

Variation in the predictability of lake plankton metric types

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Abstract

Statistical and climate models are frequently used for biodiversity projections under future climatic changes, but their predictive capacity for freshwater plankton may vary among different species and community metrics. Here, we used random forests to model plankton species and community metrics as a function of biological, climatic, physical, and chemical data from long-term (2000–2017) monitoring data collected from Lake Müggelsee Berlin, Germany. We (1) compared the predictability of well-known lake plankton metric types (biomass, abundance, taxonomic diversity, Shannon diversity, Simpson diversity, evenness, taxonomic distinctness, and taxonomic richness) and (2) assessed how the relative influence of different environmental drivers varies across lake plankton metric models. Overall, the metric predictability was highest for biomass and abundance followed by taxonomic richness. The biomass of dominant phytoplankton taxonomic groups such as cyanobacteria (adjusted- $R^2 = 0.53$) and the abundance of dominant zooplankton taxonomic groups such as rotifers (adjusted- $R^2 = 0.59$) and daphnids (adjusted- $R^2 = 0.51$) were more predictable than other metric types. The plankton metric predictability increased when grouping phytoplankton species according to their functional traits (adjusted- $R^2 = 0.37 \pm 0.14$, mean \pm SD, $n = 36$ functional groups) compared to higher taxonomic units (adjusted- $R^2 = 0.25 \pm 0.15$, $n = 22$ taxonomic groups). Light, nutrients, water temperature, and seasonality for phytoplankton and food resources for zooplankton were the main drivers of both taxonomic and functional groups, giving confidence that our models captured the expected major environmental drivers. Our quantitative analyses highlight the multidimensionality of lake planktonic responses to environmental drivers and have implications for our capacity to select appropriate metrics for forecasting the future of lake ecosystems under global change scenarios.

Freshwater ecosystems are subject to numerous anthropogenic stressors such as land use and climate change (Søndergaard and Jeppesen 2007; Vörösmarty et al. 2010). Among freshwater ecosystems, lakes are strongly threatened by global change effects (Adrian et al. 2009; Carpenter et al. 2011). Lakes are home to a diverse array of plankton species, which play vital roles in biogeochemical cycles and food webs (Falkowski et al. 1998; Field et al. 1998). Modeling lake responses to global change enables understanding of how global change might alter biological and functional community structure or lead to biodiversity loss, and how these changes might affect ecological functioning (Isbell et al. 2011; Mouquet et al. 2015). In light of the rapid decline in global freshwater biodiversity (Scholes et al. 2018) and given the

importance of plankton diversity for lake ecosystem functioning, there is an ongoing need to predict plankton responses to global change (Lürling and De Senerpont Domis 2013; Özkundakci et al. 2016). A wide variety of commonly recorded taxonomic and functional metric types such as biomass, abundance, taxonomic richness, Shannon diversity, Simpson diversity, and evenness can be used to assess the ecological effects of global change on lake ecosystems. Each of these highly relevant metric types captures different community responses to environmental changes and provides unique information on ecosystem conditions (Mouillot et al. 2006; Heino et al. 2007; Gascón et al. 2009; Gallardo et al. 2011; Özkundakci et al. 2016). For example, biomass, abundance, and taxonomic richness describe the mass or number of different species in an ecological community (Colwell 2009) that reflect abiotic constraints (Gallardo et al. 2009). Global-change effects on biotic communities alter the number of species and their abundances (Hillebrand et al. 2008). Shannon and Simpson diversity indices characterize species diversity in a community and include measurement of community heterogeneity. While Shannon diversity emphasizes the richness component of

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diversity, in Simpson diversity the relative importance of evenness to richness is higher compared to Shannon diversity (Nagendra 2002). Furthermore, evenness itself reflects how equally species abundances are distributed in a community (Wilsey and Potvin 2000). We know, for example, that global warming leads to an increase in thermophilic species (Adrian et al. 2016), favors cyanobacteria blooms consisting of only a few species (Wagner and Adrian 2009; Huber et al. 2012), or leads to a decline or extinction of cold water fish species (Jeppesen et al. 2010). All these responses to environmental drivers alter total and relative species abundances and thereby species evenness (Adrian et al. 2006; Hillebrand et al. 2008; Wilhelm and Adrian 2008; Wagner and Adrian 2011). In contrast, taxonomic distinctness or diversity (i.e., different from species diversity) characterizes the taxonomic relatedness among species in a community (Warwick and Clarke 1995), thus showing whether different functions are active. While total biomass of a community is very much related to resources, the species composition can vary substantially due to short term variability in abiotic drivers, priority effects, and competition between species or traits (Sommer et al. 2012). The differences across the metric types due to the different information they capture from the community result in variations in their predictability. Metrics types are usually addressed individually, making it difficult to evaluate which metric type would be appropriate for forecasting the future of freshwater lake ecosystems. The predictability of commonly used metric types has been assessed for benthic macroinvertebrates of river ecosystems (Heino et al. 2007; Gascón et al. 2009) or transitional water communities (Mouillot et al. 2006). However, assessing the predictability of various metric types, which capture different aspects of ecosystem functions, using environmental driver data in freshwater lake ecosystems is still required.

Assessing metric predictability requires advanced statistical models and time series data with high taxonomic resolution to sufficiently capture the complex relationship between biological communities and environmental drivers (Kremer et al. 2017). Here we apply Random Forests (RFs, a machine learning [ML] algorithm) to 18 years of lake plankton data and its major environmental drivers. ML builds on traditional correlative analyses (Kehoe et al. 2015; Rivero-Calle et al. 2015; Thomas et al. 2018) and allows the description of ecological responses to environmental drivers and captures the complex interactions among drivers.

We compared the predictability and thus the utility of eight commonly used indicators of biological communities and ecosystem functionality including lake plankton biomass, abundance, taxonomic richness, Shannon diversity, Simpson diversity, evenness, taxonomic diversity, and taxonomic distinctness. We chose these specific metric types from multiple potential metrics because they are the most common metric types recorded and measured for lake ecosystems worldwide, which allows comparability between studies. Based on data at

high temporal (weekly biological sample data and mean daily environmental data for the day of sampling) and taxonomic resolution (species/genus), we quantified the predictability of plankton taxonomic and functional communities and their relationship to major environmental drivers for the eight plankton metric types. We hypothesized that (H_1) the predictability of lake plankton communities partially depends on the metric type, and that less-derived metric types (biomass and abundance) might be more sensitive to environmental variability, thus being more predictable than other metric types. Based on common ecological knowledge, (H_2) phytoplankton composition strongly depends on light and nutrient availability, water temperature and seasonality, and (H_3) zooplankton taxa are driven by temperature, resource availability, and predation. Although this study was performed using the data from a single lake, the insights may be relevant to other comparable, temperate, freshwater lakes.

Methods

Study site

Lake Müggelsee (area 7.3 km², mean depth 4.9 m, maximum depth 8.0 m) is a shallow, polymictic, and eutrophic lake located in the southeast of Berlin, Germany (52°26'N, 13°39'E). It is situated between maritime and continental climatic zones, characterized by high intra- and interannual weather variability. It is fed by the River Spree and has a water retention time of approximately 6–8 weeks (Köhler et al. 2005). The seasonal succession pattern of the plankton typically follows the basic annually repeated seasonal successional pattern of plankton, described in the Plankton Ecological Group (PEG) model for a eutrophic lake (Sommer et al. 2012). The PEG is a verbally formulated model unfolding biotic interactions constrained by abiotic control mechanisms (Sommer et al. 2012).

Climatic, physical, and chemical data

Inflow rates from the River Spree were provided by the Berlin Senate Department for the Environment, Transport and Climate Protection (SenUVK, <https://www.berlin.de/sen/uvk/en/>). Meteorological data such as air temperature (°C), light (daily attenuation [1/m], global radiation [$W m^{-2}$], photosynthetically active radiation [$\mu mol m^{-2} s$]), relative humidity, precipitation, and wind (wind speed [$m s^{-1}$] and wind direction [°]) were recorded at the automatic Lake Müggelsee monitoring station anchored 300 m offshore. Meteorological data were aggregated to yield daily means and were used as driving forces in our models. Data gaps were filled using publicly available meteorological data from a weather station approximately 8 km away from Lake Müggelsee (Airport Schönefeld, location: 52°22'N 13°31'E, German weather service: https://www.dwd.de/DE/Home/home_node.html). We found high correlations ($0.5 < |r| < 1$) between the meteorological data of the meteorological station at Lake Müggelsee and the Airport

Schönefeld data. The missing data were simulated by applying RFs machine learning algorithm based on a multivariate regression modeling approach (see Machine learning approach below). Details on the models' performance and the correlation between the meteorological data measured at the lake station and the Airport Schönefeld weather station are summarized in Supplementary Fig. S1. Less than 15% of the data of the lake station were missing and imputed using this approach. To account for seasonality, we added Julian date (1-365) as a predictor variable to our models.

Sampling was carried out between January 2000 and December 2017 at weekly (April to October) to biweekly intervals (November to March). Volumetrically weighted mixed samples derive from samples taken at five different sampling stations across the lake from locations with various water depths (surface to bottom at 1 m intervals at each sampling station). These samples were used for chemical and planktonological analyses (Driescher et al. 1993). Water samples were taken using a 5-liter transparent hydro bios universal water sampler. Depth profiles of water temperature ($^{\circ}\text{C}$), oxygen (concentration, saturation), conductivity (μS), and pH were taken at 0.5 m intervals (surface to bottom) at the five different sampling stations. Similar to the integrated biological samples that are representative of the whole water column, these data were aggregated to yield means per sampling date.

Nutrient measurements included nitrogen (total nitrogen, total dissolved nitrogen, ammonium, and nitrate), dissolved carbon (organic and inorganic), phosphorus (total phosphorus, soluble phosphorus, and soluble reactive phosphorus) and soluble reactive silica. A full list of predictor variables is given in Supplementary Table S1.

Plankton sample processing

Phytoplankton and zooplankton were identified to the lowest possible taxonomic levels of either species or genera, resulting in 97 species and 39 genera (136 taxa) for phytoplankton, and 97 species and 32 genera (129 taxa) for zooplankton. Phytoplankton abundance (cell number L^{-1}) and total phytoplankton biomass (mg L^{-1}) were determined using an inverted microscope (Utermöhl 1958). Our phytoplankton counting effort is such that all encountered phytoplankton taxa in one sample are usually identified after less than 20–50% of the overall counted area has been processed. Zooplankton were identified and counted under a light microscope at 50X (crustacean zooplankton) to 100X (rotifers) magnification. Abundances are given as individuals L^{-1} .

The 747 phytoplankton samples included six taxonomic groups: Cyanobacteria (595 samples, 5 genera, 22 species), diatoms (419 samples, 6 genera, 31 species), chlorophytes (512 samples, 17 genera, 33 species), chrysophytes (585 samples, 7 genera, 5 species), cryptophytes (743 samples, 1 genera, 3 species), and dinoflagellates (327 samples, 3 genera, 4 species). Diatoms were additionally identified to the species level based on separate Naphrax preparations for roughly

24 samples per year (24 ± 10 , mean \pm SD; at least one sample per month) during the study period. To make use of this higher taxonomic resolution, we assessed the predictability of phytoplankton biomass, abundance, taxonomic richness, taxonomic diversity, and taxonomic distinctness with only 546 out of 747 samples, for which we had all species data, resulting in a total number of 90 species and 25 genera (115 taxa).

The 1113 zooplankton samples included 5 taxonomic groups: daphnids (632 samples, 1 genera, 5 species), bosminids (540 samples, 1 genera, 3 species), calanoid copepods (696 samples, 1 genera, 2 species), cyclopoid copepods (739 samples, 1 genera, 2 species), and rotifers (1112 samples, 15 genera, 42 species). This allowed us to assess the predictability of zooplankton abundance, taxonomic richness, taxonomic diversity, and taxonomic distinctness based on 1113 samples, 32 genera, and 97 species.

Metric types and calculations

The most relevant metric types such as abundance and biomass were calculated for the taxa of each sample while identifying the Müggelsee taxa (Table 1). Taxonomic richness (at the genus and species level) was calculated according to the number of species in each sample. The abundance, biomass, and taxonomic richness are the most common and easily calculable metric types, thus being relevant candidates of assessing the predictability of lake algae for many lakes worldwide. Shannon diversity, Simpson diversity, and Pielou's evenness were calculated in R (using vegan package of R Programming Language Software) to address community-level responses. Shannon diversity is more influenced by taxonomic richness and thus rare species than Simpson (Nagendra 2002). For each sampling date, two further community-level metric types were calculated, which provide information on the diversity and distinctiveness of the total phyto- and zooplankton communities: taxonomic diversity (different from species diversity) and taxonomic distinctness. These two metric types reflect relevant aspects of biodiversity. While, for example, taxonomic richness depicts the number of phyto- and zooplankton species and the number of functional groups (i.e., groups of taxa with similar traits such as nitrogen fixers) in a sample, taxonomic diversity and distinctness reflect evolutionary relationships by assessing the relatedness among species within a sample or community (Warwick and Clarke 1995; Clarke and Warwick 2001; Gallardo et al. 2011). Because they are reasonably uncorrelated and capture different information about the community (Gallardo et al. 2011), we also expected the metric types to differ in their predictability. Taxonomic diversity and distinctness were calculated based on abundance data by means of metric types that represent average taxonomic diversity (Δ) or distinctness (Δ^+). Both metric types measure the taxonomic relatedness in species assemblages of a lake by calculating the average path length (i.e., differences in their higher taxonomic units) between all

Table 1. The list of the eight metric types and their description.

Metric type	Description
Abundance	The total number of a species in a sample
Biomass	The mass of each species in a sample according to its abundance and size
Taxonomic richness	The number of a species/functional traits in a sample
Shannon diversity	Shannon diversity index characterizes species diversity in a community while emphasizing the species richness component of diversity
Simpson diversity	Simpson diversity index characterizes species diversity in a community while emphasizing the species evenness component of diversity
Evenness	Evenness reflects how equally species abundances are distributed in a community
Taxonomic distinctness	Taxonomic distinctness measures the average distance between all pairs of species in a community. It characterizes the taxonomic relatedness among species by calculating the differences in higher taxonomic units (i.e., genus, family, order, suborder, and subclass) between all species pairs in that community, while considering their abundances
Taxonomic diversity	Taxonomic diversity (different from species diversity) characterizes the average distance between all pairs of species in a community by calculating the differences in their higher taxonomic units, while considering their abundances. Compared to taxonomic distinctness, taxonomic diversity considers the relatedness between individuals of the same species as well

species pairs in a sample according to their abundance value and the higher taxonomic units (i.e., genus, family, order, suborder, and subclass) (Warwick and Clarke 1995; Gallardo et al. 2011). More specifically, taxonomic distinctness was calculated as: $\Delta^+ = [\sum \sum_{i < j} \omega_{ij}] / [s(s-1)/2]$, where s is the abundance of species present in the sample, and ω is the weight given to the path length between higher taxonomic unit of species i and j (Clarke and Warwick 1998). In comparison, taxonomic diversity considers the paths between individuals of the same species as well (Warwick and Clarke 1995). These two metric types enable the assessment of the evolutionary relatedness among all species assemblages of a sampling site compared to all other samples over time. These two metric types were calculated using the “taxa2dist” and “taxondive” function from the vegan package (Oksanen et al. 2019) in the R programming software (R Development Core Team 2016).

Biodiversity forecasts might use a suite of metric types despite significant collinearities and redundancy across them. For example, Shannon diversity, Simpson diversity, and

evenness were strongly and positively correlated with taxonomic diversity ($r = 0.78, 0.80, \text{ and } 0.75$; Supplementary Fig. S2). Taxonomic distinctness and diversity may provide valuable information on how many functions are active or not, mainly by indicating the existence of taxonomically diversified species. Beside the number of functions performed in a community (e.g., N-fixing), also the (relative) abundance of the species responsible for these functions should be considered, as the ecosystem-level consequences depend on process rates and therefore species evenness (Hillebrand et al. 2008). Given these assumptions, the distribution and diversity of species and thereby traits are important for the aggregated performance of communities (Norberg 2004). Therefore, the somehow redundant metric types of Shannon diversity, Simpson diversity, and evenness provide unique information at the ecosystem level. In more detail, Shannon diversity depends on species richness and is strongly sensitive to even small diversity changes (e.g., changes in the number of species), which makes it being a good indicator of the current state of the environment regarding the changes in species richness. Simpson diversity is weakly affected by less abundant species, but strongly counts on dominant species, which makes it unique in showing ecosystem-level diversity trends (Nagendra 2002) and is a good indicator for algal blooms comprised by only a few species. Changes in the environment may change the relative distribution of species by driving species to extinction or by supporting the dominance of a few species (Chapin lii et al. 2000).

Functional trait selection

Functional traits reflect species' morphological, physiological, and phenological characteristics, which indirectly impact their fitness by affecting their growth, reproduction and survival (Violle et al. 2007). We selected four phytoplankton functional traits at the species and genus level being relevant for capturing morphological, physiological, and behavioral characteristics (Litchman and Klausmeier 2008). Cell organization (the ability to build aggregations) is representative for species' morphological characteristics, while nitrogen fixation (the ability to fix nitrogen) and silica demand are proxies for physiological characteristics, and motility (the ability to move in the water column) describes the behavioral characteristics (see the functional groups for each trait on Table 2). Species were assigned to each functional group according to the quantitative data gathered by a literature search (Seltmann et al. 2019). The abundance, biomass, or taxonomic richness of the species with similar traits was summed up at each sampling date. Using these data, the predictability of functional groups was assessed based on their biomass, abundance, and functional richness as response variables. Due to the fact that the functional traits are assigned to species or genera, and detailed data on diatoms were available for fewer annual samples, the dataset on functional traits was also limited to fewer

samples (i.e., 115 taxa from 546 out of 747 samples), for which diatoms were identified up to the species level.

We further investigated phytoplankton functional traits in multidimensional combinations by assigning each species to a unique functional group according to its trait categories. For example, we grouped all species that are solitary living cells,

Table 2. Functional traits of phytoplankton species (according to Litchman and Klausmeier 2008).

Functional traits	Functional groups	Description
Cell organization	<ul style="list-style-type: none"> Solitary living cells Aggregation forming species Colony building species 	Describes the individual cell organization of the species
Motility	<ul style="list-style-type: none"> Non-motile species Passively motile species Highly motile species 	Describes the ability of species to move in the water column
Nitrogen (N) fixation	<ul style="list-style-type: none"> Non-N-fixers N-fixers 	Discriminates between species that use dissolved nitrogen and are able to fix nitrogen, and species that are unable to fix nitrogen at all
Silica demand	<ul style="list-style-type: none"> No silica demanding High silica demanding 	Defines the silica demand of species

non-motile species, non-N-fixers, and no silica demanding together, and summed up their occurrences. According to this multidimensional definition, we defined 36 possible unique combinations from the 11 trait categories. Only 13 of the 36 combinations exist in our data set, and one of these 13 categories was excluded due to being rare (only present in four samples). We assessed the predictability of the 12 remaining multidimensional functional groups to compare it with the predictability of the functional groups when assessing them separately. The 12 combinations of functional groups are shown on Supplementary Fig. S3. For zooplankton, we separated species into broad taxonomic groups, which also partially reflect differences in trophic guilds. The groups used here included daphnids (omnivorous, mostly herbivorous), bosminids (bacterivorous/ herbivorous), calanoid copepods (omnivorous with a strong herbivorous component, selective in prey size), cyclopoid copepods (omnivorous with a strong carnivorous component), and rotifers (mostly bacterivorous, herbivorous; partly carnivorous). Despite being omnivorous with a strong herbivorous component, we divided daphnids and calanoid copepods into two groups. The calanoid copepods have wider prey size spectrums and are selective in their prey.

Machine learning approach

Random forests (RFs) were recently found to be a robust and flexible machine learning tool for examining ecological systems (Thomas et al. 2018; Liu et al. 2019). The RFs algorithm generates an ensemble of de-correlated decision trees (Breiman 2001). Each tree of the RF ensemble predicts the observations based on its own particular subset of training data, which consists of values of a metric type (e.g., cyanobacteria taxonomic richness) and randomly selected one-third of the corresponding

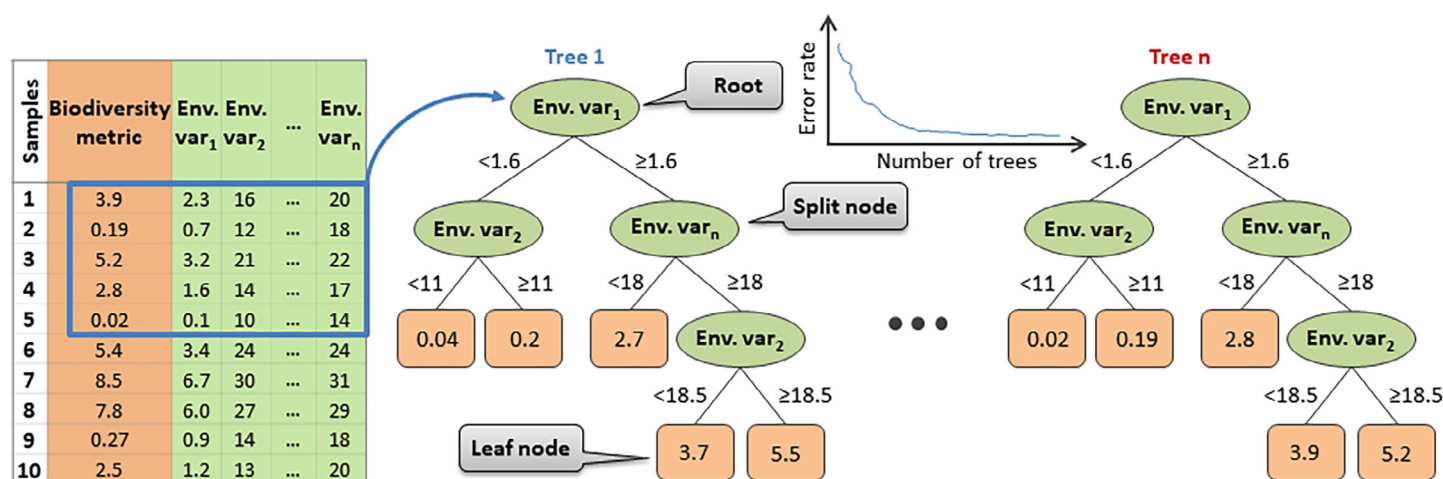


Fig. 1. The random forest modeling approach. A random forest tree accepts a random subset of data (the blue square), and each node receives the values of an environmental driver. The leaf nodes predict values of a metric based on the values of environmental drivers. The prediction error rate decreases substantially once the random forest builds further trees (bootstrapping). The predictions become more accurate with additional trees while the error rate decreases and predictions are averaged across all aggregated trees.

environmental drivers, which vary across RF trees (Fig. 1). Each node in a tree represents an environmental driver from the input subset of data. Each branch of the tree divides the gradient of environmental driver into separate categories, such as high and low temperatures. Each leaf at the end of a branch reflects a decision for the value of the metric type and represents the corresponding predicted value. By constructing an ensemble of these decision trees, the RFs develop nonlinear relationships in aggregate and quantify the predictability of any metric type (Breiman 2001). Building large collections of de-correlated decision trees is akin to bootstrapping, and RFs predict response value of a sample by averaging predictions across all regression trees, that is, an aggregation approach. The bootstrapping and aggregation approaches are designed to build models with

complex fitting shapes and low variance that avoids overfitting and increases the accuracy of predictions by averaging noisy and biased models (Breiman 2001). We took advantage of RFs' features to quantify the predictability of plankton species grouped according to their higher taxonomic unit and their functional traits, thereby assessing the performance of different metric types.

Model validation

Typical ML cross-validation approaches assume that randomly selected training and testing datasets are independent. The RF algorithm is fully non-parametric and separates the dataset into disjoint subsets (Breiman 2001). As RFs make no assumption about model residuals, they can make robust

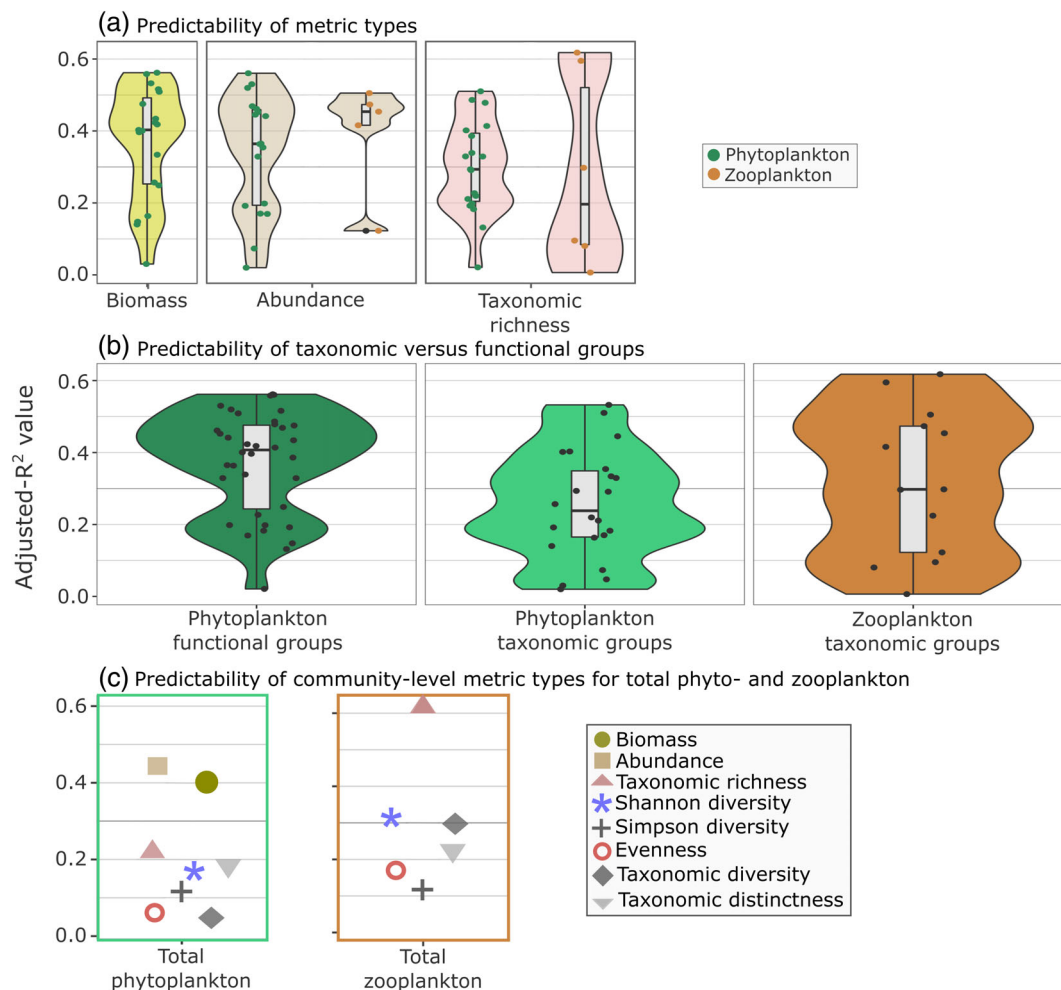


Fig. 2. Predictability of (a) different metric types (biomass [mg L^{-1}], abundance [$\text{cell number L}^{-1}$], and taxonomic richness) for phytoplankton (green dots) and zooplankton (brown dots) of Lake Müggelsee, and (b) phyto- and zooplankton when grouping them according to their higher taxonomic unit vs. their functional traits across all metric types, characterized by adjusted- R^2 . The greater the adjusted- R^2 value on the y-axis, the more predictable is the metric type or taxonomic/functional groups. The wider sections of the violin plots represent a higher density of data points on the given value, and the skinner sections represent a lower density. The predictability of each community-level metric type was higher for total zooplankton than for phytoplankton in Lake Müggelsee (c). The adjusted- R^2 values are calculated according to the out-of-bag prediction. See Supplementary Figs. S4 and S5 and Table S2 for further information on model validations, such as cross-validated correlation coefficients (Kendall and Pearson) among predictions and observations for each metric. See Supplementary Fig. S6 for detailed information on the predictability of different metric types for each functional or taxonomic group.

predictions even when data are temporally autocorrelated. But to ensure that temporal autocorrelation did not inflate the predictability of metric types, we used two cross-validation approaches to assess models' performance—standard out-of-bag (OOB) cross-validation where the entire time series is split into randomly selected 70% training and 30% test sets (Breiman 1999), and a non-random splitting (NRS) cross-validation approach where the first 70% of the time series (from years 2000 to 2012) is used to predict the last 30% (from years 2013 to 2017) as akin to forecasting. When time series are auto-correlated, training and testing datasets are more independent using the NRS cross validation, but OOB cross-

validation is the more common, standard approach and tends to have higher predictive abilities.

The predictive abilities of RF models were determined by comparing the OOB or NRS predictions with observations for the testing datasets. The predictive ability was quantified using the adjusted R^2 values from an ordinary least squares regression between predictions and observations. The adjusted- R^2 is a very reliable and promising metric to evaluate models' predictability. Due to the added information via serial dependency being known as temporal autocorrelation in time-series data, removing autocorrelation in the NRS approach is expected to decrease models' predictive ability. This results in much lower adjusted- R^2

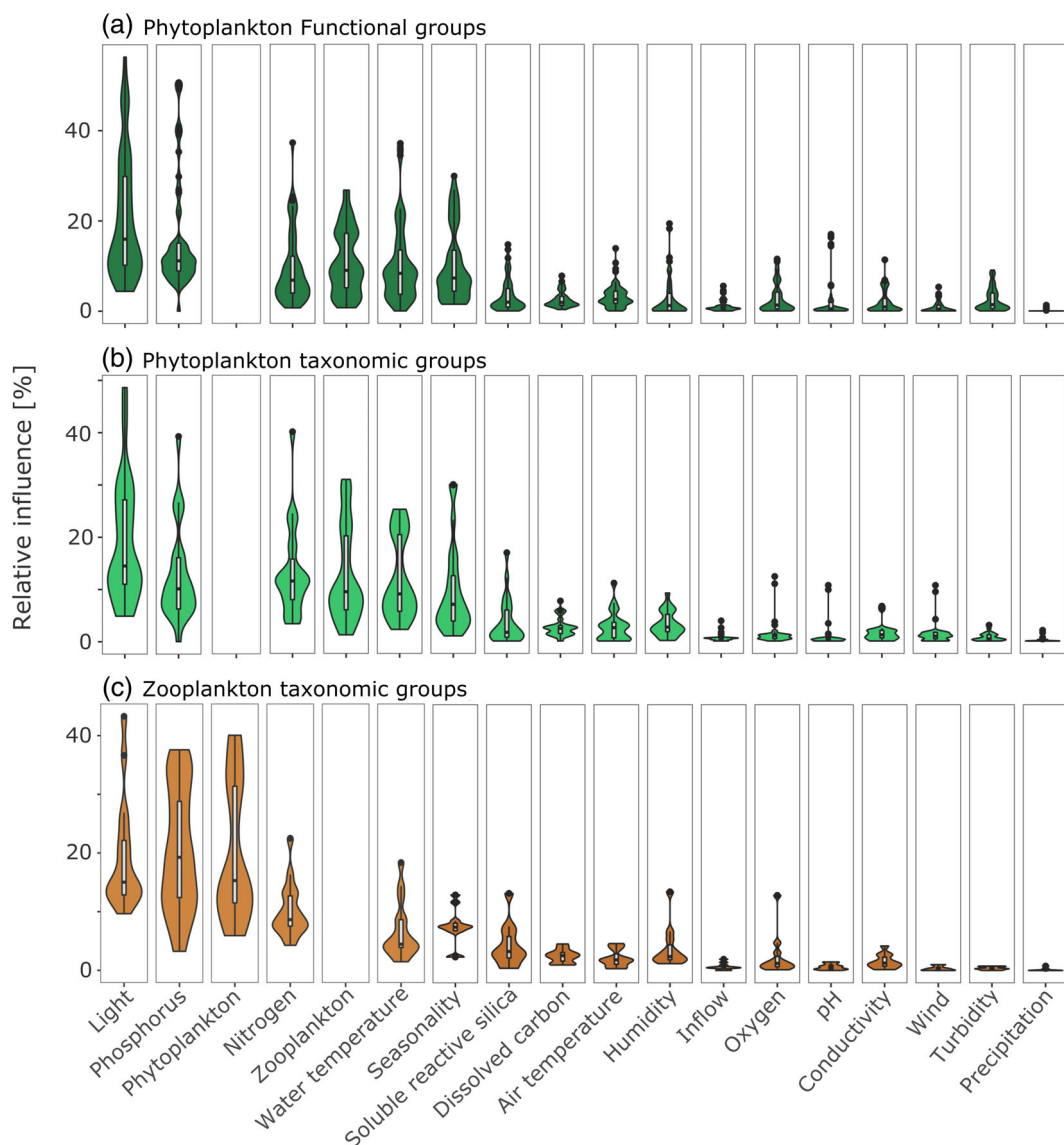


Fig. 3. Relative influence of the most important environmental drivers for all metric types for (a) phytoplankton functional groups, (b) phytoplankton community and taxonomic groups, and (c) zooplankton community and taxonomic groups from Lake Müggelsee. See Supplementary Table S3 for more details on the relative influence of all environmental variables according to the five metric types. See Supplementary Table S5 for multiple comparisons among pairs of environmental variables.

values when using NRS prediction as compared to the OOB approach. However, 28% of models showed higher adjusted- R^2 values following the NRS approach, and a further 30% showed values with less than 10% difference (Supplementary Fig. S4). According to these results and the high Pearson correlation (0.78) between the two cross-validation approaches, the OOB prediction was found to be a reliable approach to assess models' predictive ability, without the necessity of removing autocorrelation signals by, for example, differencing. Furthermore, as the whole historical period is usually used to train a model for forecasting, OOB prediction is considered in further analyses of this study.

Relative influence of environmental drivers

The relative influence of each environmental driver was assessed for each metric type and the subsequent taxonomic or functional group by using the change in models' error rate across RF trees, when the predictor variable was excluded.

All statistical analyses were carried out in R 3.5.1 (R Development Core Team 2016). To compare more than two groups, we used one-way ANOVA and Tukey's Honestly Significant Difference (HSD) post-hoc test.

Results

Model performance for different metric types and taxonomic or functional groups

The predictability of the metrics used here varied widely across metric types (e.g., abundance vs. richness), planktonic groups (phytoplankton vs. zooplankton), taxonomic groups (e.g., daphnids vs. bosminids), and functional groups (e.g., colony building species vs. aggregation forming species) (Fig. 2).

Overall our results showed that among the eight metric types, biomass, abundance, and richness were more predictable than Shannon diversity, Simpson diversity, evenness, taxonomic diversity, and taxonomic distinctness for both phytoplankton and zooplankton (H_1 , Fig. 2a). The total phytoplankton biomass and total abundance were more predictable than its taxonomic diversity or distinctness, with R^2 values decreasing from 0.40 and 0.45 for total biomass and total abundance to 0.18 for Shannon diversity and taxonomic distinctness, and 0.13, 0.07, and 0.05 for Shannon diversity, Simpson diversity, evenness, and taxonomic diversity (Fig. 2c). For zooplankton, the R^2 values decreased from 0.62 for taxonomic richness to 0.31, 0.30, 0.22, 0.16, and 0.15 for Shannon diversity, taxonomic diversity, taxonomic distinctness, Simpson diversity, and evenness, respectively (Fig. 2c).

Regardless of the variability in the metric types, the biomass, abundance, and taxonomic richness of phytoplankton functional groups ($n = 36$ models) were significantly more predictable than its taxonomic groups ($n = 22$ models) (ANOVA, Tukey's HSD test, $p = 0.04$, Fig. 2b and Supplementary Fig. S4). The unique multidimensional combinations of phytoplankton

functional groups were also better predictable than the taxonomic groups (Supplementary Fig. S3).

In addition to these key results, we found that the dominant phytoplankton and zooplankton taxonomic groups of Lake Müggelsee were more predictable than other metrics (Figs. 2b and Supplementary Fig. S5), such as the biomass, abundance, and richness of cyanobacteria ($R^2 = 0.53$, 0.35, and 0.51, respectively), the abundance and richness of rotifers ($R^2 = 0.59$ and 0.42, respectively), or the abundance of daphnids, cyclopid, and calanoid copepods ($R^2 = 0.51$, 0.47, and 0.45, respectively).

Environmental drivers

The models were able to identify the major environmental drivers—and their relative influences on the different metrics (Fig. 3). Well-known major drivers such as light and nutrients followed by water temperature and seasonality were the most important predictors of both phytoplankton and zooplankton metrics (ANOVA, Tukey HSD, $p < 0.05$) (H_2 , Fig. 3b, c). Availability of food resources (i.e., phytoplankton total biomass) was a strong predictor of the richness of the total zooplankton community and taxonomic groups such as daphnids and rotifers (ANOVA, Tukey HSD, $p < 0.05$) (H_3 , Fig. 3a). However, water temperature was less important than light or nutrients, which indirectly affect the food sources (H_3 , Fig. 3a).

Discussion

We applied RFs as an advanced ML tool to predict eight metric types as a function of climatic, physical, chemical, and biological predictors. We determined which metric types could be most reliably forecasted in a central European shallow and eutrophic lake. The phytoplankton total biomass and total abundance, as well as zooplankton taxonomic richness, were substantially more predictable than their taxonomic diversity and distinctness. We identified light, nutrients, and water temperature as the most important drivers of phytoplankton taxonomic and functional groups. Zooplankton abundance and richness were mostly driven by resource availability.

Machine learning in ecological studies

The usefulness of ML for examining specific ecological systems depends on whether the variation in the response can be sufficiently predicted by the drivers. The promise of our ML approach was demonstrated by the match between the modeled driver-response relationships and what would be expected based on current ecological understanding (Supplementary Fig. S7). For example, congruent with contemporary ecological understanding (Litchman and Klausmeier 2008), the partial effects of light and nutrients were the most important environmental variables for phytoplankton. Additionally, the abundance of predators strongly influenced the phytoplankton metrics, and the abundance of food resources strongly influenced the zooplankton metrics.

All these results strongly show that our models capture the major environmental drivers and their interactions.

Our models performed well in cross-validation despite low sample sizes for some species (please see an example in Supplementary Fig. S8). We found that the out-of-bag predictions for taxonomic and functional groups were well correlated with the testing observation sets (for details see Supplementary Fig. S7). In addition to this key evidence, despite the low variability of cryptophytes' richness over the entire period (2.1 ± 0.5 , mean \pm SD), its predictability ($R^2 = 0.33$) was above the average among the taxonomic groups (Supplementary Fig. S6 and Table S3). A convenient method to boost the predictive power of a model for forecasting is to normalizing their skewed gradient through, for example, logarithmic transformation (Johnston 1978). Due to the aim of our study on (1) assessing the relative influence of environmental drivers on the plankton metrics and metric types, and (2) comparing their predictive ability rather than predicting the future scope of lake communities, our response variables were not log-transformed prior to the modeling. However, the predictability of phyto- or zooplankton dominant taxonomic groups from Lake Müggelsee with R^2 values ranging between 0.4 and 0.6 is within the range of results from other studies (e.g., Thomas et al. 2018; Liu et al. 2019). This evidence gives us confidence that the RFs are a promising and reliable ML tool for assessing and predicting lakes' planktonic responses to global changes.

Employing ML tools on data with a weekly biological sampling resolution may be sufficient for making robust and reliable ecological predictions. However, Lake Müggelsee's data are exceptional for its time span and resolution. Similar long-term, high-resolution sampling for other freshwater lakes might be unrealistic given the costs of such monitoring especially in the context of present funding constraints. We might therefore use long-term high-frequency sample data from a handful of lakes together with low-frequency or single-date sample data from hundreds of freshwater lakes around the globe to increase model skill. In this case, we may also need to add lake attributes such as lake depth, lake area, and latitude as further predictor variables to allow the model distinguish lake characteristics. In this case, the lack of statistical power associated with coarse time series (e.g., monthly sampling) may be partially offset by including data with coarser temporal resolutions from many lakes in a single model. Furthermore, such high-skilled models would allow extrapolations of plankton responses to thousands of lakes across regional or even continental and global scales.

Model performance for different metric types

Low variability over time in taxon-specific metrics may result when the taxonomic groups in question are species-poor. This low variability can minimize the capacity of the models to detect the influence of environmental drivers. Nevertheless, our ML models explained the variation in the response metrics according to their environmental correlates,

even when the metric was based on data from species-poor communities such as cryptophytes (Supplementary Figs. S6 and S7).

A variety of metric types can be used to evaluate the ecological integrity of freshwater ecosystems (Gallardo et al. 2011). These metric types enable the assessment of signals, trends, and patterns of biological responses in the historical period, or to quantify potential future changes in freshwater ecosystems' functioning. Even slight differences in the performances of ML for different metrics shown here (Fig. 1) may have large consequences for the uncertainties while forecasting. Therefore, selecting the most predictable metric types could lead to substantially better forecasts.

Our results suggest that we should continue measuring and using the biomass, abundance, and taxonomic richness, because the models built for to these metric types are robust, provide better predictions, and allow for long-term studies. These results are comparable to other studies, in which the biomass of phytoplankton and main taxonomic groups such as cyanobacteria was reported to be highly predictable (e.g., Persaud et al. 2015; Crisci et al. 2017; Zhu et al. 2018). Hence, these metric types may be used as indicators for assessing consequences of long-term global changes for freshwater lake communities.

Some community-level metric types such as taxonomic diversity and distinctness were less predictable than the taxonomic group- and functional group-level metric types such as biomass, abundance, and taxonomic richness (Fig. 1). Community-level metrics are harder to predict because they reflect a more complex set of processes. Any given algal mass is primarily constrained by abiotic drivers (nutrients, light, temperature), while taxonomic diversity or distinctness additionally involves competition (Mouillot et al. 2006). Their low predictability can therefore be described either by their non-significant relationship to abiotic factors or trophic variables (Mouillot et al. 2005; Leonard et al. 2006; Heino et al. 2007), or by their sensitivity to long periods of environmental variability rather than the short-term changes investigated in this study. Furthermore, the low explanatory power of short-term variation in environmental drivers suggests the strong influence of stochasticity, which was reported earlier for the trait distributions of total phytoplankton communities from Lake Müggelsee (Seltmann et al. 2019). Therefore, environmental variability alone may not fully describe the variability in Lake Müggelsee's plankton taxonomic diversity or distinctness, and the influence of stochasticity might need to be considered in assessing the predictability of these metric types. Another possibility to make reliable forecasts of such low-predictability metric types is to calculate it indirectly. This could be done by first fitting many species-specific models for a high-predictability metric type like abundance and then calculating the low-predictability metric type indirectly using the abundance model outputs.

Taxonomic diversity and distinctness are minimally correlated with all other metric types (Supplementary Fig. S2), thus providing distinct information on ecosystem functioning in freshwater (Heino et al. 2007; Gascón et al. 2009) or marine realms (Clarke and Warwick 1998; Leonard et al. 2006). These two metrics are known to complement other metric types such as taxonomic richness (Gascón et al. 2009) and functional diversity (García-Girón et al. 2019). More specifically, taxonomic distinctness shows whether diversified species are available in a sample or community; therefore, a loss of taxonomic richness does not necessarily mean loss of function as a redundant trait might have been lost from that sample or community. Ecosystem functioning is also related to overall ecosystem productivity, which depends, beside others, on species abundances. Specifically, community-level consequences of a certain function may vary strongly if that function is performed by a rare species as compared to a dominant species (Hillebrand et al. 2008). Therefore, despite the lower predictability of evenness, it is an important aggregate performance indicator for freshwater communities compared to other metric types such as taxonomic distinctness or richness (i.e., number of traits) (Norberg 2004; Hillebrand et al. 2008).

Model performances for different taxonomic or functional groups

The predictability of metrics varied substantially across metric types. For example, biomass ($R^2 = 0.53$) and richness ($R^2 = 0.51$) of cyanobacteria were substantially more predictable than its abundance ($R^2 = 0.35$) (Fig. 2c,d,e). These differences in predictability reflect the differences across metric types in the information captured by them (Mouillot et al. 2006; Heino et al. 2007; Gascón et al. 2009; Gallardo et al. 2011). Although phytoplankton abundance is an important indicator of overall ecosystem productivity and lakes nutrient concentrations (Hillebrand et al. 2008; Baho et al. 2020), the higher predictability of biomass compared to abundance reveals the importance of appropriate size data, which is the necessary element in calculating species biomass from their abundance. The size of species and individuals is a key parameter in ecological food webs (Peters 1983; Ray et al. 2001) and is linked to their growth- and reproduction rates (Peters 1983; Brown et al. 2004). Global warming alters phytoplankton body size via increasing their metabolic rates (Gillooly et al. 2001). Body size can be considered as a vital ecological trait that strongly responds to environmental changes (Hooper et al. 2005; Ye et al. 2013). Large phytoplankton species usually have slow growth and high energetic requirements (Séguin et al. 2014), which makes them sensitive to environmental variability. Furthermore, global warming increases frequency and period of thermal stratification in lake ecosystems (Kraemer et al. 2015). Thermal stratification leads to decline in nutrients in the epilimnion (Winder et al. 2009). Increasing temperatures combined with low nutrient availability favors small-sized phytoplankton species due to their more

efficient nutrient uptake (Lewis 1976; Finkel et al. 2010). Individual sizes are shown to be sensitive to environmental variability; thus providing useful information that result in the better predictability of phytoplankton biomass over their abundances. However, biomass provides complementary information with other metric types such as abundance about the ecosystem state and potential global change effects in freshwater lake ecosystems.

For the phytoplankton of Lake Müggelsee, the functional groups were more predictable compared to the taxonomic groups (Fig. 2). The predictability of the unique combinations of the functional groups according to the multidimensional traits definition strongly endorsed their better predictabilities as compared to taxonomic groups. Global change effects on plankton taxa can also be tracked better by assessing their functional traits than their taxonomic diversity. For example, winter severity was found to have relatively small effect on taxonomic richness and evenness, while strong relationships were reported between phytoplankton taxa and winter severity when their functional traits were considered (Özkundakci et al. 2016). The better predictability and strong responses of phytoplankton functional groups to global changes, as compared to taxonomic groups, can be described by the key functional traits such as motility. Motility can potentially enable species to survive under thick ice coverage during severe winter conditions (Adrian et al. 1999; Dokulil and Herzig 2009; Twiss et al. 2014). More specifically, the passively or highly motile taxa are able to dive deep in the water column once the lake is covered by thick winter ice (Özkundakci et al. 2016).

The zooplankton taxa abundance was more predictable than other metric types when separated into their taxonomic/trophic guilds. This can be explained by the ability of functional traits to provide potential insight into the mechanisms underlying the changes in community structures that enables stronger mechanistic links to the environmental drivers (Hamilton et al. 2019). These findings confirm that the trait-based assessment is a promising tool to understand global change effects on freshwater biotic communities that enables the determination of climate or environmental vulnerabilities (Litchman and Klausmeier 2008; Foden et al. 2013; Hamilton et al. 2019). Nevertheless, the use of a combination of metric types for both taxonomic and functional groups provides complementary information that achieves a more comprehensive understanding of the structure and function of the lake ecosystems and potential responses to local drivers and global changes.

Environmental drivers

Our overall findings suggest that light, nutrients, water temperature, predator abundance, and resource availability are among the most significant drivers of phyto- and zooplankton in lakes. Water temperature was less important than light or nutrients, which indirectly affect food resources through, for

example, temperature increase caused by increasing light and increasing phytoplankton growth rates. We are limited in our ability to interpret the relationships between specific environmental drivers and phyto- or zooplankton responses. This limitation is mainly due to the complex web of forces linking many of these drivers to each other. For example, wind causes turbulence and enforces water mixing that leads to nutrient enrichment from deeper layers to the top layer of the water column. Precipitation also increases nutrient availability in lakes via increasing catchment runoff. The effect of temperature may capture indirect effects of temperature-induced increases in fish predation, although fish predation on zooplankton has not been considered explicitly by our models. All these interrelated processes lead to nutrient enrichment of lakes and reduction in herbivory that increases plankton growth rates in some species and enhances the risk of algal blooms (Huisman and Hulot 2005). Therefore, an environmental driver with small relative influence might impose its strong influence via its indirect effects on other drivers.

Our findings contribute to our knowledge of lake functionality and suggest frequent and continuous monitoring of lake plankton abundance and biomass by research organizations and monitoring agencies. Employing advanced ML tools on long-term monitoring data may help to elucidate the links between global change and freshwater ecological responses. It may further increase the quality of forecasting in an age of environmental change and provide complementary data that are relevant for developing strategies to sustainably manage aquatic resources. Our approach and findings contribute to our knowledge of lakes' functionality and are of great interest for use in predicting and extrapolating ecological patterns and processes to large spatial scales, especially to freshwater lakes which lack long-term biological data. Furthermore, the methods used in this study can be applied across ecological realms (freshwater, terrestrial, and marine), taxa (e.g., fish or macroinvertebrates), metrics, and environmental drivers (e.g., climate or land use) to quantify global change effects on ecological systems at different spatial scales.

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Conflict of interest

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