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Research article

Synergistic effects between global warming and water quality change on modelled macrophyte species richness

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Submerged freshwater macrophytes are crucial for the functioning of lakes. Their growth and survival follow environmental conditions like light, temperature, and nutrient availability. Hence, the impending increase in water temperature as well as changes of nutrients and turbidity will lead to changes in macrophyte geographic and depth distribution: Herein, we assess these potential changes. We apply an eco-physiological macrophyte growth model to simulate biomass growth and survival of virtual species defined by random trait combinations within expert-derived trait ranges for oligotraphentic, mesotraphentic, and eutraphentic species groups in deep lakes in Bavaria, Germany, which cover clear, moderate, and turbid lake conditions. The emergent potential species richness is compared with empirically observed species richness to evaluate general predictions for current conditions. Thereafter, we apply the model to scenarios of temperature increase and of turbidity and nutrient change to assess potential changes in species richness and the influence of species' traits on being an environmental change 'winner' or 'loser'. We find a cross-lake, hump-shaped pattern of potential species richness along depth. This largely reflects observed patterns, although mismatches were also detected and might be explained by missing processes and environmental heterogeneity within the lake. Rising temperature leads to increased richness of potential species in all lake types, species groups, and depths. Turbidity and nutrient change effects depend on depth and lake type. 'Loser species' under increased turbidity and nutrient level are light consumptive and sensible to disturbances, while 'winner species' have a high biomass production. These findings show that the hump-shaped depth distributions of submerged macrophyte diversity can emerge solely considering eco-physiology. The differential responses to environmental changes imply that management measures must account for lake type because those responses can have opposite trends depending on lake depth and type.

Keywords: aquatic plants, climate change, land-use change, process-based model, species distribution

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Introduction

Submerged macrophytes provide a broad range of ecosystem services in lakes (Thomaz 2021). They create habitat for many other species and change the lake environment by binding nutrients or stabilising the sediment. The eco-physiological processes controlling macrophyte growth and survival are strongly affected by light availability, nutrient availability, and temperature. The accelerating global biodiversity loss of macrophytes, especially of submerged ones, is well documented (Sand-Jensen et al. 2000, Körner 2002, Phillips et al. 2016, Zhang et al. 2017) despite evidence of increasing species richness in some lakes (Murphy et al. 2018). The main influencing factors for these diversity changes seem to be global climate and regional land-use changes (Zhang et al. 2017, Hofstra et al. 2020), which cause changes of light availability (due to changes in water turbidity), nutrient availability, or water temperature. The ways in which climate change influences water temperature, nutrients, and turbidity in lakes are complex and include direct and indirect effects (Lind et al. 2022). For example, lake water temperatures rise with the general increase in air temperature, which can further impact turbidity and nutrients, as higher temperatures promote algae growth and thus reduce light availability. Therefore, nutrients and turbidity normally co-vary, including with temperature. Moreover, nutrients and turbidity can also be influenced by land-use practices (e.g. due to fertilisers) and wastewater management. Therefore, different scenarios of environmental change may take place and influence macrophyte diversity in yet unpredictable ways.

All these stressors, like changes in water temperature or light and nutrient availability, have an effect on the eco-physiological processes of submerged macrophytes (Cao and Ruan 2015, Reitsema et al. 2018). Such an effect can scale up to the geographical distribution of individual species and of species richness. A practical classification of macrophytes into oligo-, meso-, and eutraphentic species groups can be based on their nutrient preferences (Melzer 1999). The presence of distinct species groups can thus indicate the water quality and ecological state of the lake (Schaumburg et al. 2004). Still, studies on macrophyte richness distribution remain observational and correlative, with synergistic effects of multiple stressors being mechanistically little understood (Lind et al. 2022). Therefore, it is paramount to assess these synergies on macrophytes.

Process-based models based on first principles, such as eco-physiological processes, are better suited to assess biodiversity response to changing conditions than correlative models (Dormann et al. 2012, Cabral et al. 2017, Higgins et al. 2020, Schouten et al. 2020). Furthermore, they help to explain how a system works and they enable to explore changes under novel conditions like increased temperature and turbidity in high elevation deep lakes. Eco-physiological models can be applied to identify important plant physiological parameters which have an influence on plant survival. Process-based models simulating the growth of submerged macrophytes have a long tradition, being proposed as early as the late 1980s (Collins and Wlosinski 1989, Wortelboer 1990, Scheffer et al. 1993, Hootsmans 1994, Best et al. 2001, Herb and Stefan 2003). Those models were developed to answer various study questions, like the effect of macrophytes on algal blooms (Asaeda and Van Bon 1997), the effect of varying light regimes on macrophyte growths (Herb and Stefan 2003), or macrophyte impact on water quality (Sachse et al. 2014). Furthermore, most models were calibrated under very specific environmental conditions for only one or a few species (van Nes et al. 2003, Gao et al. 2017). No modelling study explored macroecological distribution patterns of macrophytes or their response to environmental change due to the fact that these models are computationally and data demanding. Hence, applying eco-physiological models to assess the distribution of multiple species and thus of richness in both current and future conditions requires more efficient models and cross-species parameter calibration.

Macrophytes are still underrepresented in trait-based research and in environmental change assessments (Dalla Vecchia et al. 2020, Iversen et al. 2022). Consequently, the eco-physiological parameters have yet to be calibrated for most macrophytes. In the case of limited trait-based information, employing a virtual species pool represents the best alternative to assess potential impacts of environmental change (Dormann et al. 2012, Cabral et al. 2017). Experiments with randomly drawn trait combinations within defined functional boundaries or types can determine virtual species that are able to survive and reproduce (as done for terrestrial plants – Webb et al. 2010, Zakharova et al. 2019). In such applications, the process-based model acts as a performance filter, with the surviving virtual species representing potentially viable species. Hence, this approach could be used for the data-poor macrophytes.

In this study, we tackle two main objectives. First, we address the potential species richness of oligotraphentic, mesotraphentic, and eutraphentic submerged macrophytes under current environmental conditions. We ask: how many potential species can grow in clear, intermediate, and turbid lakes (Q1.1)? Do the potential species richness patterns along depth follow the observed distribution in all lake types (Q1.2)? Second, we assess scenarios of water temperature increase and water quality change (increase in both nutrients and turbidity). We ask: in which depth and lake types do we lose or gain oligo-, meso-, and eutraphentic species (Q2.1)? Is this change dependent on eco-physiological traits (Q2.2)?

To answer questions Q1.1 and Q1.2, we run random species parameter combinations within the three defined parameter spaces of trophic-dependent species groups (oligotraphentic, mesotraphentic, and eutraphentic) and compare emergent versus observed patterns. We expect to find the highest species richness in moderately nutrient rich lakes (Q1.1) (Lewerentz and Cabral 2021). We hypothesise to find hump-shaped patterns (Q1.2) of species richness along depth gradients (Lewerentz et al. 2021). Moreover, we expect a higher potential than observed species richness because limiting processes like herbivory have not been modelled (Q1.1 and Q1.2). We further hypothesise that the studied lakes will lose species under increased turbidity and nutrient conditions but gain

species under increased water temperature (Q2.1) (Lewerentz and Cabral 2021). To answer question Q2.2, we determine those plant traits that influence if a species will win or lose distribution within environmental change scenarios. We expect that under increased nutrient and turbidity, high biomass production is advantageous, as species can more quickly reach better conditions while utilizing available resources.

Material and methods

The model

We use an eco-physiological process-based growth model for submerged macrophytes named 'macrophytes growth model' (MGM). The MGM is a re-implemented and simplified version of the model 'Charisma 2.0' (van Nes et al. 2003) (Fig. 1a) written in the programming language *julia* (Bezanson et al. 2017) for faster performance. The model uses the super-individual approach (Scheffer et al. 1995). Each super-individual represents a number of individuals which all have the same growth rate, individual weight, and height. We simulate each species separately as one super-individual per depth. The model calculates on a daily basis the biomass, the height, and the number of sub-individuals for each of these super-individuals (Fig. 1b). The MGM considers influences of geographic factors (daylength and water depth) and environmental factors (irradiance at surface, nutrients, water temperature, and turbidity) on the growth of submerged macrophytes. The growth of macrophytes is mainly driven by photosynthesis and respiration. Photosynthesis depends

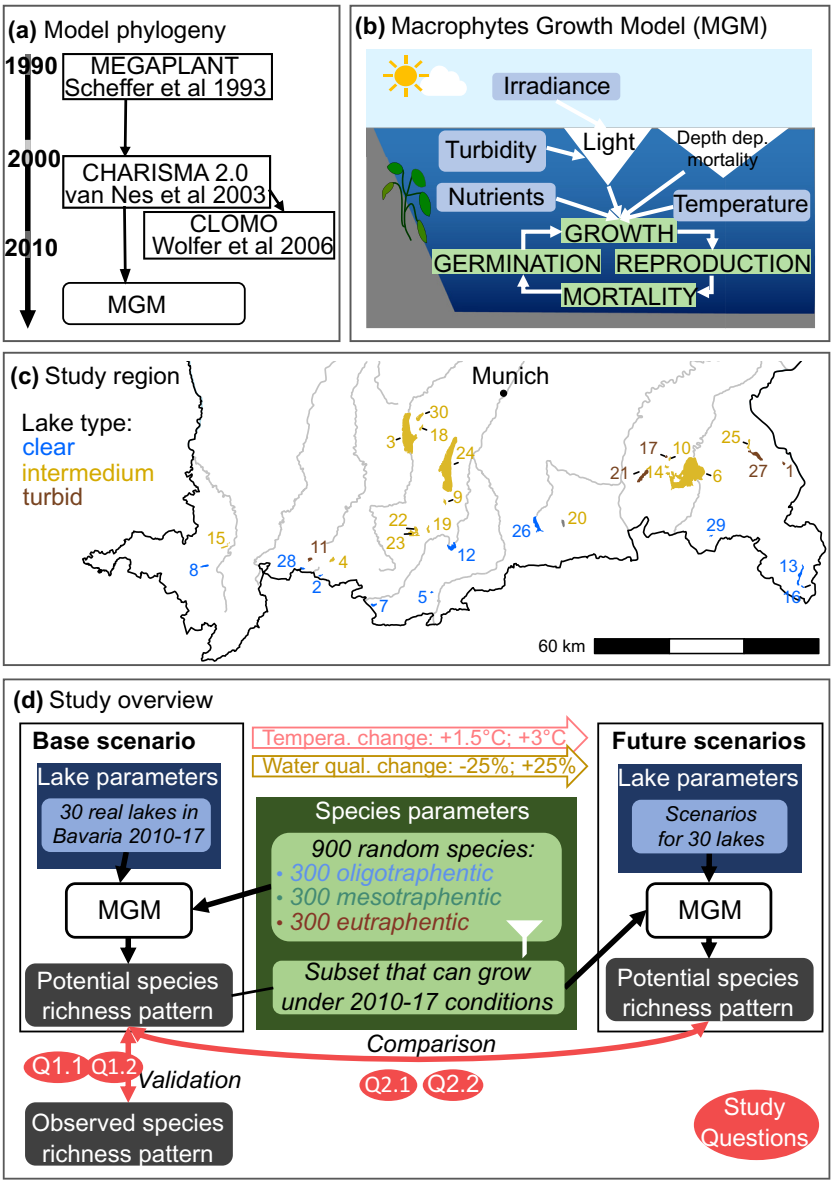

Figure 1. The model phylogeny (a), simplified processes of the macrophytes growth model (MGM) (b), an overview about the studied lakes including an ID and the lake types in different colors (c), and an overview about the study design (d).

on available light (that declines with depth), nutrients, and temperature, while respiration depends only on temperature. Furthermore, the processes of self-thinning, depth dependent mortality, plant senescence, and self-shading influence growth.

The MGM is mechanistically simplified compared to Charisma 2.0 to reduce the number of parameters (47 species-specific parameters in Charisma 2.0) by excluding processes of 1) carbonate limitation because the lakes we simulated were not carbonate limited and no evidence was found for carbon limitation; 2) spatial processes like seed dispersal, which we assume not to limit occurrence of macrophytes within the regional context (Alahuhta et al. 2020); 3) water level fluctuation because corresponding data are not available for all lakes and because the macrophyte mappings correspond always to the actual water level; 4) interspecific competition and 5) herbivory because both processes are not relevant for modelling the eco-physiological constraints on the potential distribution of species; and 6) vegetative reproduction because turions and offshoots are considered part of the mother plant during development and can be treated as reproductive units or seeds after separation. Therefore, the MGM focuses on eco-physiological rather than demographic or dispersal constraints, retaining 28 species-specific, eco-physiological parameters that determine the seasonal cycle, mortality, and growth rate dependent on light availability, nutrients, and temperature (Table 1). The detailed Overview, Design concepts, Details (ODD) protocol (Grimm et al. 2010, 2006) for MGM (Supporting information) and the model code (Supporting information) are open access and available on GitHub (https://github.com/AnneLew/MGM).

Datasets

The available dataset from the German federal state of Bavaria covers large lakes (>0.5 km² surface area). From this dataset we selected all natural and deep lakes: lakes of natural origin (without artificial influence on water level fluctuation and not of artificial origin) and with a minimum depth of 9 m. Their locations are shown in Fig. 1c. Their surface altitudes at mean water level range from 425.9 to 885.0 m a.s.l. (Supporting information). They are all carbonate-rich and stratified (formation of different thermal layers during summer), but provide a broad range of environmental conditions, e.g. from turbid to clear, or from cold to warm waters. Macrophyte occurrence in four water depth strata (0–1, 1–2, 2–4 m, > 4 m) and monthly physical-chemical measurements (e.g. water temperature, P_{tot}, and Secchi depth) are recorded in all these large lakes for the EU Water Framework Directive (WFD) monitoring and are publicly provided by the Bavarian State Office for the Environment under www.gkd.bayern.de. Secchi depth, a measure for transparency of water, was converted to kD, the extinction coefficient of light in water (Holmes 1970, Kirk 1935). Data for irradiance are obtained from the nearest German Weather Service (DWD) weather station as daily mean (StMWi 2019).

For each lake we selected the most recent macrophyte mapping data (2004–2017). We excluded all species that are sterile hybrids, emerged, with floating leaves, mosses, or non-rooted. In addition, 'indicator species' were selected, i.e. species that are oligotraphentic, mesotraphentic, or eutraphentic according to the classification by Melzer and Schneider (2014).

Experimental design

Data preparation and analyses were done in R ver. 4.0.5 (www.r-project.org). We defined parameter spaces for oligotraphentic, mesotraphentic, and eutraphentic functional types (Table 1). We selected the parameter spaces based on parameters of reference species out of the groups defined by Melzer and Schneider (2014) for which some of the parameter values are known. Reference species were *Chara aspera* (Characeae) for oligotraphentic species, *Myriophyllum spicatum* (Haloragaceae) and *Potamogeton perfoliatus* (Potamogetonaceae) for mesotraphentic species as well as *Potamogeton pectinatus* (Potamogetonaceae), *Elodea nuttallii* (Hydrocharitaceae), and *Najas intermedia* (Hydrocharitaceae) for eutraphentic species (Supporting information). As the eco-physiological parameters of most submerged macrophyte species are not known, we randomly select 300 parameter combinations for each of the three parameter spaces defined for oligotraphentic, mesotraphentic, and eutraphentic functional types respectively. Each of the resulting 900 parameter combinations represent hypothetical, virtual species.

We select lake parameter values as base scenario representing today's environmental conditions according to measured data within the 30 selected lakes from the dataset (description above, Supporting information). The lake parameters differ not just in their latitudes, but also in their maximal summer temperature, nutrient content, and turbidity. Based on these four parameters we classified the lakes into clear, medium, and turbid lakes performing a hierarchical clustering using Euclidean distance and the Ward linkage method on normalized environmental data of the lakes. All other lake parameters are identical across lakes (Supporting information).

As base scenario, we run the MGM for all 900 virtual species within the 30 lakes at four depths (0.5, 1.5, 3, 5 m) for 10 years to reach equilibrium (Fig. 1d). We determine as surviving virtual species those that can establish a mean biomass of more than 1 g of fresh weight (in sum over depth) during summer (June–August). From now on, those virtual species are termed as 'potential species' (i.e. they are physiologically plausible). In contrast, empirically observed species from the WFD mapping, i.e. those that passed through all ecological processes (including demography, interaction and dispersal) in nature, are termed 'observed species'.

As future scenarios, to study the effects of environmental change related to global warming and water quality change, we performed simulation experiments with the potential species under changed lake parameters in a full-factorial design. We set two theoretical water temperature increase scenarios of + 1.5 and + 3.0°C (reference period 2010–2020) which are

Table 1. Parameter spaces for oligotraphentic, mesotraphentic, and eutraphentic functional types. Parameters are marked as bold if they are different for the functional types. The spaces were selected based on reference species from the groups (Melzer and Schneider 2014). Reference species were *Chara aspera* for oligotraphentic species, *Myriophyllum spicatum* and *Potamogeton perfoliatus* for mesotraphentic species, and *Potamogeton pectinatus, Elodea nuttallii* and *Najas intermedia* for eutraphentic species.

Symbol	Unit	Description	Oligotraphentic min – max	Mesotraphentic min – max	Eutraphentic min – max	Source
seedsStartAge	dayno	Age of the plants where seed formation starts	10–100	10–100	10–100	(h)
seedsEndAge	dayno	Age of the plants where SeedFraction is reached	30–120	30–120	30–120	(h)
cTuber	fraction	Fraction of tuber weight loss daily when sprouts starts growing	0.1	0.1	0.1	(f)
pMax	**h^{-1}**	**Maximal gross photosynthesis**	**0.001–0.01**	**0.001–0.02**	**0.001–0.03**	(h)
q10	–	Q10 for maintenance respiration	2	2	2	(f)
resp20	day^{-1}	Respiration at 20°C	0.002	0.002	0.002	(f)
heightMax	**m**	**Maximal height**	**0.1–1**	**1–6**	**3–4**	(c)
maxWeightLenRatio	**g m^{-1}**	**Weight of 1 m young sprout**	**0.01–0.1**	**0.4–0.8**	**0.1–0.4**	(d)
rootShootRatio	**fraction**	**Proportion of plant allocated to the roots**	**0.1**	**0.05–0.09**	**0.05–0.08**	(d)
fracPeriphyton	fraction	Fraction of light reduced by periphyton	0.2	0.2	0.2	(f)
hPhotoDist	m	Distance from plant top at which the photosynthesis is reduced factor 2	1.0	1.0	1.0	(f)
hPhotoLight	**µE m^{-2} s^{-1}**	**Half-saturation light intensity (PAR) for photosynthesis**	**15–60**	**30–60**	**40–60**	(b)
hPhotoTemp	**°C**	**Half-saturation temperature for photosynthesis**	**14**	**14–15**	**14–15**	(b)
plantK	m^{-2} g^{-1}	Extinction coefficient of plant tissue	0.02	0.02	0.02	(f)
pPhotoTemp	–	Exponent in temp. effect (Hill function) for photosynthesis	2–3	2–3	2–3	(a)
sPhotoTemp	–	Scaling of temperature effect for photosynthesis	1.35	1.35	1.35	(f)
cThinning	–	c factor of thinning function	5950	5950	5950	(f)
hWaveMort	m	Half-saturation depth for mortality	0–0.5	0–0.5	0–0.5	(f)
germinationDay	dayno	Day of germination of seeds	75–150	75–150	75–150	(h)
reproDay	dayno	Day of dispersal of seeds	227–289	227–289	227–289	(h)
maxAge	day	Maximal plant age	150–300	150–300	150–300	(h)
maxWaveMort	g day^{-1}	Maximum loss of weight in shallow areas	0.1–1	0.1–1	0.1–1	(h)
pWaveMort	–	Power of Hill function for wave mortality	0–8	0–8	0–8	(h)
hNutrient	**mg l^{-1}**	**Half-saturation nutrient concentration for photosynthesis**	**0.006–0.007**	**0.005–0.013**	**0.007–0.015**	(e)
pNutrient	**–**	**Power of Hill function for nutrient**	**4–8**	**3–6**	**1–2**	(e)
seedBiomass	**g**	**Individual weight of seeds**	**0.00002**	**0.001–0.007**	**0.005–0.007**	(f) (g)
seedFraction	g $year^{-1}$	Fraction of plant weight allocated to seeds	0.13	0.13	0.13	(f)
seedGermination	$year^{-1}$	Fraction of seeds that germinate	0.8	0.8	0.8	(i)
seedInitialBiomass	g	Initial biomass of seeds	2	2	2	(f)

(a) Unpublished observations in climate chambers and in the field by Markus Hoffmann. (b) Unpublished observations in climate chambers. (c) Field observations. (d) Mean values from own growth experiments Hoffmann et al. (2013, 2014). (e) Values adjusted to the observed values within the described datasets. Derived by means of Hill function of the real distribution (quantitative) of the reference species as a function of the total phosphate values. Assumption: direct correlation between photosynthesis rate and plant quantity. (f) van Nes et al. (2003). (g) Kleyer et al. (2008). (h) Expert knowledge. (i) Arbitrary.

orientated on forecasts (RCP 2.6 and RCP 8.5 or scenarios A2–B2) for water temperatures for the end of 21st century (Jones et al. 2010, Czernecki and Ptak 2018). We combined those scenarios with two further scenarios of correlated nutrient and water turbidity increase (+25%) or decrease (−25%) (reference period 2010–2020). Although we expect an increase as result of global warming, we also include a nutrient and turbidity decrease scenario as an alternative scenario for land-use decisions that favour better water quality. We coupled these water quality components because of their high correlation within the data set and the well-established connection between nutrient content and turbidity in lakes via algae growth. This design resulted in a total of eight scenarios and allowed the investigation of interactive effects of environmental change drivers. We again run each future scenario for all potential species within the 30 lakes at four depths (0.5, 1.5, 3, 5 m) for 10 years to reach equilibrium.

Data analysis

To answer question Q1.1, we calculate the number of oligotraphentic, mesotraphentic and eutraphentic species in each lake type for observed species richness from the mapped data and for the potential species richness from the modelled data. To answer question Q1.2, we calculate the number of oligotraphentic, mesotraphentic and eutraphentic species for each

depth in each lake for observed species richness and for the potential species. We plot them as box plots grouped by the lake types as a proportion of the total species number (on % scale). To compare lake-wise the observed species richness with the modelled one, we calculated the Pearson correlation between observed and potential species richness for each species group in each lake type.

To answer question Q2.1, we analysed the individual and interactive effects of water temperature increase scenarios and water quality change scenarios by calculating per lake, depth, and species group the difference of species number between the selected scenario and the base scenario. We plotted the mean and the standard deviation between lakes to see the direction and intensity of change.

To answer question Q2.2, we selected two scenarios, turbidity and nutrient decrease (−25%) and turbidity and nutrient increase (+25%), and determined for each species whether it loses ('loser') or gains ('winner') distribution by comparing the number of lakes the species is present in between the base scenario and each selected scenario. We then performed a generalised linear model (GLM) to explain if a species is a winner or a loser within the corresponding scenario. The explanatory variables are all species-specific parameters, the response variable is the winner-/loser-classification (binomial distribution). Interactive effects among parameters are not considered. We plotted the odd ratio of all significant variables ($p < 0.05$) with the 'sjplot' package (Lüdecke et al. 2021). The goodness of the model is determined with Tjur's R^2 within the performance package (Lüdecke et al. 2022). A value $R^2 \geq 0.26$ implies a substantial explanation of the model (Cohen 1988). Traits that promote significantly ($p < 0.05$) that a species loses distribution will be called 'loser traits' and traits that promote significantly ($p < 0.05$) an increase in distribution of the species are called 'winner traits'.

All model input and output data and code for data analysis are stored and provided as research compendium on GitHub (https://github.com/AnneLew/LewerentzEtAl2023_ModelledMacrophyteSpeciesRichness) (Lewerentz et al. 2023).

Results

The individual species richness for all lakes, depths, and scenarios can be explored within a developed shiny app, showing maps for the potential, and observed species richness, and for changes within the scenarios (https://annelew.shinyapps.io/mgm_macrophytes_scenarios/).

Base scenario: potential and observed species richness

Potential and observed submerged species richness for lake types (Q1.1)

Out of the 900 randomly assigned parameter combinations, 540 can grow under the base environmental conditions. These 540 species build the pool of potential species and all following species numbers will be shown as percentage of those. Of these 540 species, 28.5% are oligotraphentic, 34.5% mesotraphentic, 37.0% eutraphentic species (Table 2). In comparison, 35 observed species build the empirical species pool of indicator species, and of these 11.1% are oligotraphentic (n = 4), 55.6% mesotraphentic (n = 20), and 33.3% (n = 12) eutraphentic species. A table listing all species names and number of occurrences is given in the Supporting information. The comparison between observed and potential species richness within the functional groups and the lake types are given in Table 2. For mean environmental conditions per lake type of the base scenario see the Supporting information.

Potential and observed submerged species richness along lake depth and in different lake types (Q 1.2)

The observed depth diversity gradient (DDG) is clearly hump-shaped for meso- and eutraphentic species across all lake types, whereas oligotraphentic species are not present in turbid lakes, but they have a linearly decreasing DDG in clear and intermediate lakes (Fig. 2a). The potential DDG is hump-shaped across all lake types and species groups (Fig. 2b). By comparing the observed species richness with the potential species richness for all lake types and species groups (Fig. 2c), we find the highest correlations within turbid lakes for meso- ($R = 0.71$) and eutraphentic species ($R = 0.65$). Within those lakes, the observed species richness is smaller than the potential species richness (below the 1:1 line) almost in all lakes and species groups. Intermediate and clear lakes also contain lakes where observed species richness is higher than the potential species richness (above the 1:1 line). In intermediate lakes, the observed and potential species richness correlates slightly positively for all species groups (Fig. 2c). In clear lakes, potential species richness correlates negatively with observed species richness for oligo- and mesotraphentic species. A direct comparison of the potential and observed DDGs for all lakes is provided in the Supporting information.

Future scenarios of water temperature increase and water quality change

Change in potential species richness along depth for lake classes and species functional groups (Q2.1)

For the increased temperature scenario (Fig. 3a), we generally see an increase in species numbers with varying intensity across all depths, lake types, and species groups. The increase is highest in clear lakes for eutraphentic species. However, for a few individual lakes, increased temperature decreases potential species number, as a high standard deviation indicates.

The effect of increased nutrient load and water turbidity on potential species richness is dependent on the lake type (Fig. 3b). The effects are almost mirrored for decrease or increase (for decrease see the Supporting information). In clear lakes, the potential species richness increases under increased turbidity and nutrient conditions. In turbid lakes, the effect is the opposite. In intermediate lakes, the effect is depth-dependent: an increase of nutrients and turbidity prevailingly increases species richness in shallow water, while in deep water the effect is the opposite.

The combination of increased water temperatures (+3.0°C) and an increase of nutrients and turbidity (+25%) (Fig. 3c) generates a very similar pattern to solely increasing turbidity and nutrient (Fig. 3b) (see the Supporting information for all interactive scenarios).

Winner and loser traits under changed nutrient and turbidity conditions (Q2.2)

Within the decreased nutrient and turbidity scenario (−25%), we find that 78.1% of the species lose distribution (are losers), while 10.6% of all species win distribution (are winners). The general fit of the GLM explaining winner and loser traits under decreased nutrient and turbidity conditions is a Tjur's R^2 of 0.344. All significant explanatory variables are shown in Fig. 4a. The loser traits ordered by increasing odds ratios are (significance codes of drop contribution in brackets): *pMax* (***), *pWaveMort* (***), *reproDay* (**), *maxWeightLengthRatio* (*) and *hNutrient* (**). If the value of these traits is bigger, it is more likely that the species is a loser under the given conditions. The winner traits are *hWaveMort* (***), *hPhotoLight* (***) and *maxWaveMort* (**). If the value of these traits is bigger, it is more likely that the species is a winner under the given conditions.

In the increased nutrient and turbidity scenario (+25%), 15.0% of all species lose distribution, while 62.4% of all species win distribution. The general fit of the winner/loser species GLM (Fig. 4b) is a Tjur's R^2 0.404. The significant loser traits (significance codes of drop contribution in brackets) are *germinationDay* (*), *hPhotoLight* (***), *hWaveMort* (***), *maxAge* (**) and *seedBiomass* (*). The significant winner traits are *pMax* (***), *pWaveMort* (***), *reproDay* (***) and *seedsEndAge* (*).

A further winner and loser traits analysis under increased temperature shows that the significant loser traits (significance codes of drop contribution in brackets) are *pMax* (***), *pWaveMort* (***), *pNutrient* (**) and *reproDay* (*), while the significant winner traits are *hWaveMort* (***) and *hPhotoLight* (*) (Supporting information).

Discussion

Species richness of submerged macrophytes along depth – current state

Potential and observed submerged species richness in different lake types (Q1.1)

The comparison across lake types shows that, for both potential and observed species richness, the highest values appear in intermediate lakes. Intermediate peaks can be explained by geometric constraints, called 'mid-domain effect' (Colwell and Lees 2000). This plays especially a role for the potential species richness, as the parameter spaces used to draw the virtual species do not go beyond the environmental conditions simulated. The mid-domain effect seems to play a role also across lakes. Most nutrients are available in turbid lakes, while most light is available in clear lakes. Intermediate lakes are thus situated in the middle of both nutrient and light gradients (Fig. 5). Therefore, the highest share of species overlaps their nutrient and light niches at intermediate lakes. Species richness along multi-dimensional, interdependent, and opposing gradients can create non-linear responses, like the observed humped shape (Pausas and Austin 2001). Single scale and single dimension are not appropriate to depict the patterns of species richness (Mirochnitchenko et al. 2021). In line with other studies (Mellin et al. 2010, Ruiz-Benito et al. 2012, Toledo et al. 2012, Lewerentz et al. 2021), we see that the multidimensionality of environmental gradients across lake types are worth disentangling to understand species richness patterns.

Potential and observed submerged species richness distribution along depth (Q 1.2)

Our results show for the first time that the empirically observed hump-shaped pattern of species richness along depth (Lewerentz et al. 2021) already emerge solely from ecophysiological processes (Fig. 2a–b). This suggests that ecophysiology alone can emulate general real-world patterns of depth distribution of macrophytes. In our study depth only affects light availability and disturbance sensibility whereas in reality other environmental factors such as temperature can also be affected by depth. This could be an interesting avenue for further research and model development. However, DDG patterns predicted for particular lakes were not always matched (Fig. 2c). A reason for lower observed than potential species richness might be missing processes within the model (e.g. interspecific competition, dispersal, or herbivory) or imperfect detection during field mapping. A higher observed than potential species richness might be explained by habitat heterogeneity within the lakes. In our experimental design, we considered a single set of mean environmental parameters for each lake, which is the only type of environmental data available. However, large lakes are known to be environmentally heterogeneous (Árva et al. 2015). We observe an underestimation of the potential species richness exclusively in clear and intermediate lakes, but not in turbid lakes. The observed lack of species richness in the turbid lakes might be the result

Table 2. Comparison of observed species richness (OSR, given in % of total species pool, n = 36) and potential species richness (PSR, given in % of total species pool, n = 540) for oligotraphentic, mesotraphentic, and eutraphentic species in clear, intermediate and turbid lakes.

	Oligotraphentic species		Mesotraphentic species		Eutraphentic species		All species	
	OSR (%)	PSR (%)	OSR (%)	PSR (%)	OSR (%)	PSR (%)	OSR (%)	PSR (%)
Clear lakes	11.1	21.3	47.2	28.0	25.0	30.0	83.3	79.3
Intermediate lakes	5.6	28.5	50.0	34.1	33.3	25.9	88.9	98.5
Turbid lakes	0.0	24.3	25.0	33.0	22.2	36.9	47.2	94.1
All Lakes	11.1	28.5	55.6	34.5	33.3	37.0	100.0	100.0

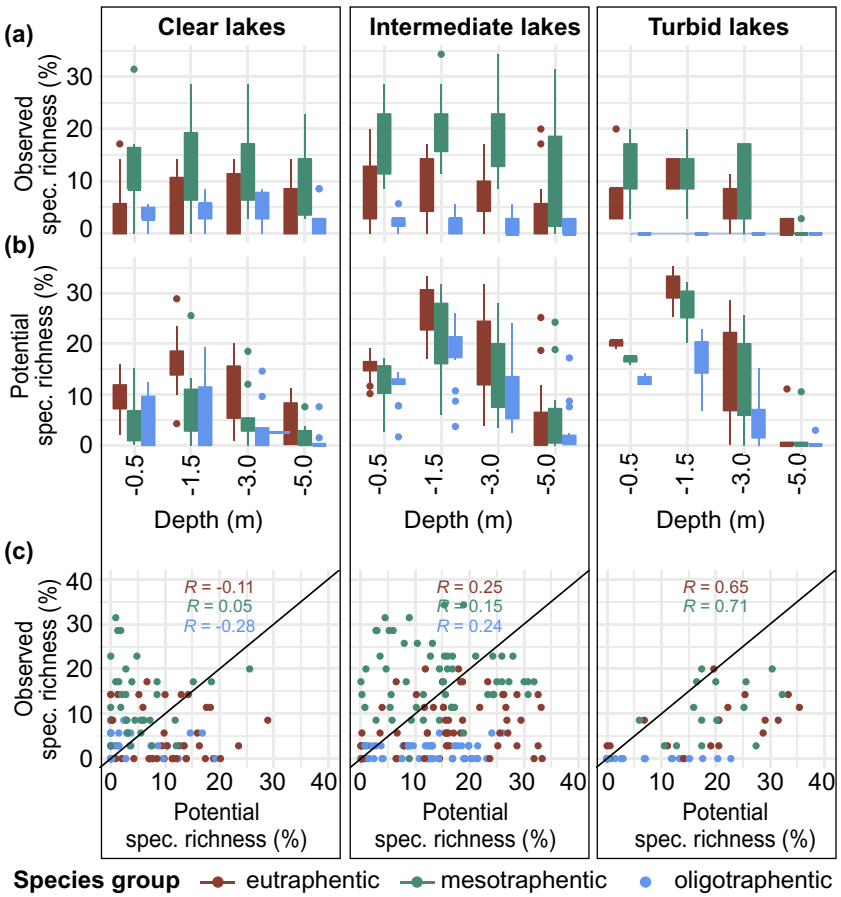

Figure 2. Number of oligotraphentic, mesotraphentic, and eutraphentic species along depth in clear, intermediate, and turbid lakes, divided into observed species richness (a) and potential species richness (b). The boxplots show the depth diversity gradient (DDG) for the individual species groups. To compare the observed and the potential species distribution within the lake types and the species groups both are plotted against each other (c), thus every point represents a species group within a lake. The black line would represent a perfect match between potential and observed species richness (1:1 line). All points below that line show a reduced observed richness, while all points above the line can be seen as an underestimated potential species richness. The *R*-values give the correlation coefficients within the species group.

of a shift in life forms from 'complex' macrophytes towards 'simple' algae. This shift indicates the increased uptake of light and nutrients by algae (Hilt 2015), reducing the fraction of resources left for the macrophyte community. Our results capture a positive, but weak correlation between observed and potential species richness for the different species groups and lake types, with the exception of eutraphentic and oligotraphentic species in clear lakes (Fig. 2c). A reason for this exception might be increased resource competition and environmental stress as clear water lakes tend to be nutrient-limited and colder. Notwithstanding such limitations, the general hump-shaped DDG and the weak yet positive correlation between potential and observed species richness proved our model to be useful to explore distribution patterns of species richness of macrophytes along the depth gradient of lakes.

Species richness of submerged macrophytes along depth under scenarios of environmental change

Species richness change (Q2.1)

Higher water temperatures caused by climate change (Woolway et al. 2020) will likely increase species richness (Fig. 3a). Indeed, higher temperatures lead to higher metabolic rates, productivity and, ultimately, also richness (Brown et al. 2004, Wang et al. 2009). Furthermore, higher maximal water temperature means that the vegetation period is prolonged, which allows slow-growing species to mature and reproduce. Species richness reduction was predicted only in particular cases, mainly for larger depths and oligotraphentic species. The eco-physiological background here might be that higher temperatures increase all biochemical reactions in the macrophytes (respiration and photosynthesis). However, as the photosynthesis can be limited by nutrients or by the available light, a netto photosynthesis that is lower than respiration can cause the death of the species (Ikusima 1970, Binzer et al. 2006).

Turbidity and nutrients in lakes can be influenced by different complex processes mostly concerning the whole catchment of a lake. During the last decades turbidity and nutrient levels of most lakes in southern Germany decreased as a consequence of improved wastewater systems and water management (Vetter and Sousa 2012, Murphy et al. 2018). However, it remains unclear if this trend will proceed in the future. Climate change might lead to a trend reversal, as it

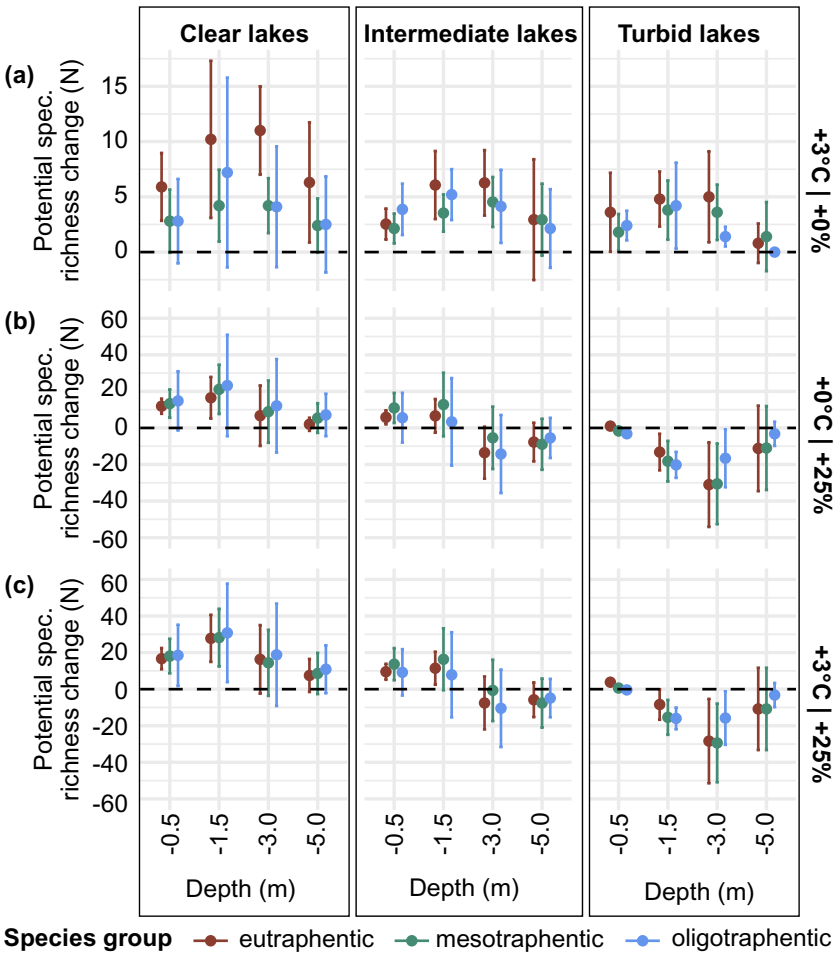

Figure 3. Depth dependent potential species richness changes under increased water surface temperature of +3°C (a), under increased (+25%) turbidity and nutrients (b), and under a combination of both environmental changes (c) for eutraphentic, mesotraphentic, and oligotraphentic species within clear, intermediate, and turbid lakes. The potential species richness change is determined in comparison to the depth dependent species richness of each species group within each lake in the base scenario and given in change of number of species. The points show the mean changes of the lakes per depth and species group, while the vertical bars show the respective standard deviation.

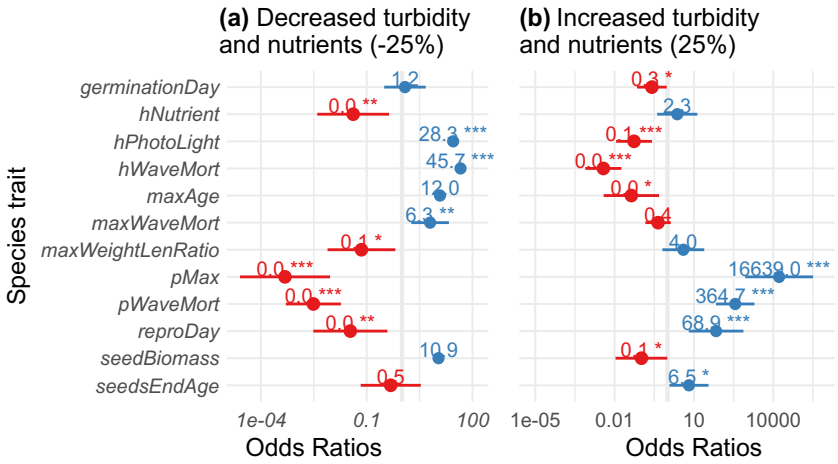

Figure 4. Traits that promote loser (Odds ratios < 1, red) or winner species (Odds ratios >1, blue) under different water quality change scenarios of decreased turbidity and nutrients (a) and increased turbidity and nutrients (b). Just traits are shown that are significant within one of the GLM models (Signif. codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Descriptions for the species traits can be found in Table 1.

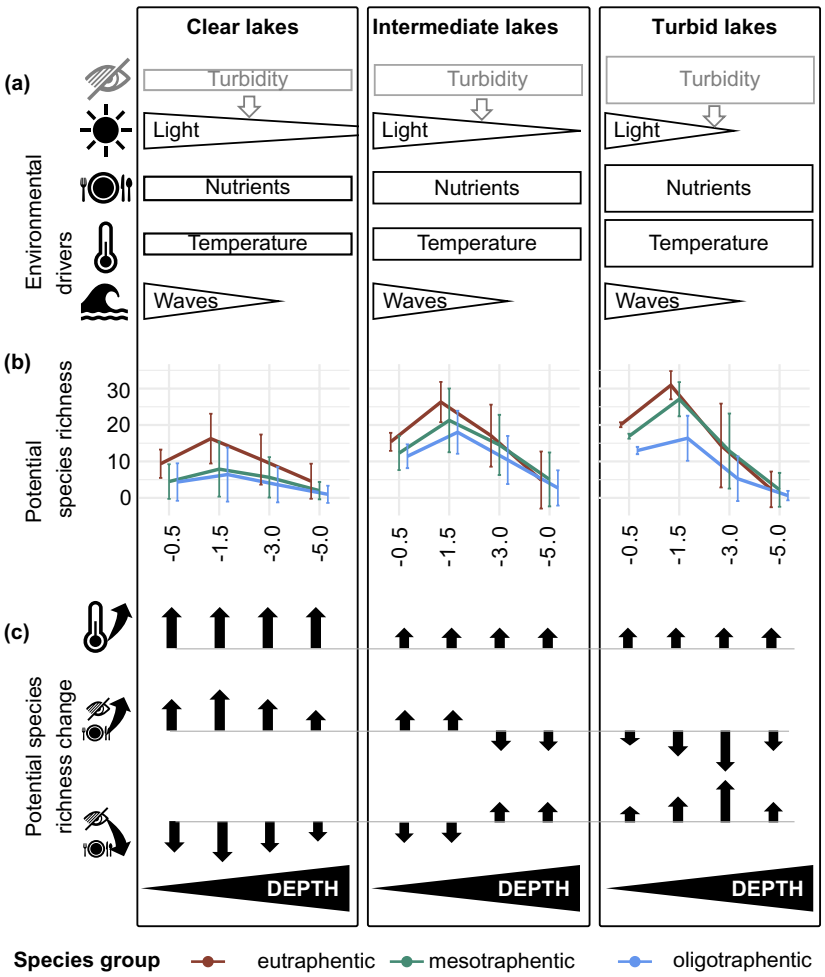

Figure 5. Summary figure showing distribution of environmental drivers (light - influenced by turbidity - , nutrients, water temperature, and waves) (a), recent potential species richness (line: mean; bars: standard deviation) (b), and scenarios of potential species richness change under temperature increase, turbidity and nutrient increase, turbidity and nutrient decrease (c) along depth in clear lakes, intermediate lakes, and turbid lakes.

enhances eutrophication processes of lakes (Moss et al. 2011, Moss 2012). Species loss in increased nutrient and turbidity conditions in turbid lakes is caused by light reduction. Alternatively, species gain in clear (i.e. nutrient-limited) lakes is a direct effect of nutrient increase. The results prove that there is no consistent trend for how changes in turbidity and nutrient levels affect the species diversity of lakes, as the effects vary depending on the type and the depth zone of the lake (Fig. 5).

In the interactive scenario of temperature increase and turbidity and nutrient increase (Fig. 3c), the potential species richness change is prevailingly dominated by the effect of turbidity and nutrient increase. This may reflect a stronger change in water quality relative to temperature and due to the higher physiological influence of light and nutrients availability in comparison to water temperature (Barko and Smart 1981). In any case, we demonstrate that changing environmental conditions will influence the potential species richness of submerged macrophytes substantially.

Traits of winner and loser species under different scenarios (Q2.2)

We identified traits of the species that statistically significantly influence if a species is a winner or a loser under increased or decreased nutrient and turbidity conditions. High correlations between the plants' responses to anthropogenic change and their traits are known for the compositional shift from submerged to emergent life forms (Zervas et al. 2019). We found traits that are sensitive to environmental change and that affect the plants' biomass production, light requirements, nutrient limitation, life cycle, and depth-dependent disturbance sensitivity (Fig. 4). This means that changes in multiple traits, and thus functions, might be required to cope with impending environmental change.

A high maximum growth rate (*pMax*) is advantageous under increased nutrient and turbidity, but disadvantageous under decreased nutrient and turbidity levels. When producing high amounts of biomass, the macrophytes can reach shallower water faster to overcome light limitation.

This rationale also explains the shift from slow-growing seagrass to fast-growing macroalgae under increasing nutrient and light limitation in oceans (Duarte 1995). This advantage of fast growth also explains a high *maxWeightLengthRatio* as a loser trait value under decreased turbidity and nutrients. If a plant needs more biomass to grow the same length as another plant, it can be outgrown, shaded, and thus outcompeted. A slow-growing species group are charophytes (Blindow 1992, Henricson et al. 2006), whereas fast growth is a trait commonly found in invasive species *Elodea canadensis* (Dawson et al. 2011, Schultz and Dibble 2012, Hussner et al. 2021). Hence, future environmental change involving increase in turbidity might cause loss of charophytes and further promote invasive species.

Several traits determine the wave mortality within the model which can be seen as any depth-dependent reduction of biomass due to disturbance (e.g. also herbivory by water birds). In the scenario with decreased turbidity and nutrients, a high wave mortality rate (*maxWaveMort*) and a depth effect (*hWaveMort*, *pWaveMort*) bring advantages for species that are susceptible to disturbance as enough light reaches deep water, where these species can survive. Under more turbid and nutrient-rich conditions, it is the other way around. In fact, the effect of waves on macrophytes in shallow areas of lakes is not negligible (Schutten et al. 2004, 2005). However, our results stress the relevance of a combined effect of wave mortality and light limitation, as disturbance-sensitive species cannot survive if light limiting.

Several life cycle traits significantly influence on whether a species becomes a winner or a loser. A later germination during the year makes the species a 'loser' in the more turbid and nutrient rich lake, as it suffers from negative carbon budget under higher temperature (i.e. respiration>photosynthesis) (Milbau et al. 2017). Furthermore, in the scenario of decreased nutrient and turbidity conditions a later reproduction is a winner trait probably due to a longer growth period and subsequent sufficient reproductive biomass for winter survival.

Conservation implications

Knowledge about the loss of potential species richness can warn against upcoming threats under different scenarios. In the presented shiny app (Supporting information) conservation practitioners can see which lakes and depths within the study region are hotspots of change under different scenarios. We confirmed that the main threatened areas within a scenario of turbidity and nutrient increase are the deep areas of turbid lakes, with some areas become even uninhabitable for submerged macrophytes (Fig. 3).

It is not the general aim of lake management and conservation to maximise species richness within lakes. The aim is to promote a species composition that represents and corresponds to the lake type (Poikane et al. 2018). Although we show that clear lakes in particular would have higher potential species diversity due to increased nutrient levels, we have to consider that they currently host a high share of the oligotrophic species that would be lost under increased nutrient and turbidity conditions (Table 2, Fig. 3). Therefore, to protect freshwater biodiversity under the multiple stressors, the restoration and conservation of suitable refugia for vulnerable species is crucial (Sarmento Cabral et al. 2013, Hofstra et al. 2020).

Limitations and perspectives

One typical limitation of eco-physiological models is complexity in terms of parameter numbers. Whereas more complex models (like Charisma 2.0) can answer complex questions (e.g. alternative stable states, spatial processes and competition), modellers must be able to interpret process interactions and overcome equifinality (i.e. different parameter combinations generating similar results). We simplified Charisma 2.0 down to 28 parameters by reducing the processes to include mostly eco-physiological ones. However, this means that spatial processes and competition are no longer considered. Spatially explicit modelling of the dispersal of seeds or other reproductive organs might shed light on the relevance of dispersal limitation and mass effects. However, due to waterfowl, including migrating species, dispersal does not tend be limiting for macrophytes.

A reason for a higher potential then observed species richness might be that environmental conditions are already changing. Consequentially, species may simply have not yet reached their full potential distribution, communities are not in equilibrium, and species may be lost in the future (Padial et al. 2014, García-Girón et al. 2019). Another factor which increased the mismatch might be inter-specific competition (Supporting information for a supporting test result of the hypothesis). In freshwater lakes, not only submerged macrophytes compete with each other for resources, they also compete with emergent species or species with floating leaves, mainly in shallow water. Emergent species and floating-leaved species have competitive advantages like a higher light availability and carbon use from air and are present within the studied lakes (Lewerentz and Cabral 2021). Moreover, submerged species compete with each other for resources above and below ground mainly by different biomass-allocation strategies (Wang et al. 2008). In addition, the model is completely deterministic. Adding stochasticity to processes like germination could increase insight into randomness effects of the processes. Moreover, other stochastic processes, such as intraspecific variation and short-term evolution, could be integrated in future model developments. Despite all these missing processes, the modelled species distribution patterns already bring valuable insights as mentioned in previous sections.

A likely reason for the underestimation of species richness within a lake might be the missing consideration of environmental heterogeneity within a lake. We use per lake the measurements of environmental parameters at just one point in the middle of the lake. To improve design of simulation experiments with MGM, a within-lake net of measurements would be necessary. Moreover, data from public monitoring

in the studied region are just available for the bigger lakes (>50 ha). However, large lakes only constitute a part of all natural water bodies (Downing et al. 2006). More information about macrophytes distribution and environmental parameters in small lakes and ponds could be integrated in future studies with MGM, as those lentic systems will likely undergo more extreme changes.

This framework of applying a process-based model in combination with random, theoretical species (Webb et al. 2010, Zakharova et al. 2019) to identify hotspots of change can be a template also for other lake regions or even other species groups, including in terrestrial systems, and is already applied e.g. for epiphytes (Petter et al. 2021) or invasive species on islands (Vedder et al. 2021). Overall, MGM can generate species richness patterns across different environmental gradients of nutrient availability, latitudes (by varying light intensity and seasonality), turbidity, water temperature, and depth.

Conclusion

Our study is the first that performs macroecological mechanistic experiments on the potential species richness of submerged macrophytes in a real-world context. Scenarios for the effects of climate and land-use change for different lake types and species groups revealed that temperature increase alone should raise the number of potentially growing species. Our experiments reveal that this is physiologically plausible even without increasing the species pool by invasive species from warmer regions. The effect of increase or decrease of turbidity and nutrients content depends on the lake type and depths. Hence, future changes in species richness are multidimensional and conservation planning needs to consider the direction of environmental change, depth, and lake, and species type (Fig. 5). The findings help to understand the physiological constraints underlying of today's distribution and to explore potential future developments of species richness of submerged macrophytes. It demonstrates that mechanistic modelling can improve the understanding of macroecological patterns of macrophytes and stress the need for process-based assessments of environmental change. This is paramount to move the predictive agenda from relying on poorly transferable correlative models to models that directly simulate the mechanics of changing environmental conditions.

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Author contributions

Anne Lewerentz: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Markus Hoffmann**: Conceptualization (supporting); Formal analysis (supporting); Writing – review and editing (supporting). **Thomas Hovestadt**: Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Uta Raeder**: Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Juliano Sarmento Cabral**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – original draft (supporting), Writing – review and editing (supporting).

Data availability statement

Original raw empirical data are publicly available, provided by Bayerisches Landesamt für Umwelt, www.lfu.bayern.de. Data and code of data analysis are available from the Zenodo Digital Repository as Research Compendium: https://doi.org/10.5281/zenodo.8036975 (Lewerentz et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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