.89	1.3	0.0009	0.0018	0.9	47.7
Grubersee	Grub	2,060	0.5	3.5	3.2	8.9	17.0	0.15	0.10	17.8	37.93	2.64	8.57	222.4	9.38	13.34	1.2	0.0009	0.0012	0.6	46.9
Grünsee ost	GruO	1,474	3.5	6.9	5.0	11.2	8.3	0.13	0.20	60.8	26.47	1.42	8.53	194.5	14.08	17.50	1.7	0.0006	0.0019	0.2	212.1
Guggersee	Gug	1,725	0.1	1.9	> 1.9	> 6.9	< 5	0.23	0.29	10.6	14.97	10.30	8.99	207.3	11.77	13.20	1.0	0.0022	0.0023	0.4	438.8
Höfersee	Hoef	1,192	0.6	1.9	> 1.9	> 6.9	< 5	0.14	0.47	5.3	20.74	10.06	8.85	220.7	14.26	15.22	0.2	0.0016	0.0016	0.1	1037.7
Mittersee	Mit	1,082	3.3	4.7	> 4.7	> 10.8	7.5	0.13	0.10	34.0	38.46	18.40	8.25	345.8	18.42	22.64	4.5	0.0008	0.0016	0.5	117.9
Rappensee	Rap	2,047	2.3	7.8	5.0	11.2	9.2	0.17	0.04	15.9	21.24	9.31	8.58	205.1	11.04	15.61	0.7	0.0006	0.0008	1.4	44.4
Seebensee	Seeb	1,657	6.4	18.4	6.9	13.1	< 5	0.14	0.52	23.3	26.95	4.35	8.76	165.9	6.81	13.84	1.1	0.0008	0.0010	0.1	824.7
Sieglsee groß	SieG	1,207	0.8	20.2	9.5	15.4	< 5	0.24	0.55	3.8	39.14	11.81	8.12	536.7	5.76	10.80	0.5	0.0008	0.0008	0.2	3748.5
Sieglsee klein	SieK	1,205	0.1	11.3	>11.3	> 16.8	< 5	0.23	0.56	99.4	38.63	10.77	8.22	382.4	741	8.82	0.3	0.0001	0.0001	0.2	4442.3
Soinsee süd	SoiS	1,458	4.0	8.2	3.2	8.9	7.9	0.27	0.61	13.4	29.76	3.92	8.29	222.1	7.28	15.04	2.8	0.0005	0.0010	0.2	533.4
Suttensee	Sut	995	1.5	1.5	> 1.5	> 6.1	< 5	0.76	0.67	60.9	41.17	6.67	8.03	280.7	14.06	17.47	0.5	0.0067	0.0067	0.5	1038.4
Taubensee	Tau	1,138	4.0	14.6	4.3	10.4	< 5	0.20	0.66	126.9	40.40	4.12	7.96	246.8	5.02	20.97	3.9	0.0018	0.0042	0.1	1202.9
Ziereiner See	Zie	1,799	3.0	15.1	5.0	11.2	7.6	0.15	0.14	26.7	22.49	1.62	8.20	219.8	6.72	13.72	2.5	0.0005	0.0010	0.4	145.8
***Röthensteiner See**	Roe	1,450	1.2	7.6	1.5	6.1	20.4	0.18	2.86	78.2	28.92	3.17	8.22	248.1	5.96	16,37	1.1	0.0009	0.0010	0.1	121.1

Table S 2: Counts of planktic diatom Taxa and share of planktic species in each of the 20 samples.

Taxon	***Asterionella formosa***	***Cyclotella comensis***	***Cyclotella comta***	***Cyclotella delicatula***	***Cyclotella distinguenda***	***Discostella stelligeroides***	***Discostella woltereckii***	***Fragilaria acus***	***Fragilaria delicatissima***	***Fragilaria gracilis***	***Fragilaria mesolepta***	***Fragilaria montana***	***Fragilaria nanana***	***Fragilaria tenera***	**Sum**	**% planktic species**
Abbreviation	A.fo	C.cs	C.ca	C.de	C.di	D.st	D.wo	F.ac	F.de	F.gr	F.me	F.mo	F.na	F.te		
Bic	1	393	56	35	0	0	0	0	2	0	0	0	0	0	487	97.4
Bre	2	22	20	0	0	0	0	0	8	0	0	0	0	0	52	10.4
DelS	0	72	25	0	0	0	0	15	12	0	0	0	18	0	142	28.4
Dra	0	0	0	0	0	24	0	0	0	0	0	0	476	0	500	100
Eng	9	0	9	0	0	0	0	0	0	0	0	17	28	7	70	14
Fri	0	500	4	0	0	0	0	0	0	0	0	0	0	0	504	100
Fun	0	0	0	2	0	87	0	0	67	0	0	0	204	0	360	72
Gru	0	95	44	0	0	0	0	0	288	1	0	0	6	5	439	87.8
GruO	0	8	0	0	0	0	337	0	6	0	0	0	221	0	572	100
Gug	0	0	39	0	0	0	0	0	0	0	1	0	27	0	67	13.4
Hoef	0	0	26	0	15	0	0	1	1	0	0	0	23	5	71	14.2
Mit	0	450	0	41	0	0	0	0	0	0	0	0	9	0	500	100
Rap	0	0	75	0	1	357	0	0	0	1	0	0	10	0	444	88.8
Seeb	0	2	3	0	0	0	0	0	0	489	0	0	0	0	494	98.8
SieG	0	0	15	0	0	0	0	0	159	6	0	21	96	10	307	61.4
SieK	0	0	0	0	4	0	0	0	0	0	0	0	78	5	87	17.4
SoiS	0	123	3	0	0	0	0	0	205	0	0	0	107	0	438	87.6
Sut	0	0	0	0	0	0	0	0	33	0	0	0	55	13	101	20.2
Tau	2	423	21	0	0	0	30	0	3	0	0	0	0	0	479	95.8
Zier	0	2	0	0	0	6	290	0	5	0	0	0	0	0	303	60.6
Sum	14	2,090	340	78	20	474	657	16	789	497	1	38	1,358	45	6,417	

Table S 3: Metrics characterising the measured environmental variables of the 43 lake set.

Parameter	Abbre-viation	Minimum	Maximum	Mean	Median	Standard Deviation
Altitude (masl)	alt	760	2,469	1,598	1,600	429.0
Lake area (ha)	area	0.1	12.0	2.3	1.9	2.4
Maximum depth (m)	depth	1.3	20.7	7.8	5.5	5.9
Secchi depth (m)	secchi	1.3	11.3	4.6	4.2	2.5
Nitrate-N (mg/l)	NO_3	0.03	2.86	0.44	0.33	0.5
Total phosphorus (µg/l)	TP	1	20.41	6.92	6.62	4.6
Silicate-Si (mg/l)	Si	0.12	0.77	0.22	0.18	0.15
Ammonia-N (µg/l)	NH_4	3.84	126.85	36.45	25.29	27.49
Sodium (mg/l)	Na	0.1	2.11	0.38	0.23	0.42
Calcium (mg/l)	Ca	12.44	49.24	28.87	27.06	9.94
Magnesium (mg/l)	Mg	0.98	19.47	7.12	6.34	4.8
pH	pH	7.9	9.0	8.4	8.5	0.3
Oxygen (%)	O_2	5.1	129.8	93.4	96.9	23.8
Conductivity (µS/cm)	cond	121.4	536.7	226.0	208.6	78.2
Ø August bottom temperature(°C)	ABT	4.6	20.9	10.0	9.4	4.0
Ø August surface temperature (°C)	AST	8.8	22.6	15.1	14.9	3.1