



Spatiotemporal dynamics of freshwater macrophytes
in Bavarian lakes under environmental change

Raum-zeitliche Dynamik der Makrophyten
in bayerischen Seen unter sich ändernden Umweltbedingungen

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A lake is a landscape's most beautiful and expressive feature. It is Earth's eye; looking into which the beholder measures the depth of his own nature.

Henry David Thoreau



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Summary

Macrophytes are key components of freshwater ecosystems because they provide habitat, food, and improve the water quality. Macrophyte are vulnerable to environmental change as their physiological processes depend on changing environmental factors, which themselves vary within a geographical region and along lake depth. Their spatial distribution is not well understood and their importance is publicly little-known. In this thesis, I have investigated the spatiotemporal dynamics of freshwater macrophytes in Bavarian lakes to understand their diversity pattern along different scales and to predict and communicate potential consequences of global change on their richness.

In the introduction (Chapter 1), I provide an overview of the current scientific knowledge of the species richness patterns of macrophytes in freshwater lakes, the influences of climate and land-use change on macrophyte growth, and different modelling approaches of macrophytes.

The main part of the thesis starts with a study about submerged and emergent macrophyte species richness in natural and artificial lakes of Bavaria (Chapter 2). By analysing publicly available monitoring data, I have found a higher species richness of submerged macrophytes in natural lakes than in artificial lakes. Furthermore, I showed that the richness of submerged species is better explained by physio-chemical lake parameters than the richness of emergent species. In Chapter 3, I considered that submerged macrophytes grow along a depth gradient that provides a sharp environmental gradient on a short spatial scale. This study is the first comparative assessment of the depth diversity gradient (DDG) of macrophytes. I have found a hump-shaped pattern of different diversity components. Generalised additive mixed-effect models indicate that the shape of the DDG is influenced mainly by light quality, light quantity, layering depth, and lake area. I could not identify a general trend of the DDG within recent years, but single lakes show trends leading into different directions. In Chapter 4, I used a mechanistic eco-physiological model to explore changes in the distribution of macrophyte species richness under different scenarios of environmental conditions across lakes and with depths. I could replicate the hump-shaped pattern of potential species richness along depth. Rising temperature leads to increased species richness in all lake types, and depths. The effect of turbidity and nutrient change depends on depth and lake type. Traits that characterise “loser species” under increased turbidity and nutrients are a high light consumption and a high sensibility to disturbances. “Winner species” can be identified by a high biomass production. In Chapter 5, I discuss the image problem of macrophytes. Unawareness, ignorance, and the poor accessibility of macrophytes can lead to conflicts of use. I assumed that an increased engagement and education could counteract this. Because computer games can transfer knowledge interactively while creating an immersive experience, I present in the chapter an interactive single-player game for children.

Finally, I discuss the findings of this thesis in the light of their implications for ecological theory, their implications for conservation, and future research ideas (Chapter 6). The findings help to understand the regional distribution and the drivers of macrophyte species richness. By applying eco-physiological models, multiple environmental shaping factors for species richness were tested and scenarios of climate and land-use change were explored.

Zusammenfassung

Makrophyten sind wichtige Bestandteile des Lebensraums See. Sie schaffen Habitate und verbessern die Wasserqualität, sind in der Öffentlichkeit jedoch kaum bekannt. Makrophyten sind sehr anfällig für Umweltveränderungen, da ihre physiologischen Prozesse von Umweltfaktoren abhängen, die ihrerseits innerhalb einer geografischen Region und entlang der Seetiefe variieren. Diese Arbeit untersucht die räumlich-zeitliche Dynamik von Makrophyten in bayerischen Seen, um die Muster ihrer Artenvielfalt auf verschiedenen Skalen zu verstehen und um die Folgen von Klima- und Landnutzungswandel auf ihre Artenvielfalt zu untersuchen.

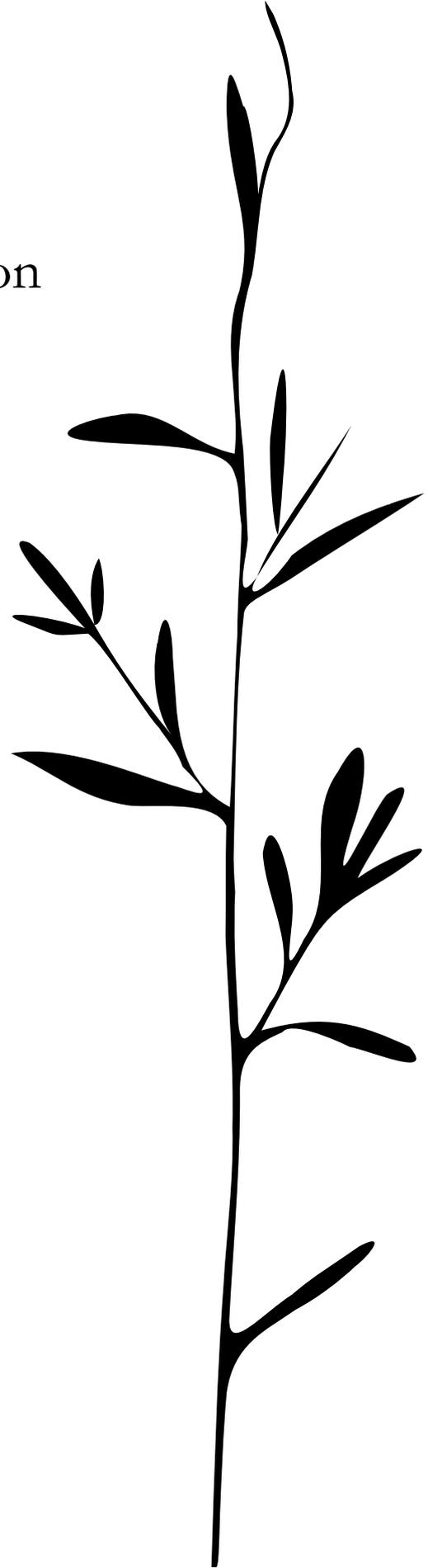
Die Einleitung (Kapitel 1) gibt einen Überblick über den aktuellen Wissensstand zur Artenvielfalt von Makrophyten in Seen, zu Einflüssen von Klima- und Landnutzungswandel auf das Wachstum von Makrophyten, sowie zu verschiedenen Modellierungsansätzen von Makrophyten.

Der Hauptteil der Arbeit beginnt mit der Analyse (Kapitel 2) der submersen und emergenten Makrophytenvielfalt in natürlichen und künstlichen Seen Bayerns. Mit Hilfe von öffentlich zugänglichen Monitoringdaten konnte gezeigt werden, dass es mehr submerser Makrophyten in natürlichen Seen als in künstlichen Seen gibt und dass sich die Anzahl an submersen Makrophyten je See besser mit physiko-chemischen Parametern erklären lässt als die von emergenten Arten. In Kapitel 3 wird die Verteilung der Artenvielfalt von submersen Makrophyten entlang des Tiefengradienten betrachtet. Entlang der Tiefe ändern sich physikalisch-chemische Parameter auf einer kurzen räumlichen Skala. Diese Studie ist die erste vergleichende Untersuchung des Tiefen-Diversitätsgradienten (DDG) von Makrophyten. Der DDG von verschiedenen Diversitätskomponenten verläuft buckelförmig. „Generalised additive mixed-effect models“ deuten darauf hin, dass die Form des DDG hauptsächlich von der Lichtqualität, der Lichtmenge, der Schichtungstiefe und der Fläche des Sees beeinflusst wird. Die Daten zeigen keine verallgemeinerbare Veränderung des höckerförmigen DDGs in den letzten Jahren. In einzelnen Seen gibt es jedoch Trends. In Kapitel 4 wird mit einem mechanistischen, ökophysiologischen Makrophyten-Wachstums-Modell (MGM) die potenziellen Veränderungen in der Verbreitung von Makrophyten unter verschiedenen Klima- und Landnutzungsszenarien untersucht. Durch die Anwendung von MGM konnte das höckerförmige Muster des DDG repliziert werden. Unterschiede zum kartierten Artenreichtum lassen sich wahrscheinlich durch nicht modellierte Prozesse wie Konkurrenz und Umweltheterogenität innerhalb des Sees erklären. Steigende Temperaturen führen zu einer Zunahme des Artenreichtums in allen Seetypen, Artengruppen und Tiefen. Die Auswirkungen von Trübungen und Nährstoffveränderungen hängen von der Tiefe und dem Seetyp ab. Merkmale, die unter erhöhter Trübung und Nährstoffgehalt "Verlierer-Arten" kennzeichnen, sind ein hoher Lichtverbrauch und eine hohe Störungsempfindlichkeit, während "Gewinner-Arten" diejenigen sind, die eine hohe Biomasseproduktion aufweisen. Kapitel 5 stellt das Imageproblem von Makrophyten dar. Unkenntnis, Unwissenheit und die schlechte Zugänglichkeit können zu Nutzungskonflikten führen. Es ist anzunehmen, dass ein verstärktes Engagement und Aufklärung dem entgegenwirken könnten. Da Computerspiele eine Möglichkeit sind, Wissen interaktiv zu transportieren und ein immersives Erlebnis zu schaffen, wird in diesem Kapitel das entwickelte Spiel bioDIVERSity vorgestellt.

Abschließend werden die Ergebnisse im Hinblick auf ihre Bedeutung für ökologische Theorien, ihre Auswirkungen auf den Naturschutz und zukünftige Forschungsideen diskutiert (Kapitel 6). Die Ergebnisse dieser Arbeit tragen dazu bei, die regionale Verbreitung und die Treiber einer oft übersehenen Artengruppe zu verstehen. Durch die Anwendung öko-physiologischer Modelle konnten verschiedene Einflussfaktoren auf den Artenreichtum von Makrophyten getestet und Szenarien von Klima- und Landnutzungswandel erforscht werden.

Part I

General introduction



Chapter 1

Freshwater macrophytes under environmental change

Fresh water is one of the key resources on which most life on earth depends. It accumulates in groundwater, but also in different forms of surface water, such as swamps, rivers, and lakes. These systems are not just resources of water, they are also biodiverse ecosystems. Climate change and land-use change not only influence the quality and availability of freshwater as a human resource but also threaten entire freshwater ecosystems and the living conditions for the species in those systems. Macrophytes are aquatic plants and macroalgae – a biodiversity component that is crucial for water quality and that is well-known to indicate long-term environmental change as its growth and thus its distribution is highly dependent on its environment. Hence, future environmental changes must have a high impact on their distribution and on species richness. Process-based eco-physiological models are an appropriate means to study scenarios of potential multifactorial changes. However, especially if the changes lead to population growth of macrophytes, the species have an image problem as they and their functions within the ecosystem are often unknown to the broad public.

In this thesis, I aim to fill relevant knowledge gaps to better understand and communicate the mechanisms influencing current and future species distribution of freshwater macrophytes under changing environmental conditions. As a study region, I selected Bavaria, Germany, since it is characterised by a high number of lakes along an environmental gradient of elevation and along different land-use intensities at the lakes' catchments.

In this chapter, I give an overview of the biodiversity of macrophytes in freshwater lakes (*Section 1.1*), the influence of environmental change on macrophyte growth and distribution (*Section 1.2*), modelling approaches (*Section 1.3*), and the study questions including a detailed structure of the thesis (*Section 1.4*).

1.1 Biodiversity of macrophytes in freshwater lakes

Macrophytes are aquatic “photosynthetic organisms, large enough to see with the naked eye” (Chambers et al., 2008). They are good and well-known long-term indicator species for the ecological functioning of freshwaters (Melzer, 1999; Melzer & Schneider, 2014; Schaumburg et al., 2004), as their eco-physiology highly depends on their aquatic environment. Macrophytes play an important role in freshwater systems, since they are primary producers and provide habitat, food, and structure for other organisms (Jeppesen et al., 1998). Macrophytes provide a broad range of 26 types of different ecosystem services, including “supporting services” such as the aforementioned provisioning of habitat and nutrient cycling, “regulating services” such as erosion regulation along shores, “provisioning services” like use for environmental monitoring, and “cultural services” such as aesthetic or educational value (Thomaz, 2021). These ecosystem services profit from more diverse macrophyte communities, as higher species richness leads to higher community resilience

(Thomaz, 2021). Macrophytes can be found globally and can belong to seven plant divisions (Table 1.1), namely Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta, Bryophyta, Pteridophyta, and Spermatophyta, thus comprising vascular plants (mostly angiosperms) and non-vascular plants (like bryophytes or macroalgae) (Chambers et al., 2008). Furthermore, macrophytes can be classified by their life forms as emergent, submerged, floating-leaved or free-floating species, depending on their relation to atmosphere contact and to the substrate.

Table 1.1: Overview of plant divisions containing freshwater macrophytes with description, representative genera, and a representative picture. Table modified after Chambers et al. (2008).

| Division | Description | Representative genera | Representative picture (if available) |
|---------------|---|---------------------------------|---|
| Cyanobacteria | Bacteria with photosynthesis (Blue-green algae) | <i>Oscillatoria</i> | |
| Chlorophyta | Green algae | <i>Chara, Nitella</i> |  |
| Rhodophyta | Red algae | <i>Lemanea</i> | |
| Xanthophyta | Yellow-green algae | <i>Vaucheria</i> |  |
| Bryophyta | Mosses and liverworts | <i>Fontinalis</i> | |
| Pteridophyta | Vascular plant that disperses spores (Ferns & allies) | <i>Salvinia, Isoetes</i> |  |
| Spermatophyta | Vascular plants that produce seeds | <i>Utricularia, Potamogeton</i> |  |

The key abiotic factors determining the growth and community composition of submerged macrophytes are light availability, temperature, water nutrient content, substrate characteristics, and

disturbances (Bornette & Puijalon, 2011). Light availability of photosynthetic active radiation is crucial for primary production (Pedersen et al., 2013), affects the thermal structure of lakes, but can also damage biota due to harming radiation (Choudhury et al., 2019). It can be differentiated by light quality (wavelength) and light quantity. Both are influenced by the solar irradiance above the lake surface (dependent on latitude, solar angle, elevation, atmospheric transparency, cloud cover, etc.) and within lake attenuation processes in the water column such as absorption and scattering. Those processes depend on water parameters, presence of algae, humic substances, and solid particles that can be summarised as turbidity. Water temperature is comparably stable in freshwaters over the year, as water has a high specific heat capacity which dampens the processes of warming up and cooling down in comparison to land. The water temperature is influenced by the air temperature, water volume, lake size, and lake depth. In deep lakes, the physical characteristics of water can lead to stratifications of temperature during summer and mixing of deep and surface water in the other seasons. High water temperatures seem to be generally an advantage for macrophyte growth until respiration exceeds photosynthesis (Santamaria & van Vierssen, 1997). The main necessary nutrients for macrophyte growth are carbon, nitrogen, and phosphorus. The availability of carbon dioxide depends mainly on pH and the surrounding geology. Nitrogen and phosphorus availability depend on the inputs into the lake, resuspension processes, mixing processes, and water chemistry. Water movements, water level fluctuations (floods and droughts), and herbivory are the main disturbances for macrophyte growth in lakes (Bornette & Puijalon, 2011). The key abiotic factors for macrophytes depend not just on the characteristics of the specific lake, such as latitude, lake size, lake depth, and climate, but on the whole catchment that drains into the lake: its geology (Iversen et al., 2019), geomorphology, hydrology, and land use including wastewater management. The abiotic factors within lakes build a complex network as they influence each other; they are specific to each lake and vary with the depth of the lake.

Globally, 3457 vascular macrophyte species are recorded that prevalingly show narrow global distributions (K. Murphy et al., 2019). For charophytes, no global study is known. In general, macrophytes show a positive relationship of species number with lake surface area, lake shoreline length or littoral zone area (species-area relationship) (as reviewed in Alahuhta et al. (2020)). The highest species richness of vascular macrophytes along latitude is recorded for sub-tropical and low-tropical latitudes (K. Murphy et al., 2019). Looking at other diversity gradients, species richness decreases with elevation (Alahuhta et al., 2020; Lacoul & Freedman, 2006; Zhou et al., 2022) and seems to decrease with lake depth (Bolpagni et al., 2016; Fu, Zhong, Yuan, Xie, et al., 2014; Fu et al., 2015; Ye et al., 2018). However, the depth diversity gradient has not yet been studied comparatively.

1.2 Macrophytes under environmental change

Global biodiversity is declining at high rates (Diaz et al., 2019). Although freshwater lakes cover just 3.7% of the Earth's non-glaciated land area (Verpoorter et al., 2014), they shelter around 12% of global fauna (Oikonomou, 2021) and up to 6% of all known species (Strayer & Dudgeon, 2010). The high biodiversity in freshwater environments worldwide is undergoing one of the most

dramatic losses of species worldwide with faster losses than in terrestrial or marine ecosystems (Dudgeon et al., 2006; McRae et al., 2017). Functioning freshwater ecosystems are crucial for human well-being, as they provide pivotal ecosystem services (Dudgeon et al., 2006). To counteract the freshwater biodiversity loss, conservation policies and a sustainable management of freshwaters are needed. These mitigation actions should be based on a thorough understanding of the processes within freshwater. Despite the high biodiversity of freshwaters and their importance, just 20% of scientific articles on biodiversity address freshwater biodiversity, and of those, just 20% study lakes (Williams-Subiza & Epele, 2021). Research gaps exist in the areas of data infrastructure, monitoring, ecology, management, and social ecology of freshwater biodiversity (Maasri et al., 2022).

For macrophytes, an accelerating decrease rate can be observed globally since the beginning of the last century (J. Y. Kim & Nishihiro, 2020; Y. Zhang et al., 2017). However, the trend is not uniform for all lakes and regions (Y. Zhang et al., 2017). The major local threats to freshwater macrophytes are assumed to be human use of lakes (e.g. boating, aquaculture, construction along shorelines) and human use of the surrounding catchment (e.g. excessive fertilisation of agricultural land leading to eutrophication, or soil sealing) (Gatti, 2016). The major global threat is climate change (Y. Zhang et al., 2017). In general, it is hard to separate climate effects from other threats in lake environments (e.g. as result of land-use change or other anthropogenic pressures), since all effects interact with each other and build a complex network of direct and indirect effects (Lind et al., 2022).

Lakes are often seen as closed systems, but they are highly connected to their surroundings (Phillips et al., 2016). Lakes are endpoints in the landscape, where influences and changes from a whole catchment come together. They integrate changes on landscape level in their catchment. Every change in intensity and type of land use can impact the water quality and hydrology of a connected lake. People have always used rivers and lakes to dispose of wastewater containing nutrients. Other sources of nutrients leading to eutrophication can be agriculture or stormwater. As a consequence of eutrophication for macrophytes, communities dominated by submerged macrophytes shift to being dominated by emergent macrophytes (Scheffer et al., 2003; Zervas et al., 2019). Besides these threats through land-use changes, direct use of lakes can also have a high impact on macrophytes. For example, boat traffic can cause significant mechanical damage to submerged vegetation (Sagerman et al., 2020). Other hydro-morphological threats are recreational exploitation (Jusik & Maciòl, 2014) and water level fluctuations caused by hydropower plants or changed run-off dynamics (Evtimova & Donohue, 2016). Since the year 2000, it is a proclaimed political aim of the European Union that all freshwater ecosystems be in at least a “good status”. By 2015, just 26.4% of all 732 monitored lakes in Germany reached that aim (Meunier, 2016). High nutrient concentrations are still the main reason for missing the target (Meunier, 2016). Macrophytes are one species group that is used in that context to determine the ecological status of lakes in combination with phyto-benthos. For less than 20% of the lakes in Germany, this quality component is rated as “good” or “very good” (Meunier, 2016). Although the ratings have improved since the start of the monitoring, it is uncertain whether the political efforts are sufficient to continue this trend in the face of upcoming stressors from future climate change.

Climate change is happening, and greenhouse gases are constantly rising. A broad range of physical, chemical, and biological consequences of climate change for lakes are already observed and are predicted to further increase under future scenarios (Adrian et al., 2009; Kraemer et al., 2020, 2021; Maasri et al., 2022; Missaghi et al., 2017; Whitehead et al., 2009; Woolway et al., 2020). Annual maximal lake surface temperature across European lakes increased with an average rate of $+0.58\text{ }^{\circ}\text{C decade}^{-1}$ even faster than the annual maximum air temperature ($+0.42\text{ }^{\circ}\text{C decade}^{-1}$) during the past decades (Dokulil et al., 2021). In fact, studies predict a summer surface water temperature increase in alpine lakes of $1.2\text{--}2.9\text{ }^{\circ}\text{C}$ until 2050 (Dokulil, 2014). In comparison, deep water temperatures showed on average almost no change ($+0.06\text{ }^{\circ}\text{C decade}^{-1}$), “but had high variability across lakes, with trends in individual lakes ranging from $-0.68\text{ }^{\circ}\text{C decade}^{-1}$ to $+0.65\text{ }^{\circ}\text{C decade}^{-1}$ ” (Pilla et al., 2020). The temperature increase is relevant for macrophytes, as their growth is influenced by temperature through metabolism and phenology. Furthermore, temperature increase has a series of indirect effects on macrophytes. It promotes the growth of algae, thereby reducing the light availability for submerged macrophytes, and it influences the lake mixing regime. The lake mixing regimes change their layering duration and layering types due to reduced ice cover and longer summer layering, and, as a consequence, many lakes will mix less frequently (Mesman et al., 2021; Woolway & Merchant, 2019). Incomplete or less frequent mixing in lakes have consequences for the whole lake, as it promotes anoxia in deep waters. A widespread decline in surface and deep-water habitats of dissolved oxygen can be observed in temperate lakes and is due to climate change (Jane et al., 2021). Anoxia in deep waters, in turn, can lead to resuspension processes of nutrients called “internal fertilisation”. Besides temperature increase and all its direct and indirect effects, climate change also affects precipitation patterns and promotes extreme events like droughts, heavy rainfalls, and floods. These can lead to more extreme water level fluctuations, nutrient increase, and turbidity enhancement with negative consequences for macrophyte growth (Kraemer et al., 2020; Lind et al., 2022). However, how the development of these multiple drivers will influence macrophytes growth and species richness is still unclear (Lind et al., 2022).

Macrophytes are often perceived as a nuisance to humans if they disturb boat traffic, fishing, swimming, hydrodynamics, or other functions (Thomaz, 2021; Verhofstad & Bakker, 2019). The main determinant characters for nuisance are vegetation cover and canopy depth below surface, as reviewed in Verhofstad & Bakker (2019). Consequently, an often-chosen management reaction is to mow the underwater vegetation. The removal of the nuisance submerged vegetation is expensive and diminishes the positive ecosystem functions of macrophytes, such as their habitat function for fishes (Thiemer et al., 2021). However, the “dis-services” of macrophytes, such as reduction of oxygen concentration or economic damage, typically occur in reaction to species introductions, eutrophication, or other ecosystem changes (possibly after re-oligotrophication) (Thomaz, 2021). Education and science communication about the reasons for those changes as well as the often-unknown positive ecosystem services seem to be highly necessary.

To summarise, environmental changes alter the physical and chemical environments of lakes in multiple, interacting ways. The concrete changes are hard to predict and can vary for different lakes. However, these changes will influence the eco-physiology of macrophytes and thus their growth, distribution, and species richness. The extent and the impact of these changes on macrophyte

biodiversity is unclear. To predict those possible future developments due to climate change and other environmental changes, we need process-based models incorporating the eco-physiological dependencies. A better understanding of the impact of environmental change on macrophyte biodiversity and better science communication can help to adapt management measures and to improve the conservation of freshwater ecosystems.

1.3 Modelling macrophytes

Models are simplified versions of reality from the perspective of a research question. They are built to obtain an understanding of processes, to make predictions and management recommendations, and to communicate possible future scenarios to society. In general, we can distinguish between two main types of models: statistical models and process-based dynamic models. Statistical models (including species distribution models) mainly describe correlations; thus, predictions beyond the integrated conditions are extrapolations and have to be understood as hypotheses (Lee-Yaw et al., 2021; Zurell et al., 2016). Process-based models incorporate mechanisms. Therefore, they are appropriate to predict temporal developments of complex systems beyond the conditions already observed. These models are also useful to find mechanistic explanations for macroecological patterns, especially under multiple interacting stressors, and are a theoretical framework for understanding mechanisms (Cabral et al., 2017; Van Nes & Scheffer, 2005).

Correlative models are used to analyse today's main environmental drivers of the species distribution via statistical methods. For example, by applying Generalised Additive Models (GAMs), hypotheses about future distribution can be drawn from knowledge about changes of the main influencing drivers. This method is applied e.g. to boreal catchments and emergent aquatic macrophytes (Alahuhta et al., 2011). With species distribution models (SDMs), which are also correlative models, multiple environmental variables are used to model the distribution of species. For example, SDMs were used e.g. to model the distribution patterns of charophyte in Switzerland (Auderset Joye & Rey-Boissezon, 2015), of macroalgae species in oceans (Martinez et al., 2015), of vascular macrophytes in rivers (Júnior et al., 2021), or of vascular macrophytes in wetlands (Murray-Hudson et al., 2019). Climate variables were not sufficient to model the distribution of Characeae in the Northwest USA; water chemistry variables were necessary as well (Sleith et al., 2018). Midwood et al. (2021) tested different correlative approaches. They found the best result by applying a random forest model. For aquatic plant communities in Japan, Kim & Nishihiro (2020) used a joint species distribution model (jSDM) to study the responses of function traits to global change. The weaknesses of correlative models are that they are based on correlations and that these correlations are based on current relationships, both of which limit their ability to predict future scenarios (Cabral et al., 2017; Dormann et al., 2012).

In light of these weaknesses, mechanistic models are a good alternative. Process-based growth models of submerged macrophytes have already a long tradition (D.-K. Kim et al., 2018). In Table 1.2, a small review is presented. Ikusima (1970) modelled the daily gross rate of photosynthesis dependent on depth dependent light intensity. Based on those photosynthesis functions, Scheffer et al. (1993) developed Megaplant, an eco-physiological model reproducing the growth of

submerged macrophytes during the seasonal cycle, implementing processes such as grazing, overwintering strategies, wave disturbances or seed dispersal. More detailed and also including more competing species is Charisma 2.0 (van Nes et al., 2003). It was for example used to show that alternative equilibria can be established due to positive feedback from macrophytes to the lake ecosystem and competition (van Nes et al., 2003). It was also used to answer lake management questions (van Nes et al., 2002). Charisma 2.0 was expanded to include clonal growth within the model Clomo (Wolfer et al., 2006), providing insights into the formation of patches. Other mechanistic “model families” focus more explicitly on nutrient dynamics (Asaeda & Van Bon, 1997), allelopathy (Mulderij et al., 2007), epiphyton and water level (C. Zhang et al., 2015), or on light limitation (Herb & Stefan, 2003, 2006) (see Table 1.2).

Several of these process-based models are designed to study competition between two functional types, such as submerged versus floating macrophytes (McCann, 2016), or several (2–5) species (Gao et al., 2017; van Nes et al., 2003). However, studies that mechanistically model species richness of macrophytes to explore future scenarios of species richness changes are not yet established. So far, most mechanistic models are limited to a few species, as they require detailed observations on the life cycle and processes of each species under consideration (Evans et al., 2016). Trait databases for a global, broad range of macrophytes are in development but not yet established (Dalla Vecchia et al., 2020; Iversen et al., 2022). Furthermore, optimization workflows to find parameters computationally are still very computationally demanding.

1.4 Study questions and structure of thesis

As suggested in “A Global Agenda for Advancing Freshwater Biodiversity Research” (Maasri et al., 2022), I “study the responses of biodiversity to multiple stressors and investigate ecological responses (...) to global change” (Maasri et al., 2022). To investigate the spatiotemporal dynamics of freshwater macrophytes in Bavarian lakes under environmental change (Figure 1.1), I first analyse existing data concerning patterns and drivers of macrophyte species richness between lakes (Chapter 2) and with depth (Chapter 3). To investigate the influence of possible future environmental scenarios including multiple stressors on species richness, I implement and use a mechanistic model (Chapter 4). The model also forms the basis for a computer game developed to make the interrelationships in lakes tangible in a way that is attractive for children (Chapter 5).

As a study region, I use the lakes within the Free State of Bavaria. Bavaria is the largest German state and is located in the south-east of the country. It ranges from the Alps in the south to the so-called “Mittelgebirge”, which include the Bavarian Forest and the Fichtelgebirge. Bavaria has a temperate climate. Two main river catchments shape the hydrology of Bavaria: Danube and Main. Bavaria provides an environmentally broad range of lakes. Most of the large lakes are carbonate-rich lakes of glacial origin and are located in the Alpine foothills. However, there are also large artificial lakes and a large number of small natural and artificial lakes.

Table 1.2: Review of process-based macrophyte models. A systematic search was done on Web of science (12.04.2022). The search terms were TITLE: ((macrophyte* OR "aquatic plant*") OR model*) AND TOPIC: ((macrophyte*) AND (model*)) AND TOPIC: (("simulation model" OR "ecophysiological processes" OR "ecological model" OR "growth model" OR "individual-based model" OR "numerical model" OR "mechanistic" OR "physiologic* model"). The search resulted in 110 publications. I excluded all publications (1) that do not fit to our study, e.g. with focus on salt water, wetlands or rivers, experimental studies, (2) where the subject was not the macrophyte itself (e.g. macrophyte presence included in a fish model, economic models, toxicity models, biogeochemical lake models), (3) with model applications, (4) with a detailed focus on photosynthesis instead of growth. Finally, 21 publications remained, which are listed in this table including model name (if available), model family (if it based on prev. model within list), main research topic, studied species, and growth form (GF). Abbreviations for growth forms are S (submerged), E (emergent) and F (floating-leaved). There are relevant models the search results did not include, and so this list is not comprehensive. (Table continues on next page.)

| Paper | Model name | Model family | Topic | Studied species (if explicitly defined) | GF |
|-------------------------|------------|----------------------------|--|--|------------|
| Duarte & Roff (1991) | | | Community structure | <i>Vallisneria americana</i> Michaux, <i>Potamogeton crispus</i> L., <i>Myriophyllum spicatum</i> L., <i>Elodea canadensis</i> Michaux, <i>Najas flexilis</i> (Willd.) Rostk. & W. L. E. Schmidt, <i>Potamogeton robbinsii</i> Oakes, <i>Heteranthera dubia</i> (Jacq.) MacMill., <i>Potamogeton praelongus</i> Wulfen, <i>Potamogeton gramineus</i> L. | S, F, E |
| Scheffer et al. (1993) | Megaplant | | Growth during the seasonal cycle | <i>Potamogeton pectinatus</i> L. | S |
| Van Dijk & Janse (1993) | Flora | Megaplant / SAGA1 | Resource allocation | <i>Potamogeton pectinatus</i> L. | S |
| Asaeda & Van Bon (1997) | | Megaplant / SAGA1 | Effects of macrophytes on algae and eutrophication | <i>Potamogeton pectinatus</i> L. | S |
| Hootsmans (1999) | SAGA | | Weed management | <i>Potamogeton pectinatus</i> L. | S |
| Asaeda et al. (2000) | | Asaeda & Van Bon (1997) | Life cycle and decomposition | <i>Potamogeton pectinatus</i> L. | S |

| Paper | Model name | Model family | Topic | Studied species (if explicitly defined) | GF |
|------------------------|--------------|----------------------------|--|---|------|
| van Nes et al. (2003) | Charisma 2.0 | Megaplant | Competition | <i>Chara aspera</i> Willd., <i>Potamogeton pectinatus</i> L. | S |
| Herb & Stefan (2003) | | | Light regimes, growth | | S |
| Wolfer et al. (2006) | Clomo | Charisma 2.0 | Clonal expansion | <i>Potamogeton perfoliatus</i> L. | S |
| | | Herb & Stefan (2003) | Light limitation & competition | <i>Myriophyllum spicatum</i> L., <i>Elodea canadensis</i> Michaux | S |
| Mulderij et al. (2007) | | | Allelopathy with phytoplankton | <i>Chara</i> sp., <i>Stratiotes aloides</i> L. | S, F |
| Best & Boyd (2008) | VALLA | Megaplant / SAGA | Biomass formation | <i>Vallisneria americana</i> Michaux | S |
| Li et al. (2012) | | | Growth & competition: flow & transport | Nymphaeaceae | F |
| Eid et al. (2014) | | Asaeda & Van Bon (1997) | Interaction: above- and below-ground or- gans | <i>Potamogeton pectinatus</i> L. | S |
| Zhang et al. (2015) | M-SAVM | | Role of epiphyton and water level | <i>Potamogeton crispus</i> L. | S |
| Eid et al. (2016) | | | Interaction: shoots and roots | <i>Pistia stratiotes</i> L. | F |
| Hidding et al. (2016) | | SAGA | Herbivory | <i>Potamogeton pectinatus</i> L. | S |
| McCann (2016) | | | Alternative stable states | | S, F |
| Gao et al. (2017) | GBAEDM | | Select appropriate species for restoration | <i>Vallisneria spinulosa</i> S. Z. Yan, <i>Hydrilla verticillata</i> (L.f.) Royle, <i>Myriophyllum spicatum</i> L., <i>Potamogeton malaiianus</i> Miq. | S |
| Onandia et al. (2018) | | | Biogeochemistry | Lemnaceae | S, F |
| Janssen et al. (2019) | PCLake+ | | Phenology | | S |

The main part of this pseudo-cumulative thesis (Part II) consists of 4 chapters, each organised as manuscript. Chapters 2 and 5 have been published in a German version in the non-peer-reviewed journal *Mitteilungen der Fränkischen Geographischen Gesellschaft*. Chapter 3 has been published in the peer-reviewed journal *Ecology and Evolution*. Chapter 4 is currently published as preprint and in preparation for submission. To prevent duplication, the references of all chapters are clustered at the end of part III.

The study questions those chapters address are summarised in Figure 1.1. In Chapter 2, I study submerged and emergent macrophytes in natural and artificial lakes of Bavaria to obtain a general overview of the recent regional macrophyte species richness. I use data for macrophyte occurrence and environmental measurements that were collected by the Bavarian State Office for the Environment for environmental monitoring of large lakes since the year 2004. I analyse how many submerged and emergent macrophyte species are observed in the large lakes of Bavaria, divided into lakes of natural and artificial origin. For each lake, I select the most recent mapping. Furthermore, I determine the most and least widespread and abundant submerged and emergent species. To figure out the geographical and chemical-physical factors that influence the number of submerged and emergent macrophyte species in Bavaria, I use GAMs (Generalised Additive Models). This provides insights into the connections between the environment and biodiversity of the different functional species groups in Bavaria today. Based on that, I develop hypotheses about future developments of biodiversity under various climate and land-use scenarios.

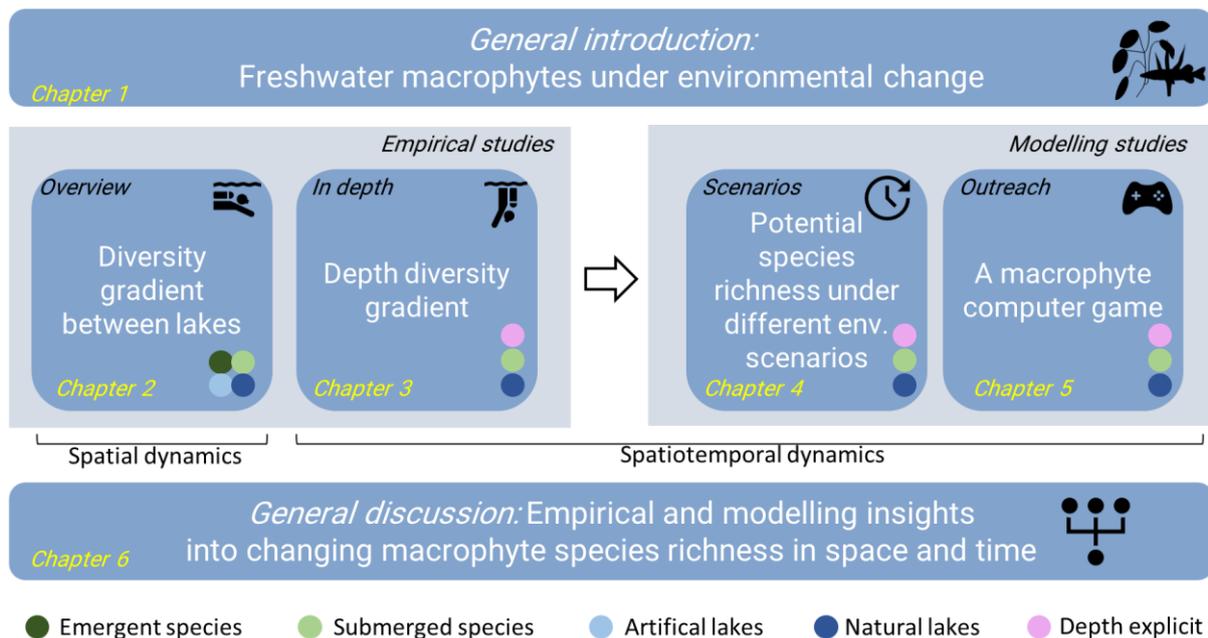


Figure 1.1: Overview of the structure of this thesis.

In Chapter 3, I take an in-depth look at the depth diversity gradient (DDG) of submerged macrophytes. Depth in freshwater lakes build a strong environmental gradient. I use the same data set as in Chapter 2 but select only deep, natural lakes to obtain a set of lakes that underlie the same environmental processes (e.g. management of artificial lakes such as reservoirs result in strong disturbances such as extreme water level fluctuations). I determine the shape of the DDG for different

diversity components (alpha, beta, gamma richness). On that basis, I examine the geographical and chemical-physical drivers of the DDG. For several lakes within the dataset, multiple monitoring campaigns between 2004 and 2017 are available. I use these repetitions to study if there is a temporal trend of the DDG. One aim of this is to highlight the potential of studying short-scale gradients in macroecological research of macrophytes.

In Chapter 4, I use a process-based macrophyte growth model to study potential changes in the future spatial distribution of submerged macrophyte species richness between lakes and with depth. I study fictional species defined by random species trait combinations within expert-derived trait ranges for oligotraphentic, mesotraphentic, and eutraphentic species groups in the same large lakes of Bavaria that are investigated in Chapters 2 and 3. I analyse if the resulting potential species richness distribution of the surviving modelled species follows the same patterns as the realised species distribution. To that end, I categorise the lakes into different lake types of clear, intermediate, and turbid lakes to evaluate the differences of the potential species richness between lake types. As a second step, I simulate the resulting potential species pool within scenarios of environmental change: temperature increase and water quality change (increase or decrease in both nutrients and turbidity). By comparing the resulting species number per lake and depth with the base scenario, I can identify in which scenarios species richness might increase or decrease. In addition, I classify the species within a scenario into “winner” and “loser” species depending on their change of habitat, and I analyse if the change depends on the species’ eco-physiological traits. This approach allows me to test mechanistically the future potential species richness of submerged macrophytes.

In Chapter 5, I focus on the image problem of macrophytes. Conflicts of use and lack of knowledge seem to be the reasons for why macrophytes are perceived as a nuisance. One reason why it is difficult to clarify the significance is the difficult accessibility and visibility of the species group under the water surface. Nowadays, computer games are one way to make places that are difficult to reach accessible. Therefore, I present a computer game for kids based on the eco-physiological growth model used in Chapter 4. The aim of the game is to educate about lake ecosystems while making their underwater world experienceable and intractable.

In part III, I discuss the implications of my findings to (1) ecological theory, (2) conservation practices, and (3) modelling approaches. Finally, I provide (4) perspectives for future research and end with (5) a short conclusion.

Part II

Study questions of the thesis



Chapter 2

Distribution of submerged and emergent macrophyte species richness in Bavaria's natural and artificial lakes

This chapter has been published in a modified German version (non-peer-reviewed):

Lewerentz, A. & Cabral, J. S. (2021). Wasserpflanzen in Bayern: Der Blick auf den See verrät nicht, was unter der Oberfläche passiert. *Mitteilungen der Fränkischen Geographischen Gesellschaft*, 67, 19-28.

Abstract:

The diversity of aquatic macrophytes remains visually hidden beneath the lake surface. Yet they have a major impact on lakes per se, as macrophytes fulfil many functions in the lake ecosystem like binding nutrients or providing habitat for other species. To obtain a general overview about their species richness, we ask in this study: How many different submerged and emergent macrophyte species grow in Bavarian lakes? Which species are the most common, which are the most abundant? How can this distribution of species richness be explained? We analyse data from the Bavarian State Office for the Environment on the occurrence of macrophytes and associated chemical-physical measurements. We use maps to show the distribution of biodiversity. Species frequencies are shown as rank-occurrence and rank-abundance curves. Influencing factors are analysed with Generalised additive models (GAMs). 71 submerged and 35 emergent species were found in the 41 lakes. We found a species count between one and 38 species per lake (mean = 17.0, $SD = 8.3$). The most widespread emergent species is reed (*Phragmites australis*) and the most widespread submerged one is *Chara contraria*. The distribution of the submerged species numbers is explained by the size of the lake and the phosphorus content, the distribution of the emergent types by the content of Cl^- , SiO_2^- , NO_3^- , NH_4^+ , O_2 , and conductivity. As these environmental factors are expected to shift due to climate and land-use changes, we use the results to develop expectations to estimate the effects of these changes on the diversity of macrophytes. These expectations can be tested in follow-up studies with the help of eco-physiological growth models.

2.1 Introduction

Freshwater lakes provide habitat for a part of the native species that often receives little public attention because it is predominantly hidden beneath the water surface. Macrophytes, aquatic photosynthetic and macroscopic organisms, are key species of lake ecosystems. They stabilise the sediment at the bottom, contribute to nutrient cycling and to primary production in lakes, and provide a food base as well as habitat for many lake animals (Jeppesen et al., 2012). At the same time, macrophytes are endangered. Land-use change in the catchment, changes in the water regime, climate change, anthropogenic eutrophication, and invasive species are altering lakes and, as a consequence, the habitat of macrophytes (Hossain et al., 2017; Lind et al., 2022).

Globally, 3457 vascular macrophyte species are known to grow in rivers, lakes, and wetlands (K. Murphy et al., 2019). In Europe, 393 vascular macrophyte species are recorded (Bilz et al., 2011). Within them, 6.6% are considered as threatened with extinction according to IUCN (Bilz et al., 2011). In Germany, 244 vascular macrophyte species can be found (Bilz et al., 2011) and additionally 36 non-vascular Charophyte species (Becker et al., 2016). Macrophytes can be divided into different functional groups of submerged and emergent species: Submerged species assimilate exclusively under water and can be rooted or free-floating. Emergent species are generally species having most of their parts (stem, leaves, flowers) above the water, but are adapted to have their roots in water-saturated soil. In the following, however, all species that assimilate carbon above water, e.g. float freely on the surface, or that have floating leaves are additionally counted as emergent species (Figure 2.1). Emergent species use carbon dioxide from the atmosphere and are not subject to the light reducing effects of water while the resource availability for submerged species depend on the water quality. Hence, the different functional groups react differently to changing environments (Alahuhta et al., 2014). For Bavaria, which is a German state with a high number of lakes and rich in lake types (Buchner, 1995), there is hitherto no overview of where most (emergent and submerged) macrophytes occur, which are the most common or rare species, and what are the drivers of the diversity distribution across lakes.

The distribution of species richness is associated with a variety of geographical factors and ecological gradients. The species-area relationship describes that more species occur in larger areas, as the diversity of habitats is also greater in larger areas (Connor & McCoy, 1979). Another influencing factor is water quality, which affects the light availability of submerged species in addition to nutrient availability (Bornette & Puijalón, 2011). The literature provides contradictory results regarding the main factors influencing macrophyte species diversity for different regions. For example, within 454 lakes in Minnesota (USA) pH and phosphorus are the main factors influencing species richness of both submerged and emergent species (Alahuhta, 2015). In another study, in boreal lakes, the main influencing factors on submerged and emergent species richness each were divergent: emergent species richness depended mainly on conductivity while submerged species richness depends mainly on alkalinity and turbidity (Alahuhta et al., 2014). Since the exact context seems to be particularly important in freshwater ecosystems, it remains unclear which environmental gradients shape species diversity in Bavarian lakes. However, knowing these is crucial for developing hypotheses for possible future scenarios.

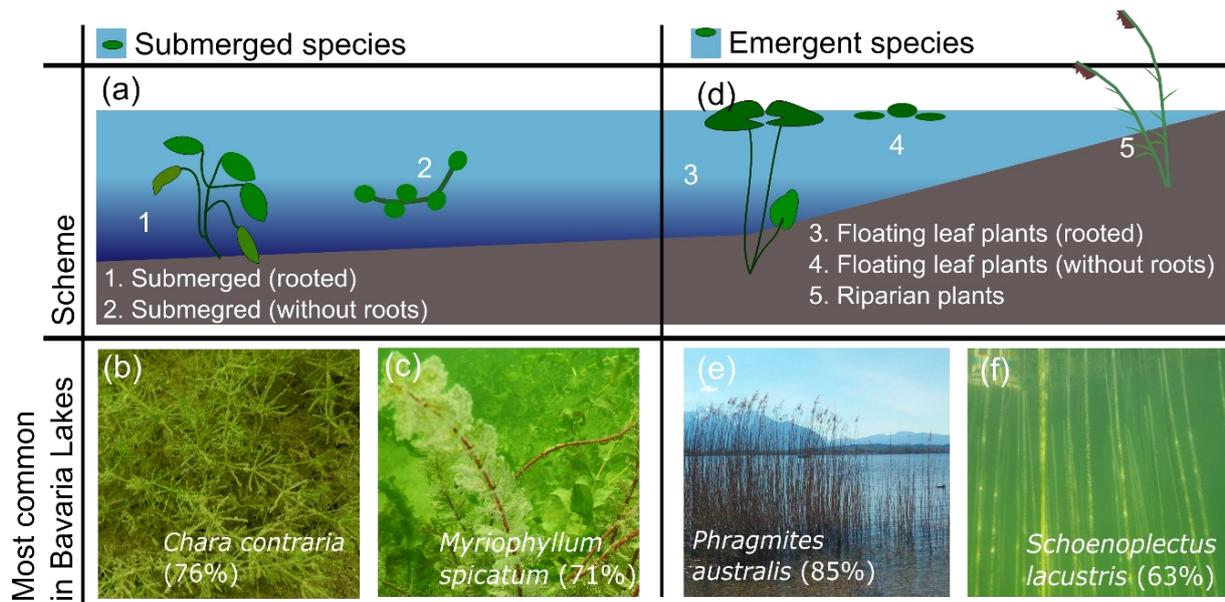


Figure 2.1: Differentiation in submerged (a) and emergent macrophytes (d). Submerged macrophytes refer to completely submerged species (1) with roots or (2) without roots. In the following, emergent macrophytes are (5) true emergent species, (4) free-floating species and (3) species with floating leaves. Photos of the most common submerged (b, c) and emergent species (e, f) are shown as examples: *Chara contraria* (b), *Myriophyllum spicatum* (c), *Phragmites australis* (e), and *Schoenoplectus lacustris* (f). The proportion of the lakes in Bavaria in which the species occurs is given in brackets. (Photo in b: Limnological Station Iffeldorf, TU Munich).

Bavaria's Landscape is dominated by lakes distributed along different elevations, land uses, and latitude. More than 1100 individual lakes are recorded (Buchner, 1995). Their sizes range from small lakes up to some of Germany's biggest lakes like Chiemsee (79.9 km²) or Lake Starnberger (58.4 km²). Lakes can be categorised by their origin in "natural lakes", e.g. formed after glaciation, and man-made lakes (in the following called "artificial lakes"), e.g. as a result of damming of rivers. Both lake types provide multiple ecosystem services like food supply (fish), drinking water supply, or recreation, but artificial lakes are mostly designed to fulfil additional services. These additional services include e.g. reservoirs that can be designed for energy production, storage of freshwater, or flood control (Cantonati et al., 2020). However, these usages can have several impacts on the lake dynamics depending on the management and the purpose of that lake. For example, reservoirs are often characterised by high water-level fluctuations, eutrophication, floods, intensive fishery, recreation use, and a high rate of invasive species (Cantonati et al., 2020) compared to natural lakes. Still, these artificial lakes provide additional habitat for freshwater species. However, the dynamics pose special challenges for macrophyte species richness, especially on rooted macrophytes (Krolová et al., 2013; Rørslett, 1989).

To obtain a basic overview of the species diversity of macrophytes in Bavarian lakes, we ask the following questions:

1. (1.1) How many macrophyte species grow in the large lakes of Bavaria? (1.2) How many of these are emergent and submerged species? (1.3) Is there a difference in species richness between natural and artificial lakes?

2. What are the most and least widespread and abundant submerged and emergent species?
3. Which geographical and chemical-physical factors influence the number of emergent and submerged species in Bavaria?

To address these questions, we use macrophyte mappings for monitoring in relation to the European Water Framework Directive. We expect a broad range of species, with a higher richness of submerged species than emergent species and higher values in natural than in artificial lakes (questions 1.1 – 1.3). We assume that *Phragmites australis* is the most widespread emergent species (Vymazal, 2013) while we have no literature based hypothesis for the most widespread submerged species (question 2). To answer question 3, we test whether the species richness of submerged and emergent macrophytes can be explained by geographic and physical–chemical characteristics of the lakes. We suppose that the main influencing factor is phosphorous content since it is the main growth limiting factor for macrophytes (Bornette & Puijalon, 2011).

Based on the findings, we develop expectations for possible future scenarios of macrophyte species diversity under climate and land-use change in Bavaria.

2.2 Material and Methods

The study is based on the surveys of the Bavarian State Office for the Environment (<https://www.gkd.bayern.de/>) for water monitoring within the European Water Framework Directive (WFD). Lakes with a minimum size of 50 ha are included in the monitoring scheme. In addition to basic chemical-physical parameters, various groups of organisms including macrophytes are examined as indicators of the water body's ecological status.

2.2.1 Abiotic data

From the monthly chemical-physical measurements at the deepest point of the lake, annual mean values for the surface measurements were calculated if measurements were available in at least eight months. The consistently available parameters are nitrate content (NO_3^-), silicon dioxide (SiO_2), total phosphorus content (P_{tot}), dissolved oxygen content (O_2), ammonium content (NH_4^+), pH value (pH), water temperature (*Temp*), conductivity (*Cond*), total nitrogen content (N_{tot}), chloride content (Cl), and water transparency (*Transp*).

Further considered lake parameters are surface area of the water body (area), the elevation of the gauge zero point (elevation), and the maximum depth of the lake (depth).

2.2.2 Biotic data

Macrophytes are mapped according to a standardised monitoring scheme (Schaumburg et al., 2015). Per lake, multiple representative transects are selected, and within four depth levels (0 – 1 m, 1 – 2 m, 2 – 4 m, > 4 m) the abundance of all present species is estimated using the Kohler (1978) five-point scale. For each lake, the total number of macrophyte species, as well as the number of submerged and emergent species, was calculated. If two growth forms of a species were present, they were considered separately. We excluded records that could not be determined down to the

exact species level. For further analyses, the most recent macrophyte mapping with a physico-chemical data set collected in the same year was selected for each lake. An overview of the biodiversity measures and environmental variables is given in Table 2.1.

Table 2.1: Median, mean, minimum and maximum values of biodiversity measures and geographical and physio-chemical variables in the 41 studied lakes.

| | Name | Short name / symbol | Unit | Me- dian | Mean | Min | Max |
|----------------------------------|---|------------------------------|---------------------|-------------|--------|--------|--------|
| Biodiversity measure | Number of submerged species | Submerged richness | n | 14.00 | 13.90 | 1.0 | 35.0 |
| | Number of emergent species | Emergent richness | n | 4.00 | 4.10 | 0.0 | 16.0 |
| Geograph- ical variables | Lake area | Area | ha | 194.00 | 722.90 | 55.0 | 7990.0 |
| | Maximal depth | Depth | m | 24.70 | 39.30 | 3.0 | 190.0 |
| | Terrain height of the gauge zero point | Altitude | m.a.s.l. | 588.00 | 605.00 | 374.0 | 885.0 |
| Physio- chemical variables | Chloride | Cl ⁻ | mg l ⁻¹ | 7.40 | 10.00 | 0.0 | 43.4 |
| | Conductivity (20 °C) | <i>Cond</i> | µS cm ⁻¹ | 312.50 | 312.00 | 111.2 | 513.9 |
| | Nitrogen, total | N _{tot} | mg l ⁻¹ | 0.67 | 1.10 | 0.2 | 4.8 |
| | Ammonium | NH ₄ ⁺ | mg l ⁻¹ | 0.03 | 0.04 | 0.0 | 0.2 |
| | Nitrate | NO ₃ ⁻ | mg l ⁻¹ | 0.27 | 0.70 | 0.0 | 4.4 |
| | Dissolved dioxygen | O ₂ | mg l ⁻¹ | 10.30 | 10.10 | 8.0 | 11.6 |
| | Phosphorous, total | P _{tot} | mg l ⁻¹ | 0.01 | 0.02 | 0.0 | 0.1 |
| | pH | pH | - | 8.40 | 8.40 | 8.1 | 8.8 |
| | Silicon dioxide | SiO ₂ | mg l ⁻¹ | 1.87 | 2.60 | 0.0 | 18.4 |
| | Water temperature | <i>Temp</i> | °C | 14.64 | 14.64 | 10.8 | 18.4 |
| Water transparency | <i>Transp</i> | cm | 320.00 | 385.90 | 83.0 | 1007.5 | |

2.2.3 Data analysis

The entire data analysis was carried out in R version 3.5.3 (R Core Team, 2021) using the *tidyverse* environment (Wickham, 2017). To investigate species distributions, the occurrence (number of lakes in which a species is present) and abundances (frequencies) were considered. The abundances mapped according to Kohler (1978) were converted into quantities according to Melzer (1988). These were summed up for each transect and then averaged for each lake. Thereafter, rank-occurrence and rank-abundance curves were generated using the R package *BiodiversityR* (Kindt, 2022). For this purpose, the occurrence / abundance of the individual species is plotted against the rank of their occurrence / abundance (most common species rank 1, etc.). Species that only occur in one lake were classified as species of low abundance. If the total abundance of a species was < 5, it was considered a low abundance species. Generalised Additive Models (GAMs) – *mgcv package* (Wood, 2011) in R – were used to identify the factors influencing submerged and emergent species diversity. A GAM was chosen to enable the detection of expectable non-linear effects. All geographical and environmental parameters were log-transformed to improve normality and included

in the full model if they were statistically independent ($r < 0.7$; Dormann et al. 2013; cf. Figure 2.2). Correlations between environmental variables were plotted using the *corrplot* package (Wei & Simko, 2017). Starting from the full model, we manually selected the minimum best model by gradually removing the parameters with the highest p -values until all remaining parameters were significant ($p < 0.05$). The individual contribution of each parameter to the model was reported as the *drop contribution*, which is the decrease in *deviance explained* by the model when the respective parameter was excluded.

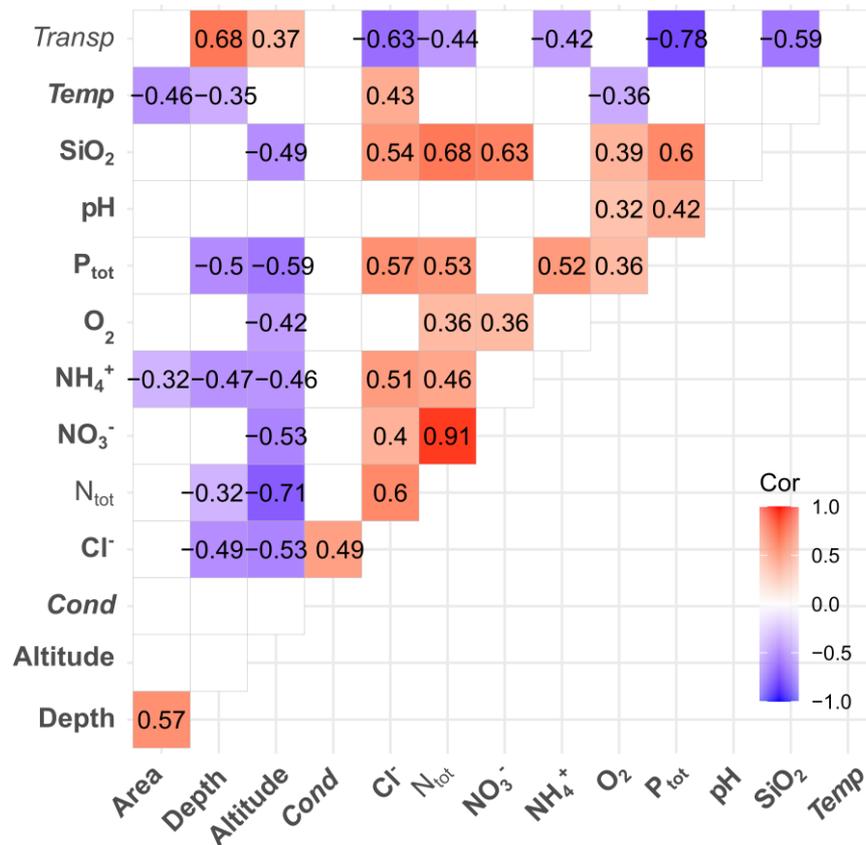


Figure 2.2: Correlations between the considered logarithmised environmental variables. Only significant correlations (including correlation coefficient) are shown. *Transp* and *N_{tot}* (not marked in bold) have been excluded from the GAM analysis because of their correlations > 0.7 . The variables considered for the full model are formatted in bold (see Table 2.1 for short names and symbols).

2.3 Results

Complete data sets were available for 41 lakes in Bavaria. While one lake is situated in northern Bavaria (Upper Franconia, Figure 2.3 a), 6 are located in the middle of Bavaria (Middle Franconia and Upper Palatinate, Figure 2.3 b), and 34 are situated in the pre-alpine and alpine regions of Bavaria (Swabia and Upper Bavaria, Figure 2.3 c). For each lake, only the most recent mapping was considered. The oldest mapping dates back to 2005 (Lake Langbürgner), the most recent mappings were in 2017 (Table 2.2).

2.3.1 Species richness

In the studied lakes, 71 submerged and 34 emergent species were found in the respective last years of monitoring. In total, 94 different macrophyte species are recorded. Within them, 4 species were Bryophytes, 18 were Charophytes, 3 were Pteridophytes, and 70 were Spermatophytes. The mean gamma richness per lake was 17.0 species ($SD = 8.3$). The mean gamma richness for emergent species was 4.1 ($SD = 3.0$) and for submerged species 13.9 ($SD = 7.7$).

Differentiating in artificial ($n = 10$) and natural lakes ($n = 31$) (locations in Figure 2.3), 49 species were observed in artificial and 82 species in natural lakes. Within the emergent species, 22 species were found in artificial lakes and 23 in natural lakes. 29 submerged species are recorded for artificial and 67 submerged species in natural lakes. The mean gamma richness in natural lakes is 3.9 ($SD = 2.4$) for emergent and 15.7 ($SD = 7.4$) for submerged species. In artificial lakes, the mean gamma richness of emergent species is 4.8 ($SD = 4.4$) and of submerged species 8.4 ($SD = 6.3$).

The largest total number of species (Table 2.2) was found in the lake Chiemsee ($n = 38$), followed by Igelsbachsee ($n = 31$) and Lake Starnberg ($n = 31$), the lowest numbers of species were found in Lake Eixendorf ($n = 1$), Barmsee ($n = 5$), Altmühlsee ($n = 6$), and Untreusee ($n = 6$). With 35 (of 38) species, the largest number of submerged macrophytes was mapped in Chiemsee, followed by Lake Starnberg ($n = 27$) and Tegernsee ($n = 26$). With one species each, Lake Eixendorf and Altmühlsee were the least species rich in submerged species. The highest numbers of emergent species were found in Igelsbachsee ($n = 16$), Lake Pelham ($n = 10$), and Lake Langbuergen ($n = 9$). No emergent species were found in three lakes (Königssee, Obersee, Lake Eixendorf).

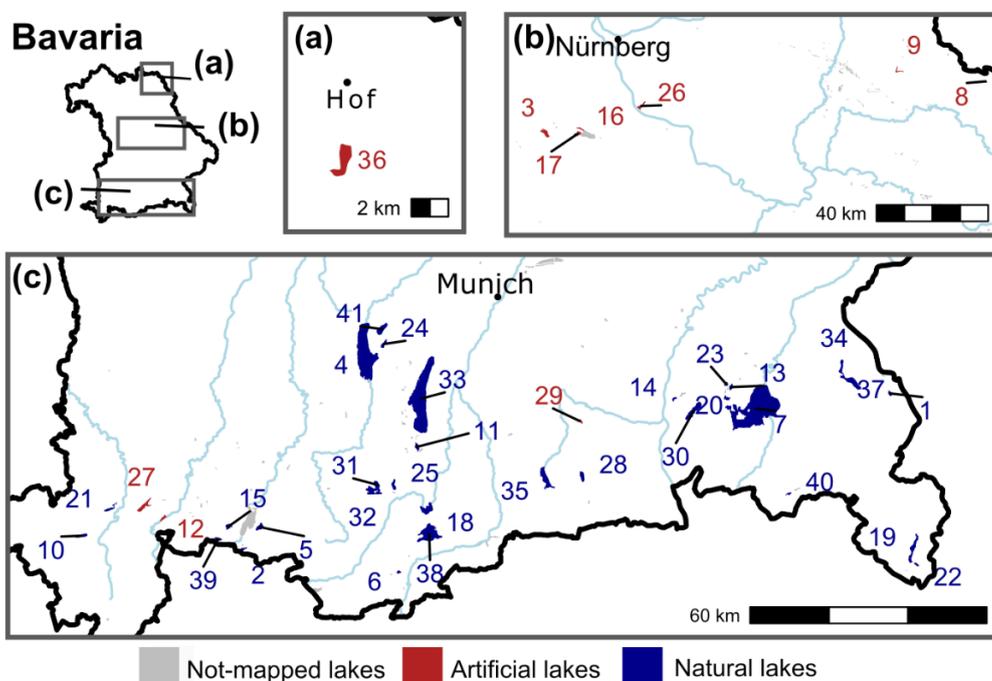


Figure 2.3: Lakes in Bavaria with complete data (red: artificial lakes; blue: natural lakes) and without any or incomplete data (grey). The lakes are located in the administrative districts of Upper Franconia (a), Middle Franconia and Upper Palatinate (b) and Swabia and Upper Bavaria (c). The respective label of the lake is an ID, which can be found in Table 2.2 showing further information about species numbers and the year of mapping.

Table 2.2: Number of submerged and emergent species and total number (Total) of species per lake. For the location of the lakes, see position of lake ID in Figure 2.3. Some species may occur in parallel as submerged and emergent forms, so the total number does not equal the sum of submerged and emergent species.

| ID | Lake name | Year | Submerged species | Emergent species | Total |
|----|----------------------|------|-------------------|------------------|-------|
| 1 | Lake Abtsdorf | 2017 | 6 | 3 | 8 |
| 2 | Alpsee | 2017 | 11 | 2 | 13 |
| 3 | Altmühlsee | 2017 | 1 | 5 | 6 |
| 4 | Ammersee | 2016 | 21 | 6 | 25 |
| 5 | Bannwaldsee | 2009 | 15 | 5 | 17 |
| 6 | Barmsee | 2015 | 3 | 2 | 5 |
| 7 | Chiemsee | 2016 | 35 | 5 | 38 |
| 8 | Drachensee | 2011 | 4 | 3 | 7 |
| 9 | Lake Eixendorf | 2010 | 1 | 0 | 1 |
| 10 | Grosser Alpsee | 2017 | 16 | 3 | 17 |
| 11 | Grosser Ostersee | 2017 | 8 | 4 | 11 |
| 12 | Grüntensee | 2017 | 9 | 3 | 12 |
| 13 | Hartsee | 2013 | 13 | 8 | 19 |
| 14 | Lake Hofstätt | 2008 | 2 | 6 | 8 |
| 15 | Hopfensee | 2016 | 17 | 3 | 19 |
| 16 | Igelsbachsee | 2015 | 15 | 16 | 31 |
| 17 | Kleiner Brombachsee | 2014 | 10 | 3 | 13 |
| 18 | Kochelsee | 2017 | 19 | 1 | 20 |
| 19 | Königsee | 2015 | 8 | 0 | 8 |
| 20 | Lake Langbürgner | 2005 | 19 | 9 | 27 |
| 21 | Lake Niedersonthofen | 2015 | 21 | 5 | 24 |
| 22 | Obersee | 2013 | 7 | 0 | 7 |
| 23 | Lake Pelham | 2016 | 14 | 10 | 22 |
| 24 | Pilsensee | 2012 | 19 | 3 | 20 |
| 25 | Riegsee | 2015 | 20 | 6 | 25 |
| 26 | Rothsee | 2015 | 18 | 2 | 19 |
| 27 | Rottachsee | 2015 | 15 | 8 | 23 |
| 28 | Schliersee | 2015 | 12 | 2 | 14 |
| 29 | Lake Seeham | 2017 | 9 | 4 | 13 |
| 30 | Simssee | 2015 | 16 | 4 | 18 |
| 31 | Staffelsee – North | 2016 | 24 | 4 | 26 |
| 32 | Staffelsee – South | 2016 | 24 | 5 | 27 |
| 33 | Lake Starnberg | 2017 | 27 | 4 | 30 |
| 34 | Lake Taching | 2012 | 17 | 4 | 18 |
| 35 | Tegernsee | 2017 | 26 | 4 | 27 |
| 36 | Untreusee | 2016 | 2 | 4 | 6 |
| 37 | Lake Waging | 2016 | 13 | 2 | 13 |
| 38 | Walchensee | 2014 | 11 | 1 | 11 |
| 39 | Weißensee | 2016 | 20 | 4 | 22 |
| 40 | Weitsee | 2011 | 10 | 2 | 11 |
| 41 | Wörthsee | 2017 | 13 | 5 | 18 |

2.3.2 Species frequency

The most widespread submerged species were *Chara contraria* (in 31 lakes $\hat{=}$ 76% of lakes), *Myriophyllum spicatum* (in 29 lakes – 71% of lakes), and *Potamogeton pectinatus* (in 28 lakes $\hat{=}$ 68% of lakes) (Figure 2.4 a). The most widespread emergent species recorded were *Phragmites australis* (in 35 lakes $\hat{=}$ 85%), *Schoenoplectus lacustris* (in 20 lakes $\hat{=}$ 49%), and *Nuphar lutea* (in 20 lakes – 49%) (Figure 2.4 b). In total, there are 8 submerged species (11% of all submerged species) and 3 emergent species (9% of all emergent species) occurring in at least half of all lakes. 23 submerged species (32%) and 14 emergent species (41%) occur in only one lake.

Among the submerged species, however, other species are more numerous, such as *Najas marina ssp. intermedia*, *Chara aspera*, and *Myriophyllum spicatum* (Figure 2.4 c). Among the emergent species, the most widespread species also correspond to the most common (Figure 2.4 d). In this context, 25% of the submerged species have a total abundance < 5 (18 species), while this applies to 53% of the emergent species (18 species).

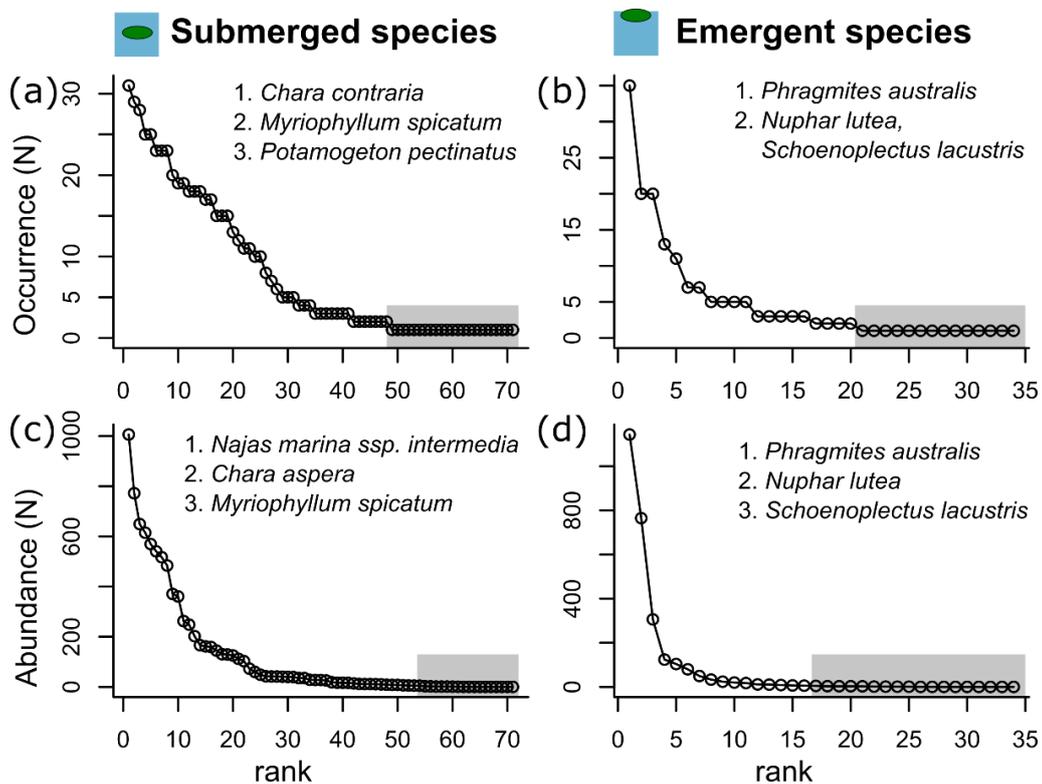


Figure 2.4: Distribution of occurrence (Panels a and b) and average abundance (Panels c and d) of submerged (Panels a and c) and emergent species (Panels b and d), sorted along the x-axis by rank of occurrence or abundance. In each case, the names of the most abundant three species are indicated. Individual average abundances were summed per transect and then averaged per lake. Rarely occurring species (in 1 lake) and with low abundance (< 10) are shaded grey.

Out of the emergent species, a number of 12 are both low abundant and low distributed (Table 2.3). This also applies to 15 of the submerged species. None of the species is threatened according

to the European IUCN red-list (Bilz et al., 2011). Two invasive species are listed: *Elodea nuttallii* and *Elodea canadensis*.

Table 2.3: Rare species, both low abundance and low distribution, divided into emergent and submerged species including note on distribution.

| Growth form | Low abundant and low common species | Comment | |
|--|-------------------------------------|-----------------------------------|--|
| Emergent species | <i>Juncus articulatus</i> | Marsh plant | |
| | <i>Filipendula ulmaria</i> | Alluvial / wetland species | |
| | <i>Menyanthes trifoliata</i> | Alluvial / wetland species | |
| | <i>Myosotis scorpioides</i> | Marsh plant | |
| | <i>Equisetum fluviatile</i> | | |
| | <i>Scutellaria galericulata</i> | Alluvial / wetland species | |
| | <i>Typha angustifolia</i> | Marsh plant | |
| | <i>Alisma plantago-aquatica</i> | Marsh plant | |
| | <i>Cicuta virosa</i> | | |
| | <i>Equisetum palustre</i> | Alluvial / wetland species | |
| | <i>Juncus inflexus</i> | Alluvial / wetland species | |
| | <i>Spirodela polyrhiza</i> | | |
| | Submerged species | <i>Chara delicatula</i> | |
| | | <i>Potamogeton × salicifolius</i> | |
| <i>Leptodictyum riparium</i> | | | |
| <i>Potamogeton natans</i> | | | |
| <i>Juncus articulatus</i> | | Marsh plant | |
| <i>Alisma plantago-aquatica</i> | | Marsh plant | |
| <i>Utricularia vulgaris</i> | | | |
| <i>Ranunculus reptans</i> | | | |
| <i>Octodicerus fontanum</i> | | | |
| <i>Potamogeton × cooperi</i> | | | |
| <i>Ranunculus × glueckii</i> | | | |
| <i>Najas marina</i> ssp. <i>marina</i> | | | |
| <i>Nymphaea alba</i> | | emergent species, here submerged | |
| <i>Solanum dulcamara</i> | | Alluvial / wetland species | |
| <i>Sagittaria sagittifolia</i> | emergent species, here submerged | | |

2.3.3 Drivers

The correlations within the influencing factors are shown in Figure 2.2. The drivers *Transp* and N_{tot} were excluded from further analysis because of their high correlation with P_{tot} and NO_3^- .

The best minimal model of the General Additive Model (GAM) shows significant correlations between species diversity and the environmental variables. The goodness of fit for the submerged species diversity model is 75.6%, while the emergent species diversity model reaches 69% (Table 2.4).

The distribution of submerged species diversity is explained by lake area and phosphorus content (Figure 2.5 a, b). The larger the area of the lake, the greater is the submerged diversity; the higher the phosphorus content, the lower is the diversity. Cl^- content has the greatest influence on emergent species diversity, followed by SiO_2 , NO_3^- , NH_4^+ , O_2 , and conductivity (Figure 2.5 c – h). There are different directions of influence: An increased Cl^- content favours species diversity, an increased

SiO₂ content reduces it and an increasing NO₃⁻ content initially shows a slightly positive influence on emergent species richness, but at higher values a negative one.

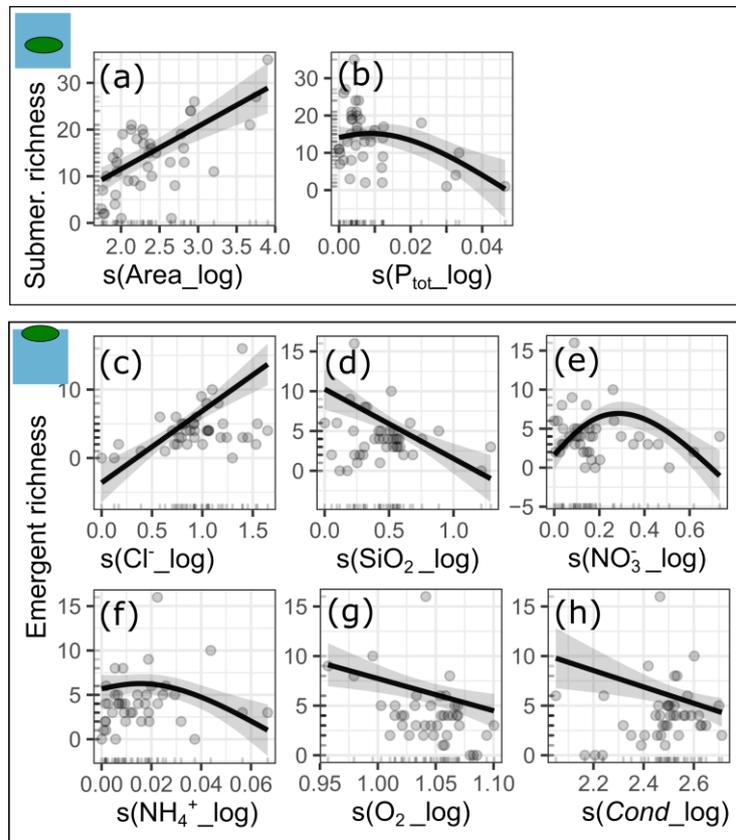


Figure 2.5: Significant factors influencing species diversity in Bavarian lakes for submerged (Panels a and b) and emergent species (Panels c – h) as a result of a GAM including standard-error curves (grey). Influencing factors are log-transformed. (See Table 2.1 for abbreviations and units).

Table 2.4: Results of the best minimal model of GAM analysis of environmental factors and biodiversity measures (see Table 2.1 for abbreviations and units). The relative contribution of each parameter to the model (% drop contribution) is the respective drop in deviance explained when the respective parameter is removed from the model. Significance ratios: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

| | Submerged species richness | | | Emergent species richness | | |
|--------------------------------|----------------------------|-------------------------|--|------------------------------|-------------------------|--|
| R ² (adj) (%) | 70.2 | | | 61.5 | | |
| Deviance explained (%) | 75.6 | | | 69 | | |
| Estimate | 13.93 | | | 4.146 | | |
| Std. deviation | 0.82 | | | 0.287 | | |
| Selected variables | Area | (57.4 8.36e-07 ***) | | Cl ⁻ | (32.7 4.28e-07 ***) | |
| (% drop contribution p value | P _{tot} | (33.3 0.0079 **) | | SiO ₂ | (19.6 0.0001 ***) | |
| Significance) | | | | NO ₃ ⁻ | (19.1 0.0007 ***) | |
| | | | | NH ₄ ⁺ | (10.8 0.0147 *) | |
| | | | | O ₂ | (6.8 0.008 **) | |
| | | | | Cond | (3.8 0.0095 **) | |

2.4 Discussion

2.4.1 Macrophytes in Bavaria: Distribution and drivers of species richness

Due to the large number of lakes, a wide range of geographical gradients as well as a high variability of chemical-physical environmental variables, Bavaria is an interesting study area with a big diversity of lakes. To manage lakes sustainably under future climate and land-use change, preserving macrophytes biodiversity, as well as having knowledge of the status quo and the regional influencing factors is crucial. The monitoring of Bavarian lakes for the EU-Water Framework Directive provides a valuable data set for studying macrophyte species richness.

2.4.1.1 Macrophyte species richness in Bavaria (Q1 and Q2)

Overall, with 94 species in the large lakes of Bavaria, the macrophytes represent a very species-rich group that rarely receives public attention (question 1.1). Hence, the studied lakes host around 2.1% of all globally known vascular macrophytes (K. Murphy et al., 2019), around 30% of all vascular macrophytes within Germany (Bilz et al., 2011) and 50% of all present Charophytes in Germany (Becker et al., 2016). Although all the natural lakes studied are located in Upper Bavaria and Swabia, almost all administrative districts are represented by artificial lakes in Middle Franconia, Upper Franconia, and the Upper Palatinate (Figure 2.3). The artificial lakes in Central Franconia also include species-rich waters such as the lake Igelsbachsee (Table 2.2). Overall, more submerged (71) than emergent (34) species were mapped (question 1.2).

Artificial lakes host a slightly higher mean species richness of emergent macrophytes (4.8) than natural lakes (3.9) (question 1.3). For submerged species we find an opposite pattern. In artificial lakes the mean species richness is clearly lower (8.4) than in natural lakes (15.7). One reason for the differences might be the different locations of the lakes. While all of the natural lakes are situated in the lower intensively used and higher situated alpine and pre-alpine region of Bavaria, most of the artificial lakes can be found in the lower central and northern parts. Besides that, the management of the artificial lakes could play a role. The frequency and intensity of artificial water level fluctuations in reservoirs puts pressure on rooted macrophytes. With changing water level, the habitat shifts as a change in depth subsequently causes a change in light availability.

As expected, the most widespread emergent species is *Phragmites australis* (question 2). The most widespread submerged species is *Chara contraria*. In general, more submerged species had a wider distribution than emergent species within the Bavarian lakes (Figure 2.4). Emergent species showed a higher share of rare species (Figure 2.4). It should be noted that a large proportion of the emergent species, the marsh plants, only form a marginal occurrence at the water's edge in the transition area from the aquatic to the terrestrial ecosystem and can also be found in other wet areas besides lakes, such as bogs or wet meadows.

2.4.1.2 Drivers of macrophyte species richness (Q3)

The distribution of the two species groups is influenced by various factors. Decreasing phosphorus content and increasing lake area explain the diversity of submerged macrophytes (Figure 2.5). On the one hand, this reflects the species-area relationship that is already shown for macrophytes in several studies (Alahuhta et al., 2014, 2020). On the other hand, increasing phosphorus content

seems to reduce the number of species due to its negative effect on light availability (see negative correlation in Figure 2.2) through increased phytoplankton. In comparison, the drivers for species richness of submerged macrophytes are similar to those within boreal catchments (Alahuhta et al., 2014). The absence of a species-area relationship for emergent diversity can be explained by the fact that, in principle, more species can be expected with a larger area, but here an opposite effect cancels out the relationship: It can be assumed that emergent species in smaller lakes offer an advantage due to lower water level fluctuations and less wave action, which counteracts the species-area relationship here. In addition, the habitats of emergent species overlap with terrestrial species, whereby the number of species is influenced by other habitats. Instead of a species-area relationship, the concentration of Cl^- , followed by SiO_2^+ and NO_3^- content, has the greatest influence on the distribution of emergent species. All three factors correlate positively with each other (0.4 – 0.63) as well as with the other nutrient factors. An increased chloride content, which mostly originates from pollution such as road salt or sewage treatment plants, apparently favours emergent species richness. In Alahuhta et al. (2014) conductivity (positively correlated with chloride content, Figure 2.2) was one of the main drivers of emergent species richness. Increased SiO_2 content, which depends among other things on the regional geology of the catchment, reduces it. An increasing nutrient content (NO_3^- and NH_4^+) initially shows a positive influence, but at higher values a negative one, which corresponds to the mid-domain hypothesis (Colwell & Lees, 2000). The high influence of chloride content on emergent diversity could be due to the fact that a missing reed belt (*Phragmites australis*) can lead to a higher emergent diversity as well as to increased inputs of chemical loads into lakes due to the missing buffer effect. This is reflected in the shown land-use effect on emergent species richness (Alahuhta et al., 2014).

The difference between the factors influencing submerged and emergent species richness shows that both species groups have to be studied: Another factor that may influence species diversity and still need to be investigated are, for example, water level fluctuations. The results confirm the main findings of boreal lakes for temperate lakes (Alahuhta et al., 2014). Still, the mechanisms are not fully understood. However, lakes provide another dimension – depth – whose influence on species richness is less intensively studied (Bolpagni et al., 2016; Fu et al., 2015; Fu, Zhong, Yuan, Ni, et al., 2014; Fu, Zhong, Yuan, Xie, et al., 2014; Ye et al., 2018). An in-depth look at the diversity gradient of species richness with depth could provide further insights as multiple chemical-physical lake properties are depth dependent.

This overview provides an important characterisation of the species diversity in Bavaria's large lakes. In the future, it would be desirable to extend this study to small water bodies, as they react even more extreme to temperature increases (Winslow et al., 2015).

2.4.2 Look into the future: Expectations for climate and land-use change scenarios

Climate change alters the chemical-physical characteristics of water bodies, which – as our results show – have a direct and indirect impact on vegetation (Lind et al., 2022). In parallel, land-use change can also influence the chemical-physical parameters of lakes. Based on the results of this study and literature, we formulate expectations of the potential consequences for submerged species richness (Figure 2.6).

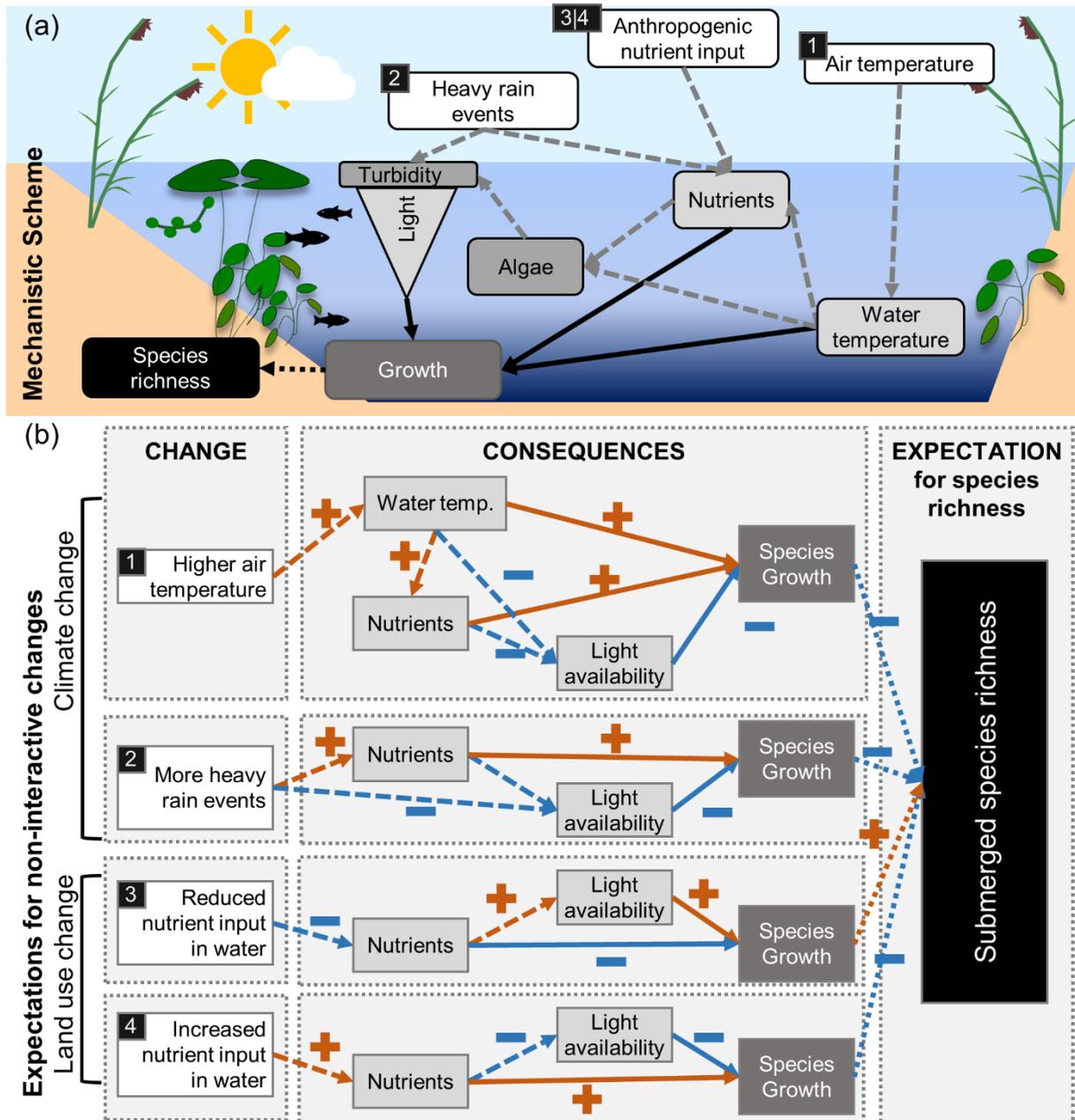


Figure 2.6: Mechanistic scheme for the dynamics of submerged macrophyte species diversity (Panel a). Expectations established for submerged species, each consisting of changes, consequences, and expectation (Panel b): 1: higher air temperatures result in higher water temperature and a direct effect of better growth and indirect effects of more nutrient availability and decreased light availability might in sum lead to decreased submerged species richness; 2: increased nutrient availability and decreased light availability due to more heavy rain events with high erosion activity could result in a decreased species growth; 3: reduced nutrient input in water by changes in land use would result in better growth and increased species richness; 4: increased nutrient input in water by changed land use would result in lower growth and decreased species richness. Numbers in A refer to the respective expectation in B. Solid lines indicate direct effects on growth, dashed lines indicate indirect effects on growth, pointed lines show effects of changed growth on species richness. The sign “+” (red colour) shows increases and “-” (blue colour) shows decreases.

For Bavaria, an increase in surface water temperature of 2.0 – 3.0 °C in large lakes and 0.8 – 1.3 °C in alpine lakes is expected by 2100 (Werner & Hesselschwerdt, 2015). In general, increased water temperature is beneficial for the metabolism and increases growth as long light is not

limited (Ersoy et al., 2020). However, previous research results indicate that the warming of lakes will lead to lower species diversity, especially of submerged species, as the growth of individual species is favoured, which could subsequently outcompete other species (Hossain et al., 2017). Furthermore, species adapted to cold water may become extinct, while species adapted to warm water may migrate. Besides that, it is predicted that emergent species will have an advantage and might outcompete submerged species (McCann, 2016). Warming waters may indirectly contribute to eutrophication. Anoxic conditions resulting from increased temperature may cause nutrients to be re-dissolved from the sediment, leading to poorer light conditions due to increased phytoplankton growth in spring (Nõges et al., 2010). This would reduce light availability and decrease growth, as also shown by the correlations between temperature and other factors (Figure 2.2). However, light availability is always also dependent on depth, so this might affect species in deeper water more than in shallow water. In summary, we would expect a decreased submerged species richness as a consequence of increased air temperatures (*Expectations 1* – Figure 2.6).

Furthermore, there is a risk that sediments and nutrients from the catchment could be introduced into water bodies during predicted more frequent heavy rainfall events (Müller et al., 2018) (*Expectation 2* – Figure 2.6). Our results show that increased phosphorus levels have a negative impact on the biodiversity of submerged species probably due to their indirect effects on light availability via enhanced algae growth. Therefore, as a result of our analysis of influencing factors, it can be expected that increased heavy rainfall events will lead to a lower species diversity of submerged macrophytes as they bring high nutrient levels in lakes through surface erosion. The direction of the impact of future land-use change on submerged species richness is unclear. For example, increased food demand could lead to an intensification of agricultural production including increased fertilisation. This could result in increased nutrient concentrations in lakes with effects on increased turbidity and decreased species growth (*Expectation 3* – Figure 2.6). On the other hand, political guidelines e.g. for wastewater treatment plants and sewage systems could decrease nutrient concentrations in lakes and generate the opposite effect (*Expectation 4* – Figure 2.6). However, all these hypotheses are considered here as single effects. In reality, climate change and land-use change happen at the same time. The complex interactions within the chemical-physical properties of lakes are hard to predict. Still, the direct effects of changed temperature, nutrient availability, and light on the growth of different macrophytes can be tested in mesocosm experiments and mechanistic macrophyte growth models.

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Further material – Processed data and code of data analysis are provided online as research compendium: https://github.com/AnneLew/LewerentzCabral_Macrophytes-Bavaria

Chapter 3

Depth diversity gradients of macrophytes: Shape, drivers, and recent shifts

This chapter has been published as:

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Abstract:

Investigating diversity gradients helps to understand biodiversity drivers and threats. However, one diversity gradient is rarely assessed, namely how plant species distribute along the depth gradient of lakes. Here, we provide the first comprehensive characterization of depth diversity gradient (DDG) of alpha, beta, and gamma species richness of submerged macrophytes across multiple lakes. We characterize the DDG for additive richness components (alpha, beta, gamma), assess environmental drivers, and address temporal change over recent years. We take advantage of yet the largest dataset of macrophyte occurrence along lake depth (274 depth transects across 28 deep lakes) as well as of physiochemical measurements (12 deep lakes from 2006 to 2017 across Bavaria), provided publicly online by the Bavarian State Office for the Environment. We found a high variability in DDG shapes across the study lakes. The DDGs for alpha and gamma richness are predominantly hump-shaped, while beta richness shows a decreasing DDG. Generalized additive mixed-effect models indicate that the depth of the maximum richness (D_{max}) is influenced by light quality, light quantity, and layering depth, whereas the respective maximum alpha richness within the depth gradient (R_{max}) is significantly influenced by lake area only. Most observed DDGs seem generally stable over recent years. However, for single lakes we found significant linear trends for R_{max} and D_{max} going into different directions. The observed hump-shaped DDGs agree with three competing hypotheses: the mid-domain effect, the mean–disturbance hypothesis, and the mean–productivity hypothesis. The DDG amplitude seems driven by lake area (thus following known species–area relationships), whereas skewness depends on physiochemical factors, mainly water transparency and layering depth. Our results provide insights for conservation strategies and for mechanistic frameworks to disentangle competing explanatory hypotheses for the DDG.

3.1 Introduction

Describing and explaining biodiversity gradients have been central goals of biogeography and ecology since the beginning of the respective fields (Gaston, 2000). Improving our understanding of the biodiversity gradients and their drivers is still an important requirement to deal with impending species loss. Therefore, many studies have explored environmental gradients as explanatory variables for biodiversity patterns along different geographic scales (Rahbek, 2004; Whittaker et al., 2007) such as (1) latitude (Stehli et al., 1969; Rohde, 1992; Pontarp et al., 2019; Etienne et al., 2019), (2) elevation (Colwell & Rangel, 2010; Graham et al., 2014; Hutchinson, 1953; Lomolino, 2001; Nogués-Bravo et al., 2008; Rahbek, 1995; Rahbek et al., 2019; Sanders & Rahbek, 2012), (3) tree height in forests (Petter et al., 2016), (4) depth in soils (Jakšová et al., 2019; Rendoš et al., 2016) or (5) depth in water (Gong et al., 2015; Rex & Etter, 1998; Smith & Brown, 2002). These geographical gradients share some environmental gradients, which are expected to influence spatial structuring of diversity gradients, e.g. temperature, light, or seasonality. However, the shorter spatiotemporal scales are, the less confounding biogeographical contingencies there are, such as the legacy of the glacial cycles on latitudinal gradients, and dispersal / connectivity limitations. Hence, studying gradients expressed at short spatiotemporal extents may provide valuable insights on drivers of biodiversity. Still, the short spatiotemporal gradients, like depth in freshwaters, are often overlooked.

Freshwater ecosystems have a high biodiversity with a high rate of species loss (Gatti, 2016; He et al., 2017; Strayer & Dudgeon, 2010), exceeding those of terrestrial systems (Dudgeon et al., 2006). Nonetheless, studies that focus on the short spatiotemporal diversity gradient in freshwater are surprisingly scarce, although light gradients in freshwater must represent a very strong driver. The few existing studies seem to show predominantly a general decrease of biodiversity along the depth gradient, e.g. for bacteria (Cantonati et al., 2014; Zhao et al., 2019), chironomids (Zhao et al., 2019) or diatoms (Kingsbury et al., 2012; Stoof-Leichsenring et al., 2020), or hump-shaped patterns along depth, e.g. for diatoms (Zhao et al., 2019) or submerged macrophytes (Ye et al., 2018). Macrophytes are, however, comparatively less studied.

Macrophytes play a pivotal role in lakes by reducing nutrient concentrations (Song et al., 2019), by providing food for a lot of other species (Bakker et al., 2016) and by giving shelter to a large number of other aquatic organisms like zooplankton, juvenile fish, and amphibians (Jeppesen et al., 1998). However, there are several knowledge gaps on macroecology of freshwater plants (Alahuhta et al., 2020). Some aspects of depth gradients in macrophytes can also be found in the literature, with previous studies mainly focus on depths limits of species (Domin et al., 2004; Middelboe & Markager, 1997; Søndergaard et al., 2013), growth of single species dependent on depth (Fu et al., 2018; Li et al., 2020; Xu et al., 2020), functional diversity along depth (Fu et al., 2017) or biomass of macrophytes along depths (Chambers & Kaiff, 1985; Collins et al., 1987). However, the depth pattern of submerged macrophyte species richness is sparsely studied (Bolpagni et al., 2016; Fu et al., 2015; Fu, Zhong, Yuan, Ni, et al., 2014; Fu, Zhong, Yuan, Xie, et al., 2014; Ye et al., 2018). The few studies that have looked at depth distribution of macrophytes in lakes mainly focussed on Lake Erhai in Yunnan Province, China. They report a hump-shaped pattern along the water depth gradient for species richness and community biomass of submerged macrophyte species (Ye et al.,

2018). Looking at all functional types including emergent species, Lake Erhai shows a significant decrease in taxonomic and functional diversity along the water depth gradient and its niche differentiation (Fu et al., 2015; Fu, Zhong, Yuan, Ni, et al., 2014; Fu, Zhong, Yuan, Xie, et al., 2014). Also, hump-shaped and decreasing patterns of species numbers along depth were found in four Italian lakes, changing patterns with time (Bolpagni et al., 2016). Still, it remains unclear if the described pattern of macrophytes is generalizable across multiple lakes and whether it stays robust over time.

The lack of macrophyte diversity gradient studies is intriguing because the environmental gradients along lake depth represent one of the sharpest found in nature, with strong variation over just few meters. With increasing lake depth, multiple abiotic factors that influence the growth of macrophytes (light, temperature, nutrients, water quality, disturbances / hydrologic variability) drastically change (Bornette & Puijalon, 2011). Light is gradually attenuated with increasing depth due to absorption and scattering, resulting in a specific reduction of light quality and quantity depending on depth and on the water turbidity. Water temperature in deep lakes does not decrease gradually, but rather abruptly with depth (Bornette & Puijalon, 2011). The formation of thermally stratified lakes results in an abrupt thermocline, especially during growing season. The thermocline influences the within-lake fluid dynamics in each thermal layer, further leading to stratified gradients in nutrients and water quality components during stratification (Bornette & Puijalon, 2011). Moreover, mechanical disturbances, like wind or waves, lose their influence gradually with depth (Van Zuidam & Peeters, 2015). The probability that water level fluctuations result in drying up the soil (Evtimova & Donohue, 2016) is also reduced, and browsing pressure by waterfowl decreases with depth (Bakker et al., 2016). How these different environmental gradients influence the species richness of macrophytes remains unclear, although knowing the processes shaping species diversity might help to predict how global change will affect biodiversity and how management strategies might mitigate potential negative diversity responses.

This study aims to describe the depth distribution of macrophyte diversity, to assess the relative importance of its drivers and to search for recent shifts. Specifically, we ask the following questions:

1. 1.1. What is the general shape of the depth diversity gradient (DDG) of submerged macrophytes in deep lakes?
 - 1.2. Are there differences between lakes and diversity components (alpha-, beta, gamma richness)?
2. What are the drivers for macrophyte DDG?
3. 3.1. Has the DDG been stable over recent years?
 - 3.2. Are temporal trends general or lake-specific?

To address these questions, we use macrophytes occurrence data of 274 transects taken over 13 years across 28 natural deep lakes in Bavaria that were mapped for monitoring in relation to the European Water Framework Directive. We expect a hump-shaped DDG (question 1.1) corresponding to previous scattered empirical evidence and following the typical patterns found along elevation (Nogués-Bravo et al., 2008). We assume no strong differences between lakes and diversity

components (question 1.2), as the pattern along elevation is shown to be generalisable for alpha and gamma richness (Bhatta et al., 2018) and as we consider beta richness as additive partitioning of alpha and gamma richness. To tackle question 2, we test whether the shape of the DDG can be explained by geographic and physical-chemical characteristics of the lakes. We expect water quality to have a high degree of influence, since water quality affects resource availability (light, temperature) (Bornette & Puijalon, 2011). Finally, we assess, with regard to questions 3.1 – 3.2, whether there have been detectable temporal changes in the DDG. We suppose that the DDG is a quite stable pattern over time, as macrophytes react slowly to changes (Bakker et al., 2013). However, due to the overall warming in annual average water temperature during the last decades we expect that species richness increases, as invasive species are expected, and warm-adapted species might expand. Our results provide the most refined and extensive assessment of macrophyte biodiversity patterns in freshwater lakes up to date, giving insights for the development of long-term conservation strategies for freshwater systems in general.

3.2 Materials and Methods

3.2.1 Data and study area

Bavaria has a wide variety of lakes, which vary in size, depth, elevation, and physiochemical parameters. Information about lake surface area, maximal lake depth and mixing regime were provided by Bayerisches Landesamt für Wasserwirtschaft (1987). We obtained data for water level statistics and physical-chemical data from the hydrological service of Bavaria (<https://www.gkd.bayern.de/>). We selected the physical-chemical parameters that were measured for the largest number of lakes: chloride (Cl), conductivity (*Cond*), total nitrogen (N_{tot}), ammonium (NH_4^+), nitrate (NO_3^-), dissolved oxygen (O_{2diss}), total phosphorus (P_{tot}), pH, silicate (SiO_2), water temperature (*Temp*), transparency (*Transp*), and spectral absorption coefficient at 254 nm (*SAC*). Although some of the parameters seem redundant at first glance all parameters are also indicators for environmental conditions with secondary or indirect effects on the macrophytes. For example, both the concentration of total nitrogen and the concentration of nitrate or even ammonium can influence biodiversity. The total nitrogen indicates the basic nutrient situation, while the ammonium or nitrate concentrations can affect species with certain nitrogen preferences (Nelson et al., 1981). We did not include Chlorophyll a measurements as they were not consistently available and phosphorus concentration is supposed to be the better predictor for trophic state and lake productivity in central European lakes. Physical-chemical data include monthly measurements at the deepest point of the lake.

Macrophyte data were also extracted from the Bavarian State Office for the Environment (www.lfu.bayern.de). The macrophyte data were recorded for the EU-Water Framework Directive Monitoring following an official sampling strategy (Schaumburg et al., 2015) and include vegetation surveys for all large lakes of Bavaria (> 0.5 km² surface area) for at least one and maximum five different years. At each lake, macrophyte data for several transects perpendicular to the shoreline at characteristic sections are available (see sampling strategy in Figure 3.1 a). Each transect is considered from shoreline to the lowest macrophyte occurrence and is subdivided along the depth

gradient into four depths (0 – -1 m; -1 – -2 m; -2 – -4 m; > -4 m). At each depth, the frequency of all species is sampled in five steps following the scale of Kohler (1978), an estimate of abundance.

3.2.2 Data preparation

Data preparation and analyses were done in R 3.5.3 (R Core Team, 2021). The pre-processed data and the code for the data analysis is provided as Research Compendium on GitHub (https://github.com/AnneLew/Lewerentz-et-al_2021_Macrophytes-DDG).

To have comparable conditions we selected all lakes from the dataset that are deep (maximum depth > 10m), not artificial, dimictic, have a natural water level dynamic (i.e. not influenced by storage power plants), and at least one sampling repetition. More information about the single selected lakes and their morphometry can be found in the Supplementary material.

To describe the local water level fluctuation (*WLF*), we calculated for each lake the difference between mean high water (*MHW*) and mean low water (*MLW*).

$$WLF = MHW - MLW$$

Based on the monthly abiotic measurements, we calculated annual means for all chemical-physical variables based on monthly measurements at the lake surface. For this calculation, we considered measurement campaigns with at least eight monthly values available. Values below the detection were assumed to be zero. To describe the water layering of the lakes, we used the standard deviation of the water temperature measurements of surface, -2 m, -4 m, and -6 m depth (*Tempsd*). The available geographic and chemical-physical variables and their mean, standard deviation, median, minimal, and maximal values are given in Table 3.1.

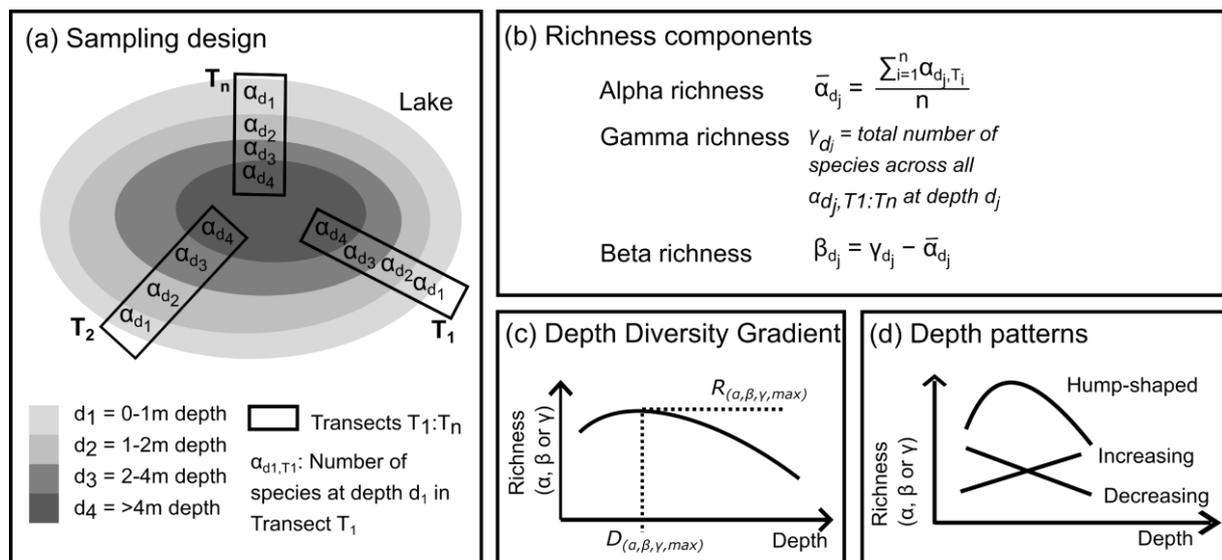


Figure 3.1: Experimental design and analysed variables. (a) Sampling design of empirical data: Each lake was mapped along representative number of transects in four different depths. Three species richness components were calculated (b) alpha richness, gamma richness, and beta richness. For all three depth curves, richness peaks (c) are characterized by D_{max} and R_{max} as depth diversity gradient measures. Resulting depth pattern types (d) can be decreasing, hump-shaped, and increasing.

From the macrophytes surveys, we excluded datasets with (I) just one plot or transect for a lake and year, (II) species that were identified as emergent or floating-leaved macrophytes, and (III) macrophytes that were not identified down to the species level. Therefore, free-floating submerged macrophytes and rooted submerged macrophytes are considered, as well as submerged forms of emergent or floating-leaved macrophytes. For further calculations, we transformed the depth ranges to decimal numbers by the mean of their limits. That is, the depth range of 0 – 1 m was converted to -0.5 m depth, the range of 1 – 2 m in -1.5 m, 2 – 4 m in -3.0 m, and > 4 m in a depth of -5.0 m.

3.2.3 Species richness components and depth diversity gradient measures

As depth-independent component of species richness, we calculated gamma richness as the total number of species per lake and year.

As depth-dependent component of species richness, we determined for every lake and year an additive alpha richness as the number of species per depth range averaged across transects (Figure 3.1 b). The gamma richness for every lake and year was defined as the total number of species per depth range (Figure 3.1 c). We then calculated an additive beta richness as gamma richness minus alpha richness (Tuomisto, 2010) (Figure 3.1 d).

Table 3.1: Overview of the number of datapoints (n), minimum values of annual means (Min), maximum values of annual means (Max), mean of annual means, standard deviation of annual means (SD), and median of annual means (Med) of the abiotic data (geographic variables: fixed values per lake; physical-chemical variables: changing over years, annual means were used) used as indicators in the studied lakes.

| | Variable (unit) | Ab-brev. | n | Min | Max | Mean | SD | Med |
|-----------------------------|--|------------------------------|----|--------|---------|--------|--------|--------|
| Geographic variables | Lake area (ha) | Area | 12 | 135 | 7990.00 | 1840 | 2654 | 624.50 |
| | Water level fluctuation (m) | WLF | 12 | 0.2 | 1.18 | 0.58 | 0.28 | 0.59 |
| Physical-chemical variables | Chloride (mg l ⁻¹) | Cl ⁻ | 27 | 0.33 | 14.98 | 7.58 | 3.94 | 7.61 |
| | Conductivity (μS cm ⁻¹) | Cond | 27 | 158.55 | 372.44 | 292.57 | 61.96 | 309.20 |
| | Total Nitrogen (mg l ⁻¹) | N _{tot} | 27 | 0.19 | 1.22 | 0.66 | 0.22 | 0.65 |
| | Ammonium (mg l ⁻¹) | NH ₄ ⁺ | 27 | 0.00 | 0.09 | 0.02 | 0.02 | 0.01 |
| | Nitrogen (mg l ⁻¹) | NO ₃ ⁻ | 27 | 0.00 | 1.09 | 0.37 | 0.28 | 0.30 |
| | Dissolved Oxygen (mg l ⁻¹) | O _{2diss} | 27 | 9.16 | 11.41 | 10.23 | 0.51 | 10.39 |
| | Total Phosphorus (mg l ⁻¹) | P _{tot} | 27 | 0.00 | 0.02 | 0.01 | 0.00 | 0.01 |
| | pH (-) | pH | 27 | 8.04 | 8.49 | 8.32 | 0.11 | 8.35 |
| | Silicate (mg l ⁻¹) | SiO ₂ | 27 | 0.00 | 2.86 | 1.68 | 0.88 | 1.64 |
| | Water temperature (°C) | Temp | 27 | 9.64 | 19.24 | 13.38 | 2.09 | 13.32 |
| | Transparency (cm ⁻¹) | Transp | 27 | 242.50 | 1197.27 | 451.74 | 198.39 | 410.00 |
| | Spectral absorption coefficient at 254 nm (m ⁻¹) | SAC | 27 | 0.00 | 24.83 | 8.85 | 7.84 | 5.35 |
| | Standard deviation of temperature measured at 0 m, -2 m, -4 m, and -6 m depth (°C) | Tempsd | 27 | 0.23 | 2.24 | 0.91 | 0.58 | 0.62 |

To further characterize the diversity depth gradient, we identified the peak of the richness depth curve (Figure 3.1 c). For each transect, we filtered the depth with the maximal species number. Thereafter, we averaged this value across transects per lake and year, from now on termed the depth with maximal alpha richness ($D_{(a,max)}$). The corresponding maximal species number averaged across transects is termed the maximal alpha richness ($R_{(a,max)}$). Similarly, the depth with maximal gamma richness ($D_{(g,max)}$) is the depth of the maximal gamma richness ($R_{(g,max)}$) along depth, and maximal beta depth ($D_{(\beta,max)}$) describes maximal beta richness ($R_{(\beta,max)}$) along depth.

3.2.4 Statistical analysis

We addressed the study questions with several analyses, focusing on different dataset levels dependent on data availability. The *biodiversity dataset* contains all macrophyte recordings (274 mapped transects in 100 field campaigns, mapping of lake in one year is called *field campaign*) of the selected 28 lakes. As no complete information is available for all mapped lakes and years, we compiled two subsets of the *biodiversity dataset*: The *environmental & biodiversity dataset* is a subset dataset with all macrophyte recordings for which all abiotic data (see Table 3.1) were available. This dataset includes data from 12 lakes, 27 field campaigns, and 147 transects. For the *biodiversity time series dataset*, we selected all lakes for which repeated mappings for at least 3 years were available. This condition was fulfilled for 17 lakes mapped in 73 field campaigns along 194 transects. Analyses for each research question are described below.

For the first question, concerning the general depth distribution pattern, we used the richness components including the different DDG measures and determined pattern types. We plotted as general DDG curves the mean and standard deviation of alpha, beta, and gamma richness for each depth (Question 1.1). We performed simultaneous tests for linear models with multiple comparisons of means using Tukey contrasts that are robust under non-normality, heteroscedasticity, and variable sample size (Herberich et al., 2010) to compare the richness across depth for significant difference. Furthermore, we plotted the different DDG peaks (DDG measures) for alpha, beta, and gamma richness and determined the corresponding regression line by fitting a linear model. We classified the DDG curves for all three richness measures in four pattern types depending on the depth of the richness curve maximum: decreasing ($D_{max} > -1$ m), shallow hump-shaped (D_{max} between -1 and -2 m), deep hump-shaped (D_{max} between -2 and -4 m), and increasing ($D_{max} < -4$ m) (Figure 3.1 d). To determine the correlations between the different diversity components (Question 1.2) we performed a Pearson correlation test between depth dependent richness components. Furthermore, we tested for correlations between DDG measures across the different richness components. A Chi-square test helped to look at associations between pattern types and biodiversity components.

For the second question, concerning the drivers of the diversity depth gradient, we analysed the influence of abiotic data on the DDG using the *environmental & biodiversity dataset*. We log-transformed the abiotic and biotic data. To show that the diversity metrics of the *environmental & biodiversity dataset* are representative for the diversity metrics of *biodiversity dataset*, we applied the PERMANOVA test *adonis2*, using the R package “vegan” which compares centroids and the variance (Oksanen et al., 2019). A non-significant result ($p > 0.05$) confirms that centroids and variance of

two groups are not different (supporting information in Appendix B). To identify the driving factors on the richness peaks we used Generalized Additive Mixed-Effect Models (GAMMs), computed with the R package “*gam4*” (Wood, 2011). $D_{(a,\beta,\gamma,max)}$ and $R_{(a,\beta,\gamma,max)}$ were used as response variables, the lake as random effect. To reduce the high correlations between abiotic factors (Pearson correlation test), we performed a Principal Component Analysis (PCA) and named the main axis ($> 80\%$ variance) after the corresponding abiotic factor, whenever an axis encompassed more than 40% of the variation of a variable. We used the loadings of the main PCA axes ($> 80\%$ variance) as explanatory variables for the GAMM. We constructed a full model with all PCA axes, then we stepwise excluded the least significant terms until obtaining a minimal model (Wood, 2008).

To answer questions 3.1 and 3.2, concerning the temporal change of the depth diversity gradient, we used the *biodiversity time series dataset*. First, we calculated the Invariability Coefficient (*IC*) as inverse of the Coefficient of Variation (*CV*):

$$IC = \frac{1}{CV} = \frac{1}{SD/mean} = \frac{mean}{SD}$$

The *IC* is a statistical tool to evaluate the degree of invariability also for datasets with different means (Question 3.1). To check for temporal trends, we built simple linear regression models for depth independent gamma richness and the DDG measures, $D_{(a,\beta,\gamma,max)}$ and $R_{(a,\beta,\gamma,max)}$, as response variables and time as explanatory variable for (a) the complete dataset and (b) each individual lake. We identified all models that showed significant linear trends ($p < 0.1$) and characterized the direction of their slopes (Question 3.2).

3.3 Results

For the dataset of all macrophyte recordings (*biodiversity dataset*), a total of 75 submerged species is documented in Bavaria. The available taxonomic groups are mainly Spermatophytes (51 species), Charophytes (20 species), Bryophytes (2 species), and Pteridophytes (2 species). The complete abiotic and biotic data (*environmental & biodiversity dataset*) cover 57 different species, whereas the *biodiversity time series dataset* included 66 species. The total (depth-independent) gamma richness per lake ranges from 5 to 34 species of submerged macrophytes. The mean gamma richness averaged across lakes is 15.36 species with a standard deviation of 6.27 species.

3.3.1 The depth diversity gradient (DDG) patterns of macrophytes

The mean depth pattern of submerged macrophytes’ alpha and gamma richness is hump-shaped, showing a peak between -1 and -2 m respectively (Figure 3.2 a, c). The mean alpha richness at the hump’s peak is 4.5 species ($SD = 2.2$), whereas the mean gamma richness peak is 11.4 species ($SD = 5.1$). In contrast, Beta richness shows a decreasing curve with its highest richness being 7.0 species ($SD = 4.0$) between surface and -1 m depth (Figure 3.2 b). However, all three richness components show high standard deviations in the different depth classes. They vary across depth classes between 1.9 and 2.3 species for alpha richness, between 3.7 and 4.1 for beta richness, and

from 5.1 until 5.6 for gamma richness (see individual DDG curves for all lakes in Appendix B, Figure B.3 – B.5).

Comparing the richness components across depths revealed only significant differences between mid- and greater depths, but not for shallower depth (Appendix B, Figure B.6).

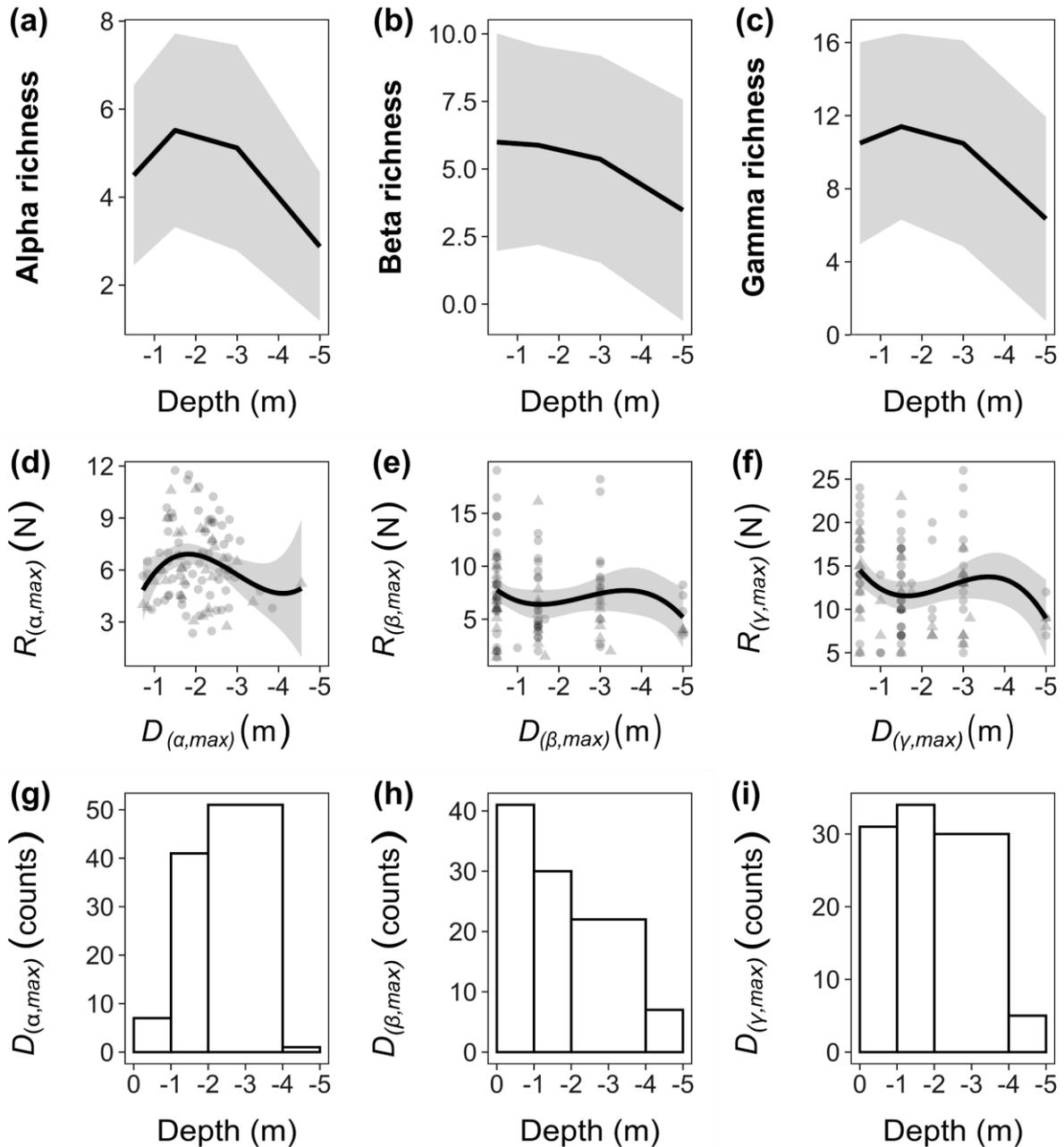


Figure 3.2: Depth diversity gradient (richness along depth) total mean (black line) and standard deviation (grey area) for alpha (a), beta (b), and gamma richness (c). The individual depth curves of alpha richness for all lakes and years are shown in Appendix B, Figures B.2 – B.5. Points show the individual DDG peaks (DDG measures) of all field campaigns (d–f). Point shapes indicate different dataset levels: round and triangular points = full dataset with all biotic data; triangular points = nested subset, for which each biotic datapoint has a corresponding abiotic datapoint. Intermediate values between depth classes result as mean from lakes with equal species numbers in two different depths. Histograms (g–i) show distribution of D_{\max} , which can be interpreted as distribution of pattern types (see definition in Figure 3.1)

Plotting the DDG measures for all three richness components (Figure 3.2 d – f), we find a hump-shaped pattern for alpha richness and a bi-modal pattern for beta and gamma richness.

Looking at the DDG patterns of single field campaigns, for alpha richness, hump-shaped curves with a peak between -2 and -4 m are most frequent (52%) (Figure 3.2 g – i). For beta richness, the majority are decreasing curves (40%), while hump-shaped curves with a peak between -1 and -2 m were slightly prevailing (39%) for gamma richness. All depth pattern types are found for all three measures.

The three depth-dependent richness measures are significantly correlated with one another ($p < 0.05$). Beta and gamma richness ($\text{cor} = 0.95$) show the strongest correlation, followed by alpha and gamma richness ($\text{cor} = 0.85$) and alpha and beta richness ($\text{cor} = 0.64$). D_{max} and R_{max} do not correlate within the respective richness components ($p < 0.05$). However, the D_{max} values across the three richness components correlate with each other. Similarly, R_{max} also correlates across the three richness components ($p < 0.05$). For correlation coefficients see supporting information in Appendix B (Figure B.7). However, a Chi-square test shows that the association between pattern types and richness components are statistically significant ($p = 0.0005$).

3.3.2 Drivers of the depth diversity gradients

The DDG measures correlate with some of the abiotic variables (Appendix B, Figure B8 and B9). $R_{(\alpha,max)}$ correlates highly significantly ($p < 0.01$) with lake area ($\text{cor} = 0.53, p < 0.01$), water level fluctuations ($\text{cor} = 0.54, p < 0.01$), conductivity ($\text{cor} = 0.53, p < 0.01$), NH_4^+ ($\text{cor} = -0.5, p < 0.01$), SiO_2 ($\text{cor} = 0.62, p < 0.01$), and spectral absorption coefficient ($\text{cor} = 0.6, p < 0.01$). $R_{(\beta,max)}$ correlates highly significantly ($p < 0.01$) with lake area ($\text{cor} = 0.55, p < 0.01$). $R_{(\gamma,max)}$ correlates highly significantly ($p < 0.01$) with lake area ($\text{cor} = 0.57, p < 0.01$) and water level fluctuations ($\text{cor} = 0.56, p < 0.01$). $D_{(\alpha,max)}$ correlates highly significantly ($p < 0.01$) with dissolved oxygen content ($\text{cor} = -0.54, p < 0.01$), total phosphorus content ($\text{cor} = 0.6, p < 0.001$), transparency ($\text{cor} = -0.67, p < 0.001$), and $Temp_{sd}$ ($\text{cor} = 0.59, p < 0.01$). $D_{(\beta,max)}$ and $D_{(\gamma,max)}$ do not correlate highly significantly ($p < 0.01$) with any of the abiotic variables.

Abiotic and biotic variables are correlated with one another in a complex fashion (Appendix B, Figure B8 and B9). Strongest positive correlations ($\text{cor} > 0.7$ or < -0.7) within abiotic data were found between N_{tot} and NO_3^- ($\text{cor} = 0.92, p < 0.01$), conductivity and SiO_2 ($\text{cor} = 0.83, p < 0.01$), and chloride and conductivity ($\text{cor} = 0.73, p < 0.01$). Strongest negative correlations showed water transparency and total phosphorus content ($\text{cor} = -0.72, p < 0.01$) and water transparency and conductivity ($\text{cor} = -0.71, p < 0.01$).

Due to the high correlation coefficients between abiotic factors, we performed a PCA (Appendix B, Figure B8 and B9). We use the first four axes (81% of total variation – Figure 3.3 a – d) to address the DDG drivers. The first axis, PC1, can be characterized as the SiO_2 & $Cond$ axis (both positive with the axis), explaining 30.1% of the variance. The PC2, the second axis, can be described as the $Temp$ & P_{tot} axis, as both abiotic variables have the highest (negative) impact (26.1% of variance). The third axis, PC3, can be named the $Temp_{sd} - Cl^-$ axis (13.3% of variance) as it ranges from most negative variable $Temp_{sd}$ to most positive variable Cl^- , while the fourth axis, PC4, shows

the $O_{2diss} - SAC$ axis (10.5% of variance) spanned between O_{2diss} (most negative) and SAC (most positive).

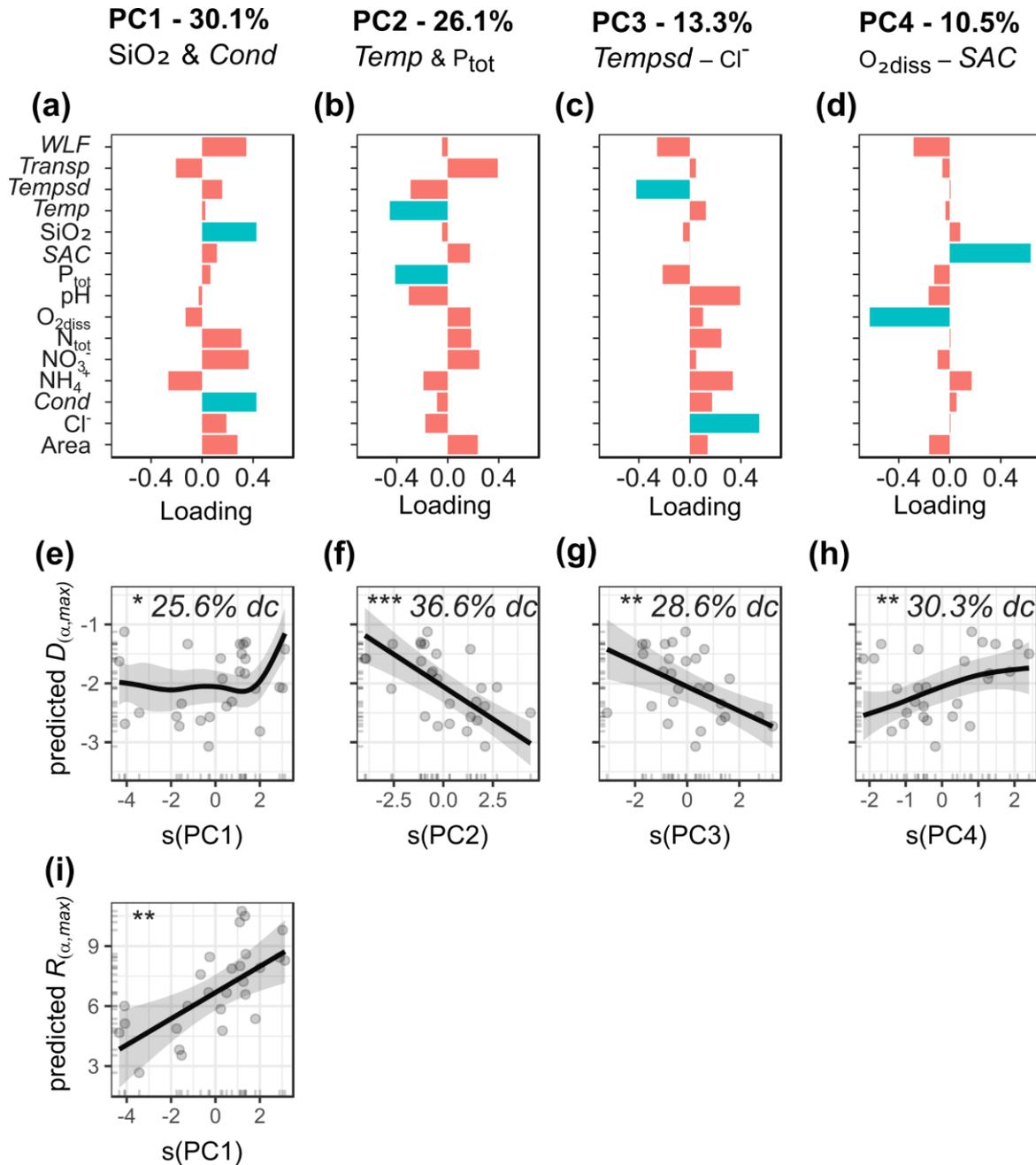


Figure 3.3: The PCA loadings (a – d) of the four first axes (81% variation) of a PCA for all abiotic variables were used as explanatory variables of the GAMM. The names of the axes are given by the variables with > 40% of the loading (highlighted in blue). The full variable names are given in Table 3.1. The panels a – d are ordered corresponding to the order of a–d. PCA biplot can be found in the Appendix B (Figure B.10). Minimal best models for generalized additive mixed models explaining $D_{(a,max)}$ by PC2 (e), PC4 (f), PC3 (g), and PC1 (h) and $R_{(a,max)}$ by PC1 (i). GAMMs without significant explanatory variables are not shown ($R_{(\beta,max)}$, $R_{(\gamma,max)}$, $D_{(\beta,max)}$, $D_{(\gamma,max)}$). The panels e – h are ordered by decreasing drop contribution (dc). The relative contribution of each variable to the full model (% drop contribution) is measured as the drop in deviance explained by the model when the predictor is removed. Significance levels of p-values: * $p < .05$; ** $p < .01$; *** $p < .001$. R^2_{adj} for $D_{(a,max)}$ is 73.5%, for $R_{(a,max)}$ 43.9%.

The GAMM showed that $D_{(a, max)}$ ($R^2 = 0.73$) significantly varies with all four PCA axes (Figure 3.3 e – h). $D_{(a, max)}$ decreases with PC2 (*Temp & P_{tot} axis*) and PC3 (*Tempsd – Cl axis*) axes, slightly increases with PC4 axis (*O_{2diss} – SAC axis*) and increases only for extreme positive values of PC1 axis (*SiO₂ & Cond axis*). The $R_{(a, max)}$ ($R^2 = 0.44$) is only influenced by the PC1 axis (*SiO₂ & Cond axis*) with a positive linear relationship (Figure 3.3 i). The GAMM analysis for $D_{(\beta, max)}$, $R_{(\beta, max)}$, $D_{(\gamma, max)}$, and $R_{(\gamma, max)}$ had all $R^2 < 2.1\%$ (see results in Appendix B, Figure B.11).

3.3.3 Temporal dynamics of the depth diversity gradients

The DDG measures of the different richness components show different degrees of invariability (IV) as measure for stability. The IV of Gamma richness (mean = 7.14, $SD = 3.69$), of $D_{(a, max)}$ (mean = 6.62, $SD = 4.11$), of $R_{(a, max)}$ (mean = 6.36, $SD = 2.87$), of $R_{(\beta, max)}$ (mean = 5.89, $SD = 2.06$), and of $R_{(\gamma, max)}$ (mean = 6.52, $SD = 2.97$) were high in comparison to the IV of $D_{(\beta, max)}$ (mean = 1.56, $SD = 0.48$) and of $D_{(\gamma, max)}$ (mean = 1.78, $SD = 0.53$).

Table 3.2: Linear model results of the time series analysis of DDG variables (D_{max} and R_{max}) across richness components for each lake. Here, +: positive slope of linear model (Meaning for D_{max} : becomes shallower; Meaning for R_{max} : more species); -: negative slope of linear model (Meaning for D_{max} : becomes deeper; Meaning for R_{max} : less species); significance levels of p -values: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘?’ 0.1

| Lake | Gamma richness | $D_{(a, max)}$ | $R_{(a, max)}$ | $D_{(\beta, max)}$ | $R_{(\beta, max)}$ | $D_{(\gamma, max)}$ | $R_{(\gamma, max)}$ |
|---|----------------|----------------|----------------|--------------------|--------------------|---------------------|---------------------|
| Lake Abtsdorf | – | – | – | – | + | – | – |
| Ammersee | – | + | – | + | – | + | – |
| Chiemsee | +++ | + | – | – | + | + | + |
| Gr. Alpsee | + | –* | + | – | – | – | + |
| Grosser Ostersee | – | + | – | + | – | + | – |
| Hopfensee | + | – | + | – | ++ | – | + |
| Lake Niedersonthofen | – | + | – | + | + | + | – |
| Lake Pelham | + | – | + | + | – | – | + |
| Riegsee | + | + | + | ++ | + | + | + |
| Schliersee | – | + | – | + | – | – | – |
| Simssee | + | + | + | + | + | + | + |
| Staffelsee-Nord | ++ | + | + | + | + | + | + |
| Staffelsee-Sued | ++ | + | + | – | + | + | + |
| Lake Starnberg | + | + | ++++ | + | ++ | + | ++++ |
| Tegernsee | + | ++ | + | + | + | + | + |
| Lake Waging | + | – | + | + | + | + | + |
| Woerthsee | – | –* | + | + | + | + | + |
| Sign ($p < 0.1$) pos. slope (number of lakes) | 4 | 2 | 2 | 1 | 5 | 3 | 4 |
| Sign ($p < 0.1$) neg. slope (number of lakes) | 0 | 2 | 0 | 0 | 0 | 0 | 0 |

For all lakes, depth-independent gamma richness showed a small but significant trend ($p < 0.1$) towards more species (Appendix B, Figure B.14 – B.15). Analysing all lakes together, the DDG measures revealed no significant common trend ($p > 0.05$) (Appendix B, Figure B.16). For individual lakes, slopes of significant linear models of the D_{max} and R_{max} over years showed mostly positive trends (richness increasing and peaking at shallower depths, see Appendix B, Figure B.17 – B.19).

The $D_{(\alpha, \max)}$ shows two significant positive trends (peak shifting towards water surface – Lake Starnberg and lake Tegernsee) and two significant negative trends (peak shifting to deeper waters – lakes Großer Alpsee and Wörthsee). The $D_{(\beta, \max)}$ increases significantly at lake Riegsee, while $D_{(\gamma, \max)}$ increases for lakes Riegsee, Staffelsee Nord, and Tegernsee. For total gamma richness, lakes Chiemsee, Staffelsee Nord, Staffelsee Süd, and Lake Starnberg show positive trends (Table 3.2).

3.4 Discussion

3.4.1 The DDG patterns of macrophytes

We showed that submerged macrophytes in deep lakes have in general a hump-shaped depth diversity gradient (DDG) for alpha richness, a prevailing decreasing pattern for beta richness and a dominantly hump-shaped pattern for gamma richness (Figure 3.2 a – c) (question 1.1). As we had only significant differences between mid and greater depths for all richness components, an even coarser species mapping resolution might be helpful. Our results are congruent to the few existing studies, which also show a hump-shaped pattern (Ye et al., 2018) for alpha richness of submerged macrophytes. A simple explanation for the predominantly hump-shaped pattern of alpha and gamma richness might be the mid-domain effect (Colwell et al., 2004): Niches along environmental gradients overlap and build a peak of richness following geometric constraints. Furthermore, the generally decreasing beta DDG might be explained by a change in local species between transects in shallower depths. In shallow water, disturbances resulting from the surface might be more diverse, which may increase coexistence with spatial partitioning of occurrences. As disturbances are coming from the surface, we propose the hypothesis that shallow water has a higher environmental heterogeneity which might be the reason for an increased beta diversity.

We see a high variety of DDG shapes between lakes, as all these DDGs vary in their maximum richness (R_{\max}) and the corresponding depth (D_{\max}), but a robust hump-shaped pattern can be seen for alpha richness (Figure 3.2 d – f) (question 1.2). The high variety of R_{\max} and D_{\max} is not surprising, as we studied lakes showing a range of physical-chemical properties (Table 3.1) and gamma richness between 2 – 35 species per lake. This wide range of species richness and environmental conditions broadens our understanding of the DDG, previously limited to one single lake in China (Fu, Zhong, Yuan, Ni, et al., 2014; Fu, Zhong, Yuan, Xie, et al., 2014). Although for alpha and gamma richness, hump-shaped curves along depth are predominant (Figure 3.2 g, i), we also see increasing and decreasing patterns at single lakes. Increasing curves must be hump-shaped, as we can safely assume that plant richness should decrease to zero further down in deep lakes. We detected more decreasing DDGs for gamma than for alpha richness, which reflects predominantly decreasing beta richness curves. Nevertheless, besides geometry and disturbances, there must be further variables affecting the DDG, as DDG shape varies between lakes, which themselves have different properties.

3.4.2 The DDG drivers

The drivers of the macrophyte DDGs strongly differed for DDG measures and richness components. Whereas pairwise correlations detected many strong relationships across richness components, multiple models revealed significant variables only for DDG measures of alpha richness.

The R_{max} correlate of the different richness components with a very similar set of abiotic parameters. All R_{max} correlate with area. This reflects species-area relationships (SARs) (Connor & McCoy, 1979; Lomolino, 2000; Patiño et al., 2014; Qian et al., 2007) for macrophytes, which is also shown by high correlation of area with total gamma richness. Looking at the GAMM results for non-linear responses $R_{(\beta,max)}$ and $R_{(\gamma,max)}$ did not show any significant results, but $R_{(a,max)}$ is exclusively influenced by the SiO_2 & *Cond* axis (PC1) (Figure 3.3). Lake area, spectral absorption coefficient, and water level fluctuations also have a high contribution to PC1 and thus, area might be the key driving force again. The SAR of macrophytes was already shown in a several studies (Alahuhta et al., 2020), and still a study comparing SAR of macrophytes with terrestrial plants would be very informative. Here, it would be interesting to add information about lake bathymetry, as lake area is just a proxy for the colonisable area per depth. Still, very generalizing indices like volume development index are also not suitable to determine the colonisable area in this case because the lake's morphology is very diverse (from kettles with several deep funnel-shaped basins to v-shaped glacial lakes, and lake basins created by glacial erosion). However, it was not shown yet that the size of lakes also influences the shape of DDG.

The $D_{(\beta,max)}$ and $D_{(\gamma,max)}$ could not be explained with abiotic variables, neither by correlations nor by a GAMM. Unlike $D_{(a,max)}$, the gamma, and consequently beta, values along DDG are more variable, indicating spatial heterogeneity and possibly unsaturation (Karger et al., 2014). Still, $D_{(a,max)}$ correlates positively with total phosphorus content and *Tempsd* (higher P_{tot} and *Tempsd* evoke a $D_{(a,max)}$ in shallower water), and negatively with O_{2diss} and water transparency. Furthermore, looking at non-linear influences, the $D_{(a,max)}$ is affected by all four PCA-axes.

The PC2 (*Temp* & P_{tot} axis) shows the highest influence (Figure 3.3). This means that in lakes with high total phosphorus concentration and / or high water temperature the DDG peaks in shallower waters. P_{tot} is the limiting factor for phytoplankton growth and phytoplankton reduces the light availability for macrophytes. In contrast, it is still debatable whether the P_{tot} concentration in the water is a limiting growth factor for macrophytes (Carr et al., 1997). One important point to consider in this debate is that rooted submerged macrophytes can also take up nutrients from the sediments (Lacoul & Freedman, 2006). Hence, P_{tot} might affect macrophytes by promoting phytoplankton growth, which then reduces light availability and shifts DDG to shallower depths. Besides P_{tot} , water temperature is a major factor influencing metabolic processes as photosynthesis and respiration. Additionally in lakes, higher and prolonged high water temperature result in higher nutrient levels due to increased mineralization and internal fertilization processes (Moss, 2012). Internal fertilization processes occur when longer high water temperature lead to increased layering stability, prolonged oxygen consumption, anoxia in deep waters, resulting in anoxic resuspension of phosphorus from the lake sediments. These resuspended nutrients promote phytoplankton growth, thus reducing light for macrophytes. Therefore, the PC2 (*Temp* & P_{tot} axis) describes the

productivity gradient in lakes, caused by lower light availability leading to a shallower maximum of species richness.

Besides light quantity, light quality also influences $D_{(a,max)}$, which is indicated by the influence of the PC4 ($O_{2diss} - SAC$ axis). With high O_{2diss} content and low spectral absorption coefficient at 254nm (SAC , a measure of coloured dissolved organic matter – CDOM), we observe richness peaks at deeper waters. On the one hand, CDOM reduces damaging UV-B radiation. On the other hand, it reduces light availability. Therefore, we see a diametrically opposed effect of light quantity and light quality which might contribute to the prevailing pattern of highest species richness at medium depth level. In general, if light resource represents the main component of productivity in lakes, the mid-depth DDG might follow the intermediate productivity hypothesis (Huston, 2014; Rajaniemi, 2003; VanderMeulen et al., 2001).

Besides light, temperature also seems to influence $D_{(a,max)}$, via surface water temperature and its influence on light availability (as explained above) and via the lake's layering depth. This second mechanism by which temperature layering affects DDG is demonstrated by the fact that along PC3 ($Temp_{sd} - Cl$ axis) $D_{(a,max)}$ decreases. A high $Temp_{sd}$ (shallow epilimnion – the upper temperature layer in a stratified lake) promotes a shallow $D_{(a,max)}$, while a low $Temp_{sd}$ (broad epilimnion) allows deeper $D_{(a,max)}$. $Temp_{sd}$ is positively correlated to water temperature demonstrating that higher temperatures can lead to a shallower upper warm layer in water bodies as the stratification is more stable (Adrian et al., 2009).

The weakest influencing effect (lowest drop contribution) is provided by PC1 ($SiO_2 \& Cond$ axis). Just at very high values of PC1 $D_{(a,max)}$ becomes shallower. As $Cond$ is negatively correlated with $Transp$ ($cor = -0.71, p < 0.001$), we speculate that also here transparency is the actual mechanism that influences $D_{(a,max)}$.

In summary, the main influences on $D_{(a,max)}$ seem to be, as expected, factors of water quality that influence light quantity ($Transp$, influenced by P_{tot} and $Temp$), light quality (SAC), and layering depth ($Temp_{sd}$). The main influence on $R_{(a,max)}$ is the lake surface area.

3.4.3 DDG temporal change

We showed that the stability of the pattern depends on the DDG measure (question 3.1). $D_{(\beta,max)}$ and $D_{(\gamma,max)}$ were quite variable measures over years, while $D_{(a,max)}$, $R_{(a,max)}$, $R_{(\beta,max)}$, and $R_{(\gamma,max)}$ are comparatively stable measures. This may be related to the fact that there is neither pair-wise correlation between nor an explaining model for $D_{(\beta,max)}$ and $D_{(\gamma,max)}$.

Contrary to our expectations, we see no general trend of increasing species richness or decreasing D_{max} . (question 3.2). Although we observe high variety in DDG temporal change between lakes, the DDG temporal change for single lakes, especially for $D_{(a,max)}$, is low and develops into different directions for different lakes. Still, we see linear trends that are consistent over time within lakes. These patterns suggest that global change effects will be more complex than anticipated. In fact, climate and land-use change influence all the highly connected chemical and physical gradients known to significantly affect DDG (Hossain et al., 2017). Therefore, the following hypotheses can be formulated (Figure 3.4): (1) As temperatures rise, so do lake surface water temperatures (O'Reilly

et al., 2015; Pilla et al., 2020). This seems to result in shallower epilimnion (Kraemer et al., 2015) and generally shallower D_{max} and a lower R_{max} . (2) Furthermore, rising temperatures entail higher *phosphorus* content, as they promote internal fertilization. But extreme weather events combined with enriched fertilization in agriculture can also cause fertilization events (Rose et al., 2016), which might result in shallower light depth and consequently in shallower DDG. (3) Browning, which is generally increasing due to temperature induced decomposition rates and changes in precipitation events (Guarch-Ribot & Butturini, 2016; Sobek et al., 2007; Weyhenmeyer & Karlsson, 2009), leads to a shallower D_{max} . (4) However, water management reduced the external nutrient loading of European lakes enormously during the last decades (Eigemann et al., 2016; F. Murphy et al., 2018). This trend is still ongoing and might still lead towards lower nutrient contents and thus to deeper D_{max} . All these opposing environmental trends make it hard to draw a general trend for multiple lakes for short timespans. However, for long timespans it seems to be a race between climate change impacts (Hypothesis 1 – 3 in Figure 3.4) that might lead to a shallower D_{max} and thus generally less macrophytes and water management impacts that might deepen the D_{max} via improved water quality (Hypothesis 4 in Figure 3.4). In summary, this study sets a good comparison for future studies once longer timeseries become available.

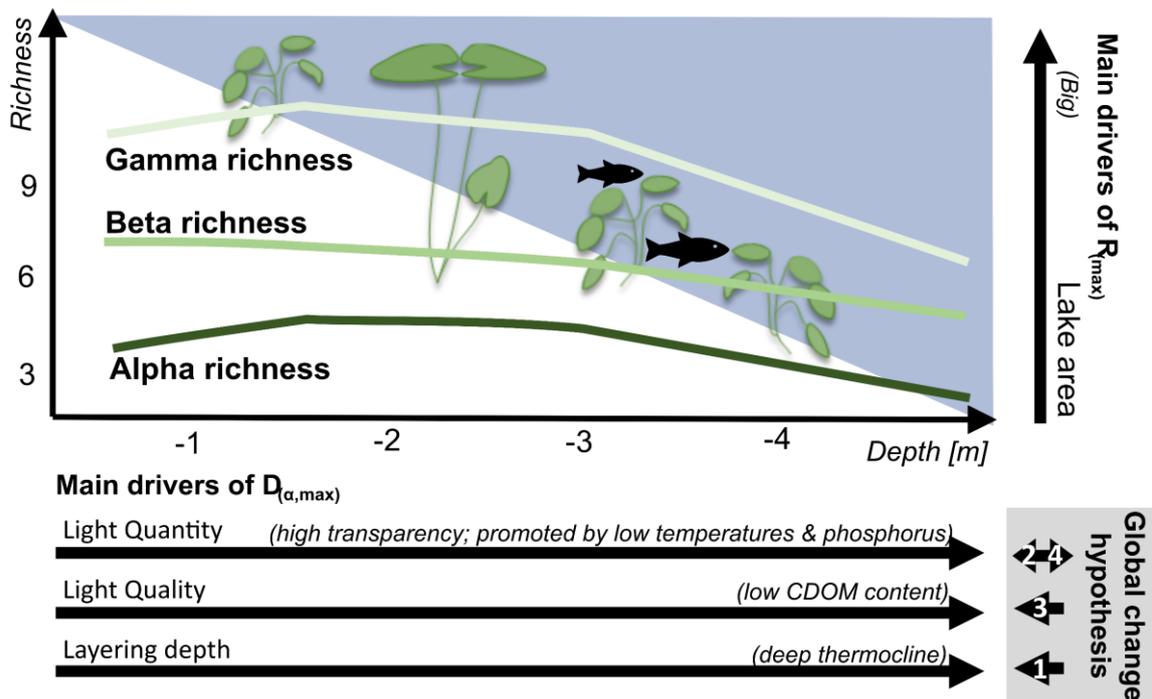


Figure 3.4: Summary figure showing the submerged macrophytes depth diversity gradient for alpha, beta, and gamma richness as well as the main drivers (black arrows) of the alpha richness peak, characterized by $R_{(alpha,max)}$ and $D_{(alpha,max)}$. Additionally, hypotheses for global change influences on the alpha richness peak for Bavaria are given in the grey box. The hypotheses are: (1) layering depth might become shallower due to rising water temperature. (2) Light quantity might be lowered due to lowered transparency. (3) Light quality is said to decrease. (4) Light quantity might be increased if water management gets adapted.

3.4.4 Implications for diversity gradients and hypotheses in general

Comparing different diversity gradients might provide deeper insights into mechanisms shaping species richness. Here, the DDG of macrophytes brings advantages compared to other gradients. The DDG assembles over shorter spatial scales than the latitudinal diversity gradient (LDG) or the elevational diversity gradient (EDG), which implies a lower importance of dispersal or connectivity and an easier replicability. For LDG, the options for replicates are restricted to two hemispheres (Pontarp et al., 2019), whereas EDG comparative studies require a high logistic sampling effort (Kessler et al., 2011; Nogués-Bravo et al., 2008). Because of these advantages, other small-scale diversity gradients may also be insightful. One example is the vertical diversity gradient (VDG) from forest floor to tree crowns, which involves sharp gradients of light intensity, temperature, and humidity. Therefore, we discuss below the potential explanatory hypotheses with all mentioned diversity gradients.

One explanation of the observed hump-shaped DDG might be the Intermediate Productivity Hypothesis (IPH). The IPH states that at low productivity level (deep waters with low light quantity and low temperature) only few specialized species survive, whereas at high productivity level (shallow waters) only few competitive species survive. Previous LDG study of freshwater macrophytes revealed its peak at sub-tropical to low tropical latitudes (K. Murphy et al., 2019), thus peaking at intermediate level of solar productivity and reflecting our analysis of DDG. Intermediate light intensity and temperature would also match the mid-canopy VDG peak for vascular epiphytes (Acebey et al., 2017; Krömer et al., 2007; Petter et al., 2021). Although quantification of productivity along depth should be attempted, our findings and the evidence from other diversity gradients already indicate a key role of light quantity and temperature in shaping DDG.

Another hypothesis is the Mid-Domain Effect (MDE), which proposes mid-gradient peaks due to geometric constraints (Colwell et al., 2004). If depth ranges from shallow-water species overlap with ranges of deep-water species a species richness peak in the middle of the gradient can be expected. The MDE is used to explain hump-shaped patterns of the LDG (Pontarp et al., 2019) and the EDG (Colwell & Lees, 2000). Indeed, the overlap of light and temperature preferences may explain the subtropical peak (K. Murphy et al., 2019) in LDG of macrophytes and our reported mid-depth peak in DDG as well as the mid-canopy VDG peak in vascular epiphytes (Petter et al., 2021). Still, an adequate evaluation of the MDE requires quantification of environmental preferences for each species – an important direction for future empirical research. In this regard, the MDE evaluation may be more feasible to perform for DDG, as it considers a smaller regional species pool than the LDG and a better experimental feasibility than VDG given the faster life cycles of macrophytes compared to vascular epiphytes.

Another explanation is the Intermediate Disturbance Hypothesis (IDH). It suggests species richness peaking at mid-levels of disturbance as species of early and late successional phases coexist (Connell, 1978). Whereas the disturbances along EDG are caused by human activities at lower elevation (Nogués-Bravo et al., 2008) and the disturbances along VDG can be associated with higher branchfall toward the outer crown of a tree (Cabral et al. 2015, Petter et al. 2021), depth-dependent disturbances in water can be caused by anthropogenic use, waves, herbivory, ice cover,

and water level fluctuations (Evtimova & Donohue, 2016). Water level fluctuation was already integrated in our study in a very simple way, but showed no strong effect on richness, thus did not explain the DDG. Nevertheless, considering that several disturbances in shallow waters should happen in lakes, future monitoring schemes should quantify more types of disturbances.

3.4.5 Limitations and Perspectives

The main limitation is that, in some lakes, the deeper end of the DDG was not clearly quantified. This is, however, most critical for the lakes with increasing DDG (For alpha richness: Eibsee 2016; for beta richness: Eibsee 2011, Grosser Ostersee 2008 & 2014, Lake Taching 2006, Woerthsee 2008, Eibsee 2016, Schliersee 2008; for gamma richness: Eibsee 2011 & 2016, Grosser Ostersee 2008, Lake Taching 2006, and Woerthsee 2008). For these lakes, which are mostly lakes with a high water transparency, it might be interesting to split up the lowest depth level to have a finer resolved depth gradient and to quantify a metric termed “the lower macrophyte limit” (Søndergaard et al., 2013). This metric is often used as indicator for water quality and might be useful to further characterize the DDG as it defines the lower limit and the occupied space.

Additional limitations of our analyses can be viewed rather as perspectives for further studies focusing on explaining the underlying causes of the DDG (see previous section) and to disentangle the presented hypotheses, as these limitations require data yet unavailable. This includes 1) depth measurements of the variables that also show depth gradients (i.e. light, temperature, or nutrients) and 2) further variables that vary across transects and lakes, such as littoral area, transect distance, slope, soil properties (components, grain size distribution, and nutrient content), average lake depth, ice cover duration, productivity, and different disturbance factors like anthropogenic use intensity (boats, mowing, swimming) or herbivory pressure (fish, water birds). Nevertheless, our analyses already indicate that light quality and quantity may play a main role in forming the DDG in freshwater lakes and will inspire further empirical studies on the DDG as well as comparative studies with other diversity gradients.

A promising direction for future research might be combining eco-physiological experiments with mechanistic modelling to test the different species richness hypotheses. Such an approach might help to clarify the influencing force of disturbances or geometry on DDG on small scales.

3.5 Conclusion

Our study makes a step towards a cross-lake generalizable understanding of the depth diversity gradient (DDG) of submerged macrophytes, their regional and temporal heterogeneity as well as the drivers of the DDG shape. Submerged macrophytes richness peaks predominantly at intermediate depth forming a hump-shaped pattern for alpha and gamma richness, but a decreasing pattern for beta richness (Figure 3.4). Well-known hypotheses of biogeography shape diversity gradients in general, such as mid-domain effect and mean productivity hypothesis. The latter is already supported by our findings on the role of light and temperature as DDG drivers. The key advantage of DDG in contrasting these hypotheses is the logistic feasibility of short-distance scales and the exclusion of confounding effects associated with dispersal constraints. The key drivers of DDG

we determined were area influencing the species richness peak height ($R_{(a,max)}$) and light quality, light quantity, and layering depth influencing the species richness peak depth ($D_{(a,max)}$). However, as there are many other possible factors for which we did not have data, but which could play a role, further research is needed before general conclusions can be drawn from this study. Although we found that the DDG in general remained stable over the past few years for most lakes, we still found shifting trends for richness metrics for some lakes. However, these trends are diverse across lakes. Whereas climate change might be more ubiquitous, land-use change may be lake specific. This suggests that water management strategies should also consider, besides global warming, lake characteristics and change in the surrounding land use. The interaction of these aspects also means that although higher temperatures lead to a reduction in the quantity of light available to aquatic plants in lakes, land-use measures can be taken to counteract this. Nevertheless, our findings already indicate that warmer water temperatures may still lead to a shift in species along depth dependent on further efforts to hold or increase water quality of lakes.

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Further material – Further analysis and supporting information are shown in Appendix B. Data and code of data analysis are published as Research Compendium: [DOI: 10.5281/zenodo.5255571](https://doi.org/10.5281/zenodo.5255571)

Chapter 4

Potential change in the future spatial distribution of submerged macrophyte species and species richness: the role of today's lake type and strength of compounded environmental change

This chapter is in preparation as: Lewerentz, A., Hoffmann, M., Hovestadt, T., Raeder, U., & Cabral, J. S. Potential change in the future spatial distribution of submerged macrophyte species and species richness: the role of today's lake type and strength of compounded environmental change. A preprint is published on *Authorea*: DOI: 10.22541/au.165401091.12520929/v1

Abstract:

Aim: Eco-physiological processes underlying biomass growth and survival of submerged macrophytes follow environmental conditions like light, temperature, and nutrient availability. These processes and conditions further delimit potential geographical and depth distribution of these species. Hence, the impending increase in water temperature as well as changes of nutrient and turbidity could potentially lead to changes in macrophyte geographic and depth distribution and occurrence. Here, we assess these potential changes.

Location: Deep lakes in Bavaria, Germany, which cover clear, moderate, and turbid lake conditions.

Methods: We apply an eco-physiological macrophyte growth model to simulate biomass growth of virtual species defined by random trait combinations within expert-derived trait ranges for oligotraphentic, mesotraphentic, and eutraphentic species groups. The emergent potential species richness is compared with realised observed species richness to evaluate general predictions to current conditions. Thereafter, we apply the model to scenarios of temperature increase, and turbidity and nutrient change to assess potential richness changes and the influence of the species traits on being an environmental change “winner” or “loser”.

Results: We find a hump-shaped pattern of potential species richness along depth across all lake types, which largely reflect observed patterns, with differences being explained by environmental heterogeneity within the lake and missing processes. Rising temperature leads to increased species richness 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 possess high light consumption and sensibility to disturbances, while “winner species” have a high biomass production.

Main conclusion: These findings show that the hump-shaped pattern of submerged macrophytes along depth can be largely explained by eco-physiology and that the differential response to future changes implies that management measures must account for lake type.

4.1 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. Most importantly, the eco-physiological processes controlling their growth and survival are strongly affected by environmental conditions, as they depend on light availability, nutrient availability, and temperature. However, the accelerating global biodiversity loss, especially of submerged macrophytes, is well documented (Körner, 2002; Phillips et al., 2016; Sand-Jensen et al., 2000; Y. Zhang et al., 2017) despite evidence of increasing species richness in some lakes (F. Murphy et al., 2018). The main influencing factors on the change of species richness seem to be global climate and regional land-use changes (Hofstra et al., 2020; Y. Zhang et al., 2017) resulting in 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 highly complex including direct and indirect effects (Lind et al., 2022). For example, lake water temperature rises due to climate change which can also have indirect impacts on turbidity and nutrients in lakes, as higher temperature can promote algae growth (lower light availability). Therefore, nutrients and turbidity seem to co-vary, while temperature could change independently. However, nutrient content and turbidity can also be influenced by land-use practices (e.g. content and timing of fertiliser on fields), and wastewater treatment management. Overall, the direction and impact of future climate change on submerged macrophytes seems to be more obvious than changes in land use.

All these stressors have an effect on the eco-physiological processes of macrophytes (Cao & Ruan, 2015; Reitsema et al., 2018). Hence, changes in these stressors likely affect the geographical distribution of individual species and of species richness of submerged macrophytes. Because of their response to their physio-chemical, geomorphological, hydrological, and biotic surroundings (O'Hare et al., 2018), species can be differentiated into oligo-, meso-, and eutraphentic species by their preference for nutrient conditions (Melzer, 1999). The presence of distinct species can then be an indicator of the water quality and ecological state of the lake (Schaumburg et al., 2004). However, studies on macrophyte species richness distribution remain largely based on observational and correlative studies, while there is a need to understand how simultaneous stressors combine and may result in synergistic effects on biodiversity (Lind et al., 2022). Therefore, it is paramount to assess these potential effects on macrophytes.

Process-based models based on first principles and known ecophysiology are better suited to assess biodiversity response from changing conditions than correlative models (Cabral et al., 2017; Dormann et al., 2012; Higgins et al., 2020; Schouten et al., 2020). To predict the potential distribution of species based on environmental factors, process-based models incorporating critical ecophysiological processes are necessary. The application of process-based models describing the growth of submerged macrophytes have a long tradition, already stemming as early as the late 1980s (Best et al., 2001; Collins & Wlosinski, 1989; Herb & Stefan, 2003; Hootsmans, 1994; Scheffer et al., 1993; Wortelboer, 1990). The majority of those models were developed to answer different study questions, however, like the effect of macrophytes on algal blooms (Asaeda & Van Bon,

1997), the effect of varying light regimes (Herb & Stefan, 2003), or their impact on water quality (Sachse et al., 2014). Furthermore, most models were only used and calibrated for one or a few species (Gao et al., 2017; van Nes et al., 2003) and under very specific environmental conditions. None of these models was used to study the macroecological distribution patterns of macrophytes or its response to environmental change. Among the reasons for the delay in applying any of these models to multiple species and under different environmental conditions is the lack of computationally efficient models and empirical data to constrain both eco-physiological and environmental parameters. Hence, applying eco-physiological models to assess the species and richness distribution in both current and future conditions deserves further attention for this neglected group of species.

Macrophytes are still underrepresented in trait-based research and in environmental change assessments (Dalla Vecchia et al., 2020; Iversen et al., 2022). Consequently, the determination of a broad range of eco-physiological parameters has yet to be established for most macrophytes. In the case of low trait-based information, applying eco-physiological models to a virtual species pool remains the best alternative to assess impacts of environmental change on macrophytes (Cabral et al., 2017; Dormann et al., 2012). As computational power and methods are evolving (Pérez-Sánchez et al., 2015), experiments with a broad range of randomly selected species within defined functional types can be a way of determining trait combinations (potential species) that allow species to survive and reproduce, as already 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 those trait combinations able to cope with the environmental conditions given the considered mechanisms. However, this approach was not yet used for macrophytes.

In this study, we tackle two main objectives. First, we address the potential species richness of oligotraphentic, mesotraphentic, and eutraphentic submerged macrophytes under recent environmental conditions. We ask: How many observed and potential species of the species pool can grow in clear, intermediate, and turbid lakes (Q1.1)? Do the potential species richness patterns across the depth follow the observed distribution in all lake types (Q1.2)? Second, we assess scenarios of water temperature increase and water quality change (increase or decrease in both nutrients and turbidity). Here, 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 oligotraphentic, mesotraphentic, and eutraphentic species and analyse the resulting distribution patterns of the growing species by comparing them with the corresponding observed pattern. We expect to find the highest species richness in moderately nutrient rich lakes (Q1.1) (Lewerentz & Cabral, 2021). We hypothesise to find hump-shaped patterns (Q1.2) of species richness along depths (Lewerentz et al., 2021). In general, we hypothesise that we see a higher potential species richness than observed species richness because limiting processes like herbivory have not been modelled (Q1.1 and Q1.2). To answer question Q2.1 and Q2.2, we run scenarios of water temperature increase and scenarios of water quality change for the recent potential species pool. We hypothesise that the studied lakes will lose species under increased turbidity and nutrient conditions but gain species under decreased turbidity and nutrient conditions and

under increased water temperature (Q2.1) (Lewerentz & Cabral, 2021). To answer question Q2.2, we determine the plant traits that significantly influence if a species will win or lose habitat within two selected scenarios of turbidity and nutrient decrease or increase. We hypothesise that under increased conditions, high biomass production is the main advantage, as species can grow at high rates even under limited conditions.

4.2 Methods

4.2.1 The model

We use an eco-physiological process-based growth model for submerged macrophytes named Macrophyte Growth Model (MGM). It is based (Figure 4.1 a) on the model Charisma 2.0 (van Nes et al., 2003), which in turn builds on the model Megaplant (Scheffer et al., 1993). The MGM is a re-implemented and simplified version of Charisma 2.0 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 rates, individual weight, and height. We simulate each species separately as one super-individual per depth. The model calculates the daily biomass, the height, and the number of sub-individuals for each of these super-individuals (Figure 4.1 b). 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 on depth-dependent light, 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.

We simplified the model compared to Charisma 2.0 to reduce the number of parameters (47 species-specific parameters in Charisma 2.0) by excluding processes of i) carbonate limitation because the lakes we simulated were not carbonate limited and no proof was found for the process; ii) spatial processes like seed dispersal, which we assume not to limit occurrence of macrophytes within the regional context (Alahuhta et al., 2020); iii) water level fluctuation, because corresponding data are not available for all lake and because the macrophyte mappings correspond always to the actual water level; iv) interspecific competition and v) herbivory because both processes are not relevant for modelling the eco-physiological constraints on the potential distribution of species; and vi) vegetative reproduction because we focus on eco-physiological constraints rather than demographic or dispersal constraints. After that, MGM still includes 28 species-specific parameters. The detailed Overview, Design concepts, Detail (ODD) protocol (Grimm et al., 2006, 2010) for MGM can be found in Appendix D. The model code, data, and data analysis code are open access and available on GitHub (see links in Appendix A).

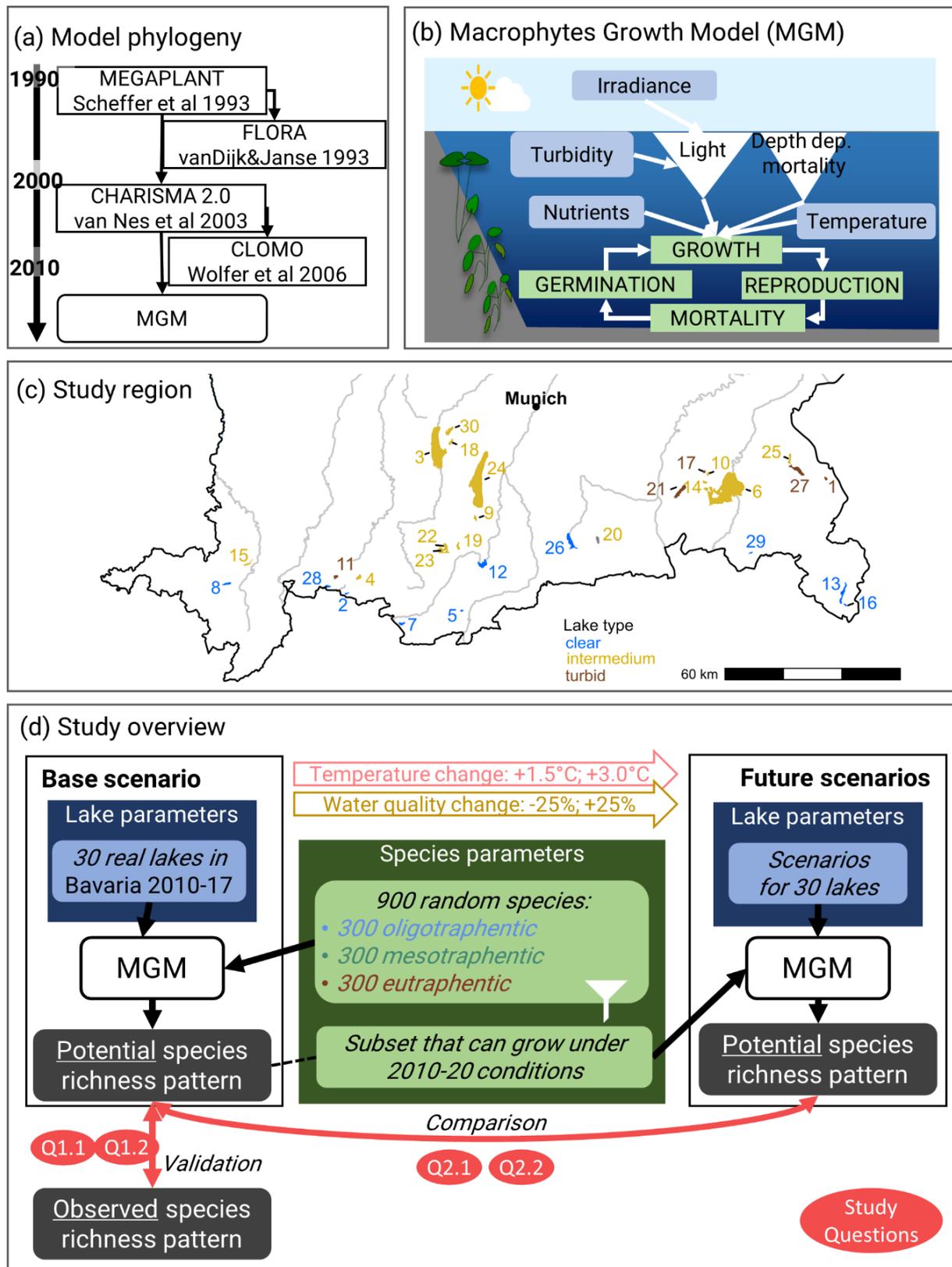


Figure 4.1: The model phylogeny (a), simplified processes of the Macrophyte Growth Model (MGM) (b), an overview about the studied lakes including the lake types (c), and an overview about the study design (d).

4.2.2 Datasets

The available dataset from the German federal state of Bavaria consists of large lakes ($> 0.5 \text{ km}^2$ surface area). We selected all lakes of natural origin (without artificial influence on water level fluctuation and not of artificial origin) and with a minimal maximal depth of 9 m. Their locations are shown in Figure 4.1 c. 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 depths (0 – 1 m; 1 – 2 m; 2 – 4 m; $> 4 \text{ m}$) and monthly physical-chemical measurements (e.g. water temperature, total phosphorus content, 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, and are non-rooted. In addition, “indicator species” were selected, i.e. species that are oligotraphentic, mesotraphentic, or eutraphentic (Melzer, 1999).

4.2.3 Experimental design

Data preparation and analyses were done in R 4.0.5 (R Core Team, 2021). We defined parameter spaces for oligotraphentic, mesotraphentic, and eutraphentic functional types. We selected the parameter spaces based on parameters of reference species out of the groups 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. As the eco-physiological parameters of 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 (Table 4.1). Each of the resulting 900 parameter combinations represent hypothetical, virtual species.

We select lake parameter values according to measured data within the 30 selected lakes from the available dataset (see description above). The lakes 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 by using a clustering method (hclust, “ward.D2”). All other lake parameters are identical across lakes and are given in the supporting information (Appendix C, Table C.1).

Table 4.1: 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. Reference species were *Chara aspera* for oligotraphentic species, *Myriophyllum spicatum* and *Potamogeton perfoliatus* for mesotraphentic species, *Potamogeton pectinatus*, *Elodea nuttallii*, and *Najas intermedia* for eutraphentic species. (Table continues on next page.)

| Symbol | Unit | Description | OLIGO- TROPIC (Min – Max) | MESO- TROPIC (Min – Max) | EU- TROPIC (Min – Max) | Source |
|---------------------------------------|---|---|---|--|--------------------------------------|--------|
| <i>seedsStartAge</i> | day no | Age of the plants where seed formation starts | 10 – 100 | 10 – 100 | 10 – 100 | (h) |
| <i>seedsEndAge</i> | day no | Age of the plants where SeedFraction is reached | 30 – 120 | 30 – 120 | 30 – 120 | (h) |
| <i>cTuber</i> | fraction | Fraction of tuber weight loss daily when sprouts start growing | 0.1 | 0.1 | 0.1 | (f) |
| <i>pMax</i> | h⁻¹ | Maximal gross photosynthesis | 0.001 – 0.01 | 0.001 – 0.02 | 0.001 – 0.03 | (h) |
| <i>q10</i> | - | Q10 for maintenance respiration | 2 | 2 | 2 | (f) |
| <i>resp20</i> | d ⁻¹ | Respiration at 20 °C | 0.002 | 0.002 | 0.002 | (f) |
| <i>heightMax</i> | m | Maximal height | 0.1 – 1 | 1 – 6 | 3 – 4 | (c) |
| <i>max- WeightLenRatio</i> | g m⁻¹ | Weight of 1 m young sprout | 0.01 – 0.1 | 0.4 – 0.8 | 0.1 – 0.4 | (d) |
| <i>rootShootRatio</i> | fraction | Proportion of plant allocated to the roots | 0.1 | 0.05 – 0.09 | 0.05 – 0.08 | (d) |
| <i>fracPeriphyton</i> | fraction | Fraction of light reduced by periphyton | 0.2 | 0.2 | 0.2 | (f) |
| <i>hPhotoDist</i> | m | Distance from plant top at which the photosynthesis is reduced factor 2 | 1.0 | 1.0 | 1.0 | (f) |
| <i>hPhotoLight</i> | μE m⁻² s⁻¹ | Half-saturation light intensity (PAR) for photosynthesis | 15 – 60 | 30 – 60 | 40 – 60 | (b) |
| <i>hPhotoTemp</i> | °C | Half-saturation temperature for photosynthesis | 14 | 14 – 15 | 14 – 15 | (b) |
| <i>plantK</i> | m ⁻² g ⁻¹ | Extinction coefficient of plant issue | 0.02 | 0.02 | 0.02 | (f) |
| <i>pPhotoTemp</i> | - | Exponent in temp. effect (Hill function) for photosynthesis | 2 – 3 | 2 – 3 | 2 – 3 | (a) |
| <i>sPhotoTemp</i> | - | Scaling of temperature effect for photosynthesis | 1.35 | 1.35 | 1.35 | (f) |
| <i>cThinning</i> | - | c factor of thinning function | 5950 | 5950 | 5950 | (f) |
| <i>hWaveMort</i> | m | Half-saturation depth for mortality | 0 – 0.5 | 0 – 0.5 | 0 – 0.5 | (f) |

| Symbol | Unit | Description | OLIGO- TROPIC (Min – Max) | MESO- TROPIC (Min – Max) | EU- TROPIC (Min – Max) | Source |
|---------------------------|--------------------------|--|---------------------------------|--------------------------------|------------------------------|--------|
| <i>germinationDay</i> | day no | Day of germination of seeds | 75 – 150 | 75 – 150 | 75 – 150 | (h) |
| <i>reproDay</i> | day no | Day of dispersal of seeds | 227 – 289 | 227 – 289 | 227 – 289 | (h) |
| <i>maxAge</i> | day | Maximal plant age | 150 – 300 | 150 – 300 | 150 – 300 | (h) |
| <i>maxWaveMort</i> | g d ⁻¹ | Maximum loss of weight in shallow areas | 0.1 – 1 | 0.1 – 1 | 0.1 – 1 | (h) |
| <i>pWaveMort</i> | - | Power of Hill function for wave mortality | 0 – 8 | 0 – 8 | 0 – 8 | (h) |
| <i>hNutrient</i> | mg l⁻¹ | Half-saturation nutrient concentration for photosynthesis | 0.006 – 0.007 | 0.005 – 0.013 | 0.007 – 0.015 | (e) |
| <i>pNutrient</i> | - | Power of Hill function for nutrient | 4 – 8 | 3 – 6 | 1 – 2 | (e) |
| <i>seedBiomass</i> | g | Individual weight of seeds | 0.00002 | 0.001 – 0.007 | 0.005 – 0.007 | (f)(g) |
| <i>seedFraction</i> | g year ⁻¹ | Fraction of plant weight allocated to seeds | 0.13 | 0.13 | 0.13 | (f) |
| <i>seedGermination</i> | year ⁻¹ | Fraction of seeds that germinate | 0.8 | 0.8 | 0.8 | (i) |
| <i>seedInitialBiomass</i> | 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 (M. Hoffmann et al., 2013; M. A. Hoffmann et al., 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

We run the model for all 900 virtual species within the 30 lakes at four depths (0.5m, 1.5m, 3m, 5m) for 10 years to reach equilibrium (Figure 4.1 d). We select as potential growing species those that can establish a mean biomass of more than 1 g (per depth and in sum over depth) during summer (June – August). Those species that passed through the considered processes within MGM in the given lake conditions are denoted as “potential species”. Species that passed through all ecological processes (including demography, interaction, and dispersal) in nature will be called “observed species”.

To study the effects of environmental change related to global warming and water quality change, we performed simulation experiments with the surviving virtual species under changed lake parameters in a full-factorial design. We chose two water temperature increase scenarios of +1.5 °C and +3.0 °C (reference period 2010 – 2020) and combined those scenarios with two further scenarios of correlated nutrient and water turbidity increase (+25%) or decrease (-25%). We coupled these water quality components because of the high correlation of both parameters within the data set and the well-known 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.

4.2.4 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 and for the potential species richness. To answer question Q1.2, we calculate the number of oligotraphentic, mesotraphentic, and eutraphentic species for each depth in each lake to obtain an observed species richness from the mapped data and to obtain the potential species from the modelled data. We plot them as box plots grouped by the lake groups as a proportion (on % scale) of the total species number. 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 and lake type.

To answer question Q2.1, we analysed the individual 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. Furthermore, we explored interactive scenarios of temperature increase and turbidity and nutrient increase by plotting the species richness changes after subtracting the single effects from the combined effects.

To answer question Q2.2, we selected two scenarios, turbidity and nutrient decrease and turbidity and nutrient increase, and determined for each species if it loses (“loser”) or gains habitat (“winner”) by comparing the number of lakes the species is present between the base scenario and each selected scenario. Then, we performed a Generalised Linear Model (GLM) to explain if a species is a winner or a loser (binomial distribution) within the corresponding scenario by all available species-specific parameters, with traits as the explanatory variables. The explanatory variables are

all species-specific parameters, the response variable is the winner- / loser-classification. Interactive effects 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 habitat will be called “loser traits” and traits that promote significantly ($p < 0.05$) an increase in habitat of the species are called “winner traits”.

4.3 Results

4.3.1 Base scenario: potential and observed species richness

The individual changes for all lakes, depths, and scenarios can be explored within the 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/).

Environmental conditions of the base scenario

Environmental variables of the 30 lakes correlate with each other, mainly nutrient and turbidity (kD) (0.79***), and latitude and maximal annual temperature ($maxTemp$) (0.51**). The mean latitude of the lakes within the groups are for clear lakes 47.56° , for intermediate lakes 47.81° and for turbid lakes 47.86° . The mean maximal summer temperature is in clear lakes 21.0°C , in intermediate lakes 24.4°C , and in turbid lakes 25.1°C . The mean extinction coefficient of light (kD , as measure for turbidity) is in clear lakes 0.27 m^{-1} , in intermediate lakes 0.40 m^{-1} , and in turbid lakes 0.64 m^{-1} . The mean total phosphorus content is in clear lakes 0.0069 mg l^{-1} , in intermediate lakes 0.0117 mg l^{-1} , and in turbid lakes 0.0292 mg l^{-1} .

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

Out of the 900 randomly assigned parameter combinations, 540 can grow under the base environmental conditions. These 540 species build the potential species pool and all following species numbers will be shown as percentage of those. Of these, 28.5% are oligotraphentic, 34.5% mesotraphentic, 37.0% eutraphentic species (Table 4.2). In comparison, 36 observed species build the empirical species pool, and of these 11.1% are oligotraphentic ($n = 4$), 55.6% mesotraphentic ($n = 20$), and 33.3% ($n = 12$) eutraphentic species.

The comparison between observed and potential species richness within the functional groups and the lake groups are given in Table 4.2.

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

The observed DDG is clearly hump-shaped for meso- and eutraphentic species across all lake types, whereas oligotraphentic species have a linear DDG in clear and intermediate lakes and are not present in turbid lakes (Figure 4.2 a). The potential depth diversity gradient (DDG) is hump-

shaped across all lake types and species groups (Figure 4.2 b). By comparing the observed species richness with the potential species richness for all lake types and species groups (Figure 4.2 c), 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 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 line). In intermediate lakes in all species groups observed species richness and potential species richness correlate slightly positive (Figure 4.2 c). In clear lakes, potential species richness correlates negatively with observed species richness for oligo- and mesotraphentic species. The DDG for all individual lakes are plotted in the supporting information (Appendix C, Figure C.1 – C.10).

Table 4.2: 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 |

4.3.2 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 increased temperature scenarios (Figure 4.3 a), we see a general increase in species numbers across all, depth, lake types, and species groups. The effect is highest in clear lakes, especially for eutraphentic species. However, for individual lakes increased temperature can also lead to a decreased species number, as the standard deviation indicates.

The effect of changed nutrient load and water turbidity is higher (Figure 4.3 b) than the effect of temperature. The effects are almost mirrored for decrease or increase. While in clear lakes the potential species richness increases under increased turbidity and nutrients, it decreases under decreased turbidity and nutrients. In turbid lakes, the effect is the opposite. In intermediate lakes, the effect depends on the depth. In shallow water, an increase / decrease of nutrients and turbidity results prevailingly in an increase / decrease of species, while in deep water the effect is the opposite.

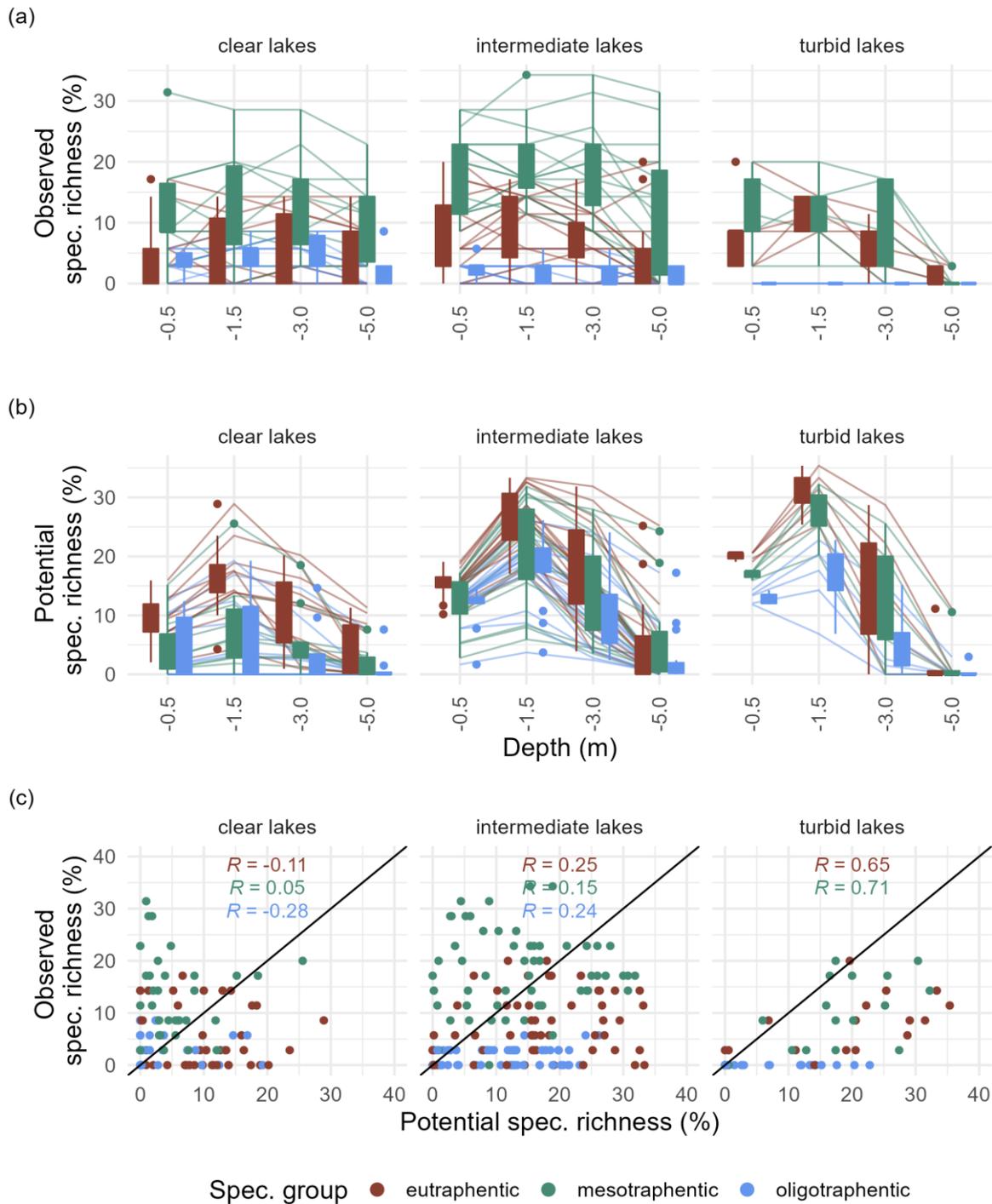


Figure 4.2: Number of oligotraphentic, mesotraphentic, and eutraphentic species along depth in clear, intermediate, and turbid lakes, divided into observed species richness (a) and potential species richness (b). The lines show the depth diversity gradient of individual lakes and the boxplots their summarised course along depth 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 and every line a linear model combining both. The black line would represent a perfect match between potential and observed species richness. All points below that line show a reduced observed richness, while all plants above the line can be seen as an underestimated potential species richness. The R -values give the correlation coefficients within the group.

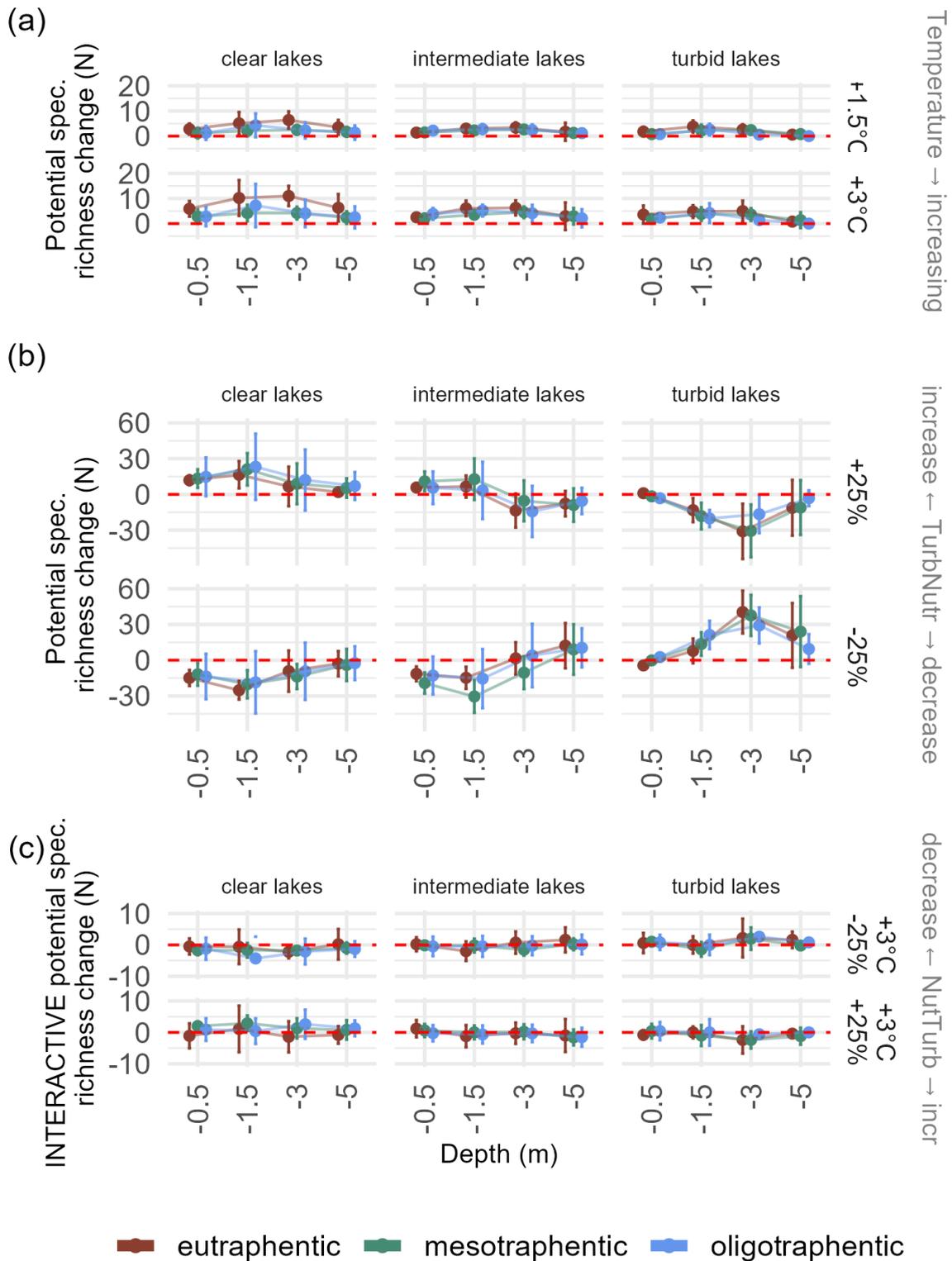


Figure 4.3: Depth dependent potential species richness changes under increased water surface temperature of +1.5 °C or +3 °C (a) and under increased (+25%) or decrease (-25%) turbidity and nutrients (b) for eutraphentic, mesotraphentic and oligotraphentic species within clear, intermediate, and turbid lakes. The 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. Besides the single effects of temperature increase (a) and coupled turbidity and nutrient change (b), we show the pure interactive effects of a temperature increase of +3 °C and an increased or decreased turbidity and nutrient level, by subtracting the single effects from the combined effects (c).

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

Within the decreased nutrient and turbidity scenario of -25% (without temperature increase), we find that 78.1% of the species lose habitat (are losers), while 10.6% of all species win habitat (are winners). Differentiated into water depth zones, more species lose habitat in shallow water (78.7%) than in deep waters (29.4%), but more species win in deep water (43.7%) than in shallow water (7.0%). 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 shown in Figure 4.4 a. 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 it is a winner under the given conditions.

In the increased nutrient and turbidity scenario (+25%) 15.0% of all species lose habitat, while 62.4% of all species win habitat. Here, we observe more losers in deep water (59.6%) than in shallow water (11.7%), but more winners in shallow water (63.7%) than in deep water (12.2%). The general fit of the GLM (Figure 4.4 b) that explains by traits if a species in this scenario is a winner or loser under increased nutrient and turbidity conditions (+25%), 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 is given in the supporting information (Appendix C, Figure C.11).

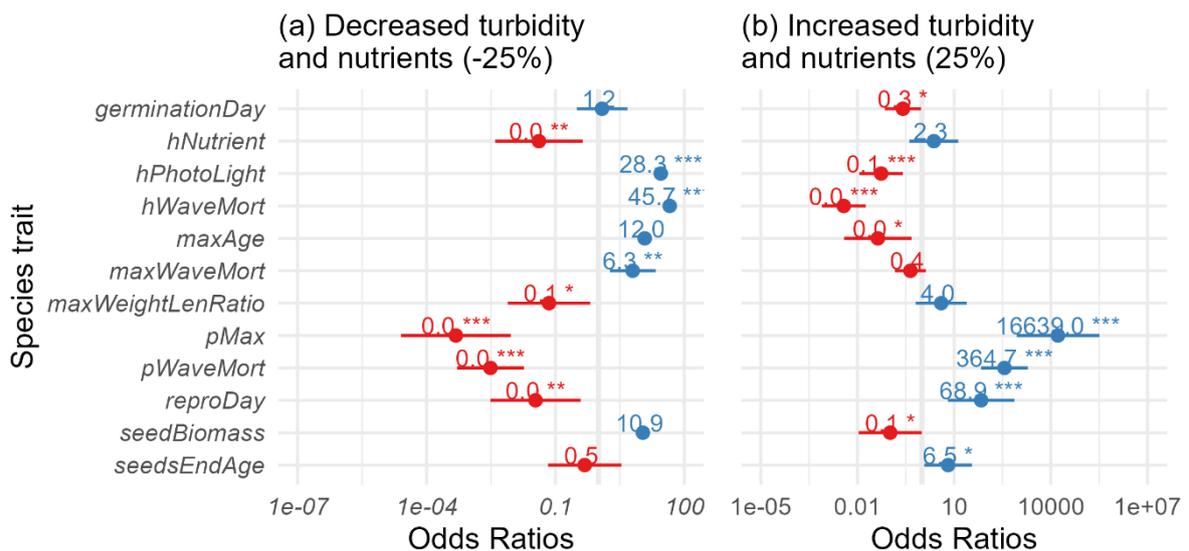


Figure 4.4: Traits that promote loser (Odds Ratios < 1, red) or winner species (Odds Ratios > 1, blue) under different water quality change scenarios of decreased turbidity and nutrients (a) and increased turbidity and nutrients (b). Just traits are shown that are significant within one of the GLM models (Signif. codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Descriptions for the species traits can be found in Table 4.1.

4.4 Discussion

4.4.1 Patterns of potential species richness of submerged macrophytes along depth – current state and changes under different environmental scenarios

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

The comparison of the species richness of submerged macrophytes across lake types shows that in both – observed and potential species richness – the highest species richness appears in intermediate lakes. Intermediate peaks can be explained by geometric constraints of boundary effects, called “mid-domain effect” (Colwell & Lees, 2000). This could play a role especially for the potential species richness as the selected parameter spaces correspond to the given conditions and might create overlap effects. Furthermore, the resources that macrophytes need for growth are differently distributed between lake types. Most nutrients are available in turbid lakes, while most light is available in clear lakes. Intermediate lakes are situated in the middle of that gradients, providing an intermediate level of both resources at the same time (Figure 4.5). Therefore, the highest share of species can find their niches at the crossing point of multi-dimensional resource availability. Species richness along multi-dimensional, interdependent, and opposing gradients of resources can create non-linear responses (Pausas & Austin, 2001). Single scale and single dimension are not appropriate to depict the patterns of species richness (Mirochnitchenko et al., 2021). In future studies, the community structures could be explored more in depth with this framework. In line with other studies (Lewerentz et al., 2021; Mellin et al., 2010; Ruiz-Benito et al., 2012; Toledo et al., 2012), we see that the multidimensionality of environmental gradients are worth disentangling to understand species richness patterns.

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

Our results show that the observed hump-shaped pattern of species richness along depth (Lewerentz et al., 2021) can emerge from an eco-physiological growth model for macrophytes (Figure 4.2 a, b). This means that eco-physiological processes alone can emulate general real-world patterns of depth distribution of macrophytes. However, patterns specific for particular lakes were not always matched (Figure 4.2 c). A reason for smaller observed than potential species richness might be missing processes within the model (e.g. interspecific competition or herbivory) or imperfect detection during field mapping. A larger 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. However, large lakes are known to be highly environmentally heterogeneous (Árva et al., 2015), which must be the case in Bavaria. This missing representation of habitat heterogeneity within lakes is due to the low spatial resolution of the measurements. Unexpectedly, 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 of a shift in life forms from complex macrophytes towards “simple” algae. This shift increases the competition for light and nutrients between algae and macrophytes (Hilt, 2015). The model is able to capture a positive, but weak correlation between observed and potential species richness for the different species groups and lake types, but with the exception of eutrphentic and oligotrphentic species in clear lakes (Figure 4.2 c). A reason for this

exception might be increased competition and stress as clear water lakes tend to be nutrient-limited and colder. Notwithstanding such limitations, our model proved to be useful to explore distribution patterns of species richness of macrophytes along the depth gradient of lakes.

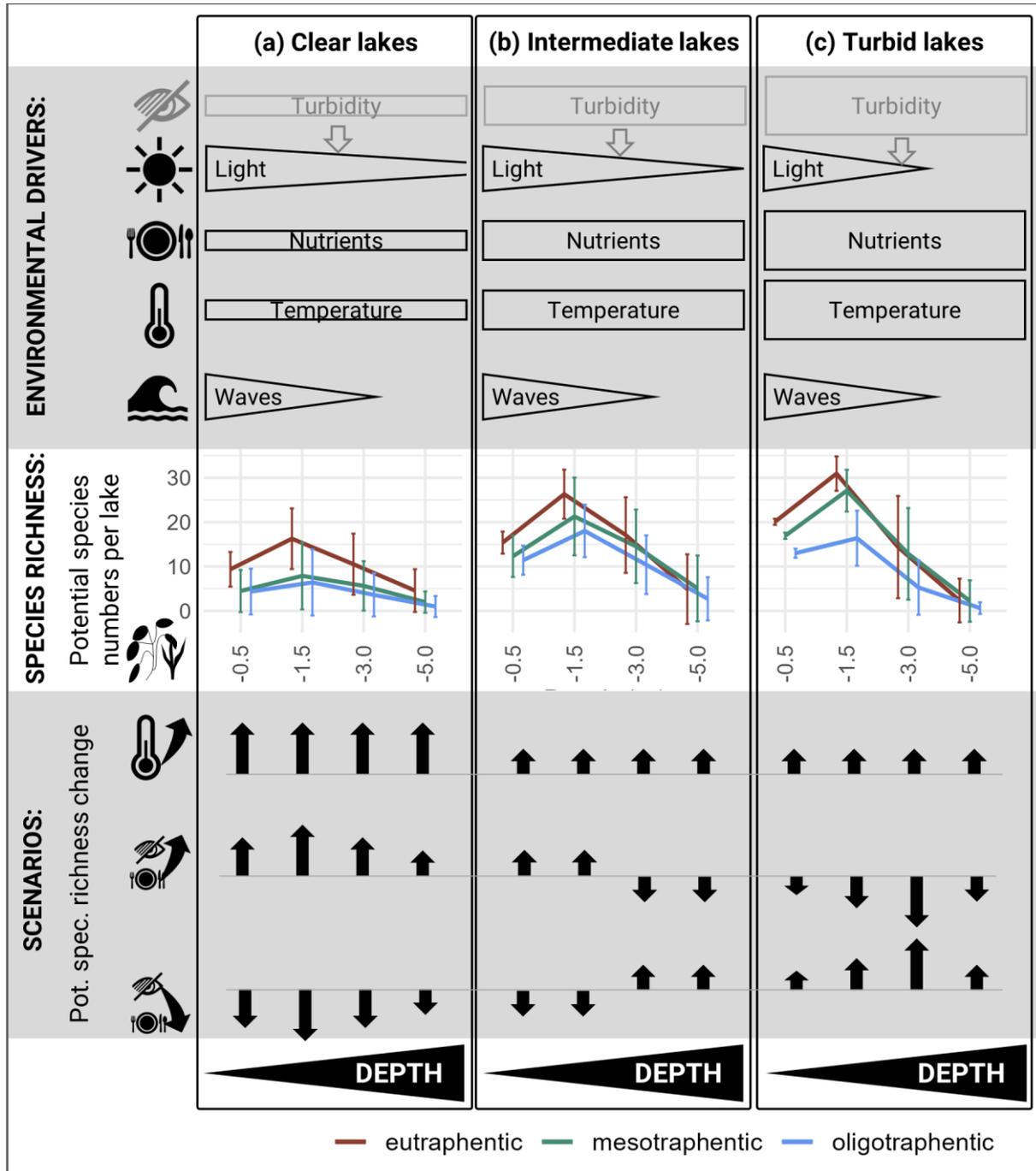


Figure 4.5: Summary figure showing distribution of environmental drivers (light (influenced by turbidity), nutrients, water temperature, and waves), recent potential species richness (line: mean; bars: standard deviation), and scenarios of potential species richness change (temperature increase, turbidity, and nutrient increase, turbidity, and nutrient decrease) along depth in clear lakes (a), intermediate lakes (b), and turbid lakes (c).

4.4.2 Patterns of potential species richness of submerged macrophytes along depth – changes under different environmental scenarios

Species richness change (Q2.1)

Climate change results in higher lake water surface temperatures (Woolway et al., 2020). Within our model, higher water temperatures promote higher potential species richness (Figure 4.3 a). This is expected, as higher temperatures leads to higher metabolic rates, productivity, and, ultimately, also richness (Brown et al., 2004; Z. Wang et al., 2009). Furthermore, higher maximal water temperature means that the vegetation period is also prolonged, which allows slower growing species to mature and reproduce. A reduction in potential species richness was predicted only in particular cases, mainly for deeper depths and oligotrophic 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 might be limited by the available light or nutrients this might result in a net photosynthesis that is lower than respiration, resulting in the death of the species (Binzer et al., 2006; Ikusima, 1970). In general, metabolic theory alone is a debatable predictor of diversity gradients (Hawkins et al., 2007).

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 decreased as a consequence of improved wastewater systems and water management (F. Murphy et al., 2018; Vetter & Sousa, 2012). However, it remains unclear if this trend will proceed in the future. Climate change might lead to a trend reversal, as it enhances eutrophication processes of lakes (Moss, 2012; Moss et al., 2011). The loss of species in increased nutrient and turbidity conditions in currently turbid lakes is caused by light reduction. Alternatively, the gain of species in today's clear lakes (i.e. nutrient-limited lakes) is a direct effect of nutrient increase. Consequently, the differences of the effects according to the lake types show that there is no generalizable trend for the potential species richness of lakes under turbidity and nutrient change (Figure 4.5). Overall, 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 traits of aquatic plants and anthropogenic pressures are known for the compositional shift from submerged to emerged life forms (Zervas et al., 2019). However, direct comparisons with Zervas et al. (2019) are challenging because they use different traits. 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 (Figure 4.4). This means that changes in multiple traits, and thus in different functions, might be required to cope with impending environmental change.

A high maximum growth rate ($pMax$) of the species is advantageous for species under increased nutrient and turbidity and a disadvantage under decreased nutrient and turbidity levels. If species are capable of producing high amounts of biomass, they can reach shallower depth faster to

overcome light limitation. This is also observed in the shift from slow-growing seagrass to fast-growing macroalgae in oceans under increasing nutrient and light limitation conditions (Duarte, 1995). This advantage of fast growth towards the water surface is also reflected in the fact that a high *maxWeightLengthRatio* is a loser trait value under decreased turbidity and nutrients. If a plant needs more biomass to grow the same length as another plant, it has a physiological and competitive disadvantage because it can be outgrown and shaded. A species group that has slow growth rates and might have a disadvantage under increased turbidity and nutrients are charophytes (Blindow, 1992; Henricson et al., 2006). In fact, a high maximum growth rate is a trait commonly found in invasive species (e.g. *Elodea canadensis*) because a high biomass production in general helps to outcompete slower growing species (Dawson et al., 2011; Hussner et al., 2021; Schultz & Dibble, 2012).

Several traits within the model 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). Within the scenario with decreased turbidity and nutrients, a high wave mortality rate (*maxWaveMort*) and a depth effect (*bWaveMort*, *pWaveMort*) bring advantages for species that are susceptible to disturbance as enough light reaches deep water, where they can exploit as newly available habitat. 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. Light limitation in deeper areas of the lake puts pressure on disturbance-sensitive species.

Several traits that determine the life cycle have significant 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 has to deal with higher temperature (higher respiration) (Milbau et al., 2017). Furthermore, in the scenario of decreased nutrient and turbidity conditions a later reproduction is a winner trait probably because it implies a longer growth period. With a longer growth period it is more likely that sufficient seed biomass can be produced for regrowth during the next year.

In summary, the change of species richness depends on their eco-physiological traits and for each scenario there are specific traits that determine the success of submerged macrophytes. The learnings about the traits are highly informative especially in the light of the fact that few of these traits are studied under environmental change. Therefore, the approach is a useful tool to study loser and winner traits in the absence of empirical data and for making risk assessments under environmental change.

4.4.3 Conservation implications

Knowledge about the loss of potential species richness can warn against upcoming threats under different scenarios. In the presented shiny app conservation practitioners can see which lakes and depths 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 (Figure

4.3). They not just lose species richness, some of them become even uninhabitable for submerged macrophytes.

It is the aim of lake management and conservation within the European water framework directive monitoring is not to maximise species richness within lakes in general. 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 host under recent conditions a high share of the oligotrophic species that would be lost under increased nutrient and turbidity conditions (Table 4.2 and Figure 4.3). Therefore, to protect the freshwater biodiversity under the multiple stressors of land-use change, eutrophication, and climate change, the restoration and conservation of suitable refugia for vulnerable and rare species is crucial (Hofstra et al., 2020; Sarmiento Cabral et al., 2013).

4.4.4 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) are useful to answer multiple complex questions (e.g. alternative stable states, spatial processes, and competition), modellers must be able to interpret process interactions and overcome equifinality. 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 bring findings about the speed of the dispersal of macrophytes from lake to lake. A reason for a higher potential than observed species richness might be that environmental conditions are already constantly changing. It might be that the observed species simply have not yet reached their full potential habitat (García-Girón et al., 2019; Padial et al., 2014). Another factor which increased the mismatch might be inter-specific competition. 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-leave species have competitive advantages like a higher light availability and carbon use from air. Moreover, submerged species compete with each other for resources above and below ground mainly by different biomass-allocation strategies (J.-W. Wang et al., 2008). Despite the fact that these not considered processes would bring further insights into spatial processes and communities, the modelled distribution patterns of species richness already bring valuable insights.

Our experimental design provides starting points for further approaches that were not yet realised due to limited data availability. A likely reason for the underestimation of species richness within a lake might be the missing implementation of environmental heterogeneity within a lake. We use per lake the measurements of environmental parameters at one point in the middle of the lake, which just represents the general state of a lake, but not its internal heterogeneity. To depict the environmental heterogeneity within a lake a denser net of measurements would be necessary. Moreover, data from public monitoring is in the studied region just available for the bigger lakes (> 50ha). 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 would help to close a knowledge gap and to integrate those in analysis of future scenarios, as those lentic systems will change at the most extreme level. With a broader data base on small lakes, MGM could be applied to include those ecosystems within studies about future changes of macrophyte species richness.

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 also within 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.

4.5 Conclusion

Our study is the first to present scenarios for the effects of climate and land-use change of the potential species richness of submerged macrophytes for different lake types and species groups. Temperature increase should raise the number of potentially growing species, even without increasing the species pool by invasive species from warmer regions. The effect of increase or decrease turbidity and nutrients content depend on the lake type and depths. We see those future changes of species richness are multi-dimensional. The study helps to fill knowledge gaps concerning today's distribution and potential future developments of species richness of submerged macrophytes. It shows 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 conditions.

Acknowledgements – We thank the Landesamt für Umwelt Bayern (LfU) for data provision. Thank you, Dr. Egbert van Nes for his support in the re-implementation of the macrophyte model. Thank you, André Bauer und Tim Seizinger for your help in optimising the model code. A special thanks goes to Ludmilla Figueiredo, Jana Blechschmidt, and Stefan Fallert for comments on a first version of the manuscript. AL, MH, TH, UR, and JSC acknowledge funding by the Bavarian Ministry of Science and the Arts in the context of the Bavarian Climate Research Network (BayKliF).

Further material – Additional analysis are provided in Appendix C. The model is open-access available on GitHub: <https://github.com/AnneLew/MGM>. Data and data analysis code is stored on GitHub as research compendium: <https://github.com/AnneLew/LewerentzEtAl2022>. Furthermore, I developed a shiny app showing all scenarios as interactive maps: https://anne-lew.shinyapps.io/mgm_macrophytes_scenarios/.

Chapter 5

The image problem of macrophytes and how to face it with a computer game

A modified German version of this chapter has been published (non-peer-reviewed) as:

Lewerentz, A., Schantz, D., Gröh, J., Knotz, A., Mammen, S. von, & Cabral, J. S. (2021). bio-DIVERSity. Ein Computerspiel gegen das Imageproblem von Wasserpflanzen. *Mitteilungen der Fränkischen Geographischen Gesellschaft*, 67, 29–36.

Abstract:

Submerged macrophytes have an image problem in the public perception. They are perceived as interfering while bathing in lakes and as a general nuisance. Terms like “algae” or “weed” are used incorrectly and have negative connotations. In addition, the many valuable functions of macrophytes in the lake ecosystem and their beauty are often unfamiliar and difficult to show to a broader public due to the challenging accessibility. Nowadays, virtual simulations can give us access to places that are hardly accessible in real life. Computer games have the potential to bring nature conservation and sustainability issues to a broader audience. This paper presents the serious game bioDIVERSity which was developed as part of an interdisciplinary course of the working group *Games Engineering* at the *Institute of Informatics* in collaboration with the *Center for Computational and Theoretical Biology* at the *University of Würzburg*. The game aims to teach children about the lake ecosystem, macrophytes, and the effects of changing water quality and climate conditions on macrophytes. Information about the ecosystem can be collected as reward of mini-games. Depending on the success in a quiz at the end of each round, the water quality of the lake in the next round is improved or worsened. The water quality is visualised and has direct effects on the growth of the macrophytes simulated with a process-based macrophyte growth model. By making the ecological consequences visual, we expect an increasing awareness of the lake ecosystem and a better understanding of the importance of macrophytes. In general, the combination of serious games and mechanistic ecological models is an interesting interdisciplinary approach for teaching ecology and communicating models.

5.1 The image problem of macrophytes

„Algen, Gräser, Schlingpflanzen. Dieses Grünzeug wächst in unseren Badeseen. Wie gefährlich ist es für Badegäste?“ (bild.de, 2020).

„Unterschätzte Gefahr aus der Tiefe - Nach tödlichem Badeunfall: Wie gefährlich sind Schlingpflanzen in unseren Seen?“ (rtl.de, 2020)

These questions were recently raised in German mass media asking what danger macrophytes pose to swimmers. Macrophytes are hardly perceived by the general public in everyday life because they are rarely visible and tangible. If they are noticed while swimming or boating, they are often seen as disturbing, slimy, creepy, or disgusting. As in in the above cited articles, macrophytes are in German language often mistakenly referred to as “Algen” (algae) or as “Schlingpflanzen” (climbing plants). However, they are botanically only partially algae. Most macrophytes are “higher plants”, also called “vascular plants”. But macroalgae (algae that can be determined with the naked eye) are also macrophytes. Talking about “algae” most people seem to think about micro-algae such as green algae. They grow en masse in nutrient-rich lakes at high water temperatures, which means they are often associated with the “eutrophication” of a lake. The term “Schlingpflanzen” refers to climbing plants that twine around trees or pillars. It implies that these plants can actively twine around a bather and pull him down under the water surface, which is not true. Furthermore, in the English language there is a similar phenomenon. The term “weed” describes unwanted plants but is often used in an aquatic context for all types of macrophytes instead of only being used for unwanted mass development. Therefore, it implies that all of them are not wanted. All these terms stir up fears and bring with them a negative connotation, although there are no documented cases in which macrophytes harmed humans in Germany. Furthermore, the term “limnology”, which describes the whole field of research within lakes is highly unknown and papers using the term have a lower publication output and scientific impact than papers using e.g. “lake ecology” (Fontaneto et al., 2021). Therefore, scientists have to be aware of the consequences of using scientific jargon outside and inside the science community. It can cause misunderstanding or simply being less heard (Bullock et al., 2019).

Some people are afraid of macrophytes and of bathing in natural waters (Shank, 1987). For example, in the United States, where 37% of the population are not able to swim, around two thirds of the people are afraid of open bodies of water like lakes, rivers, or the ocean (Lachocki, 2012). This fear is not innate, it is learned e.g. by transmission of the parents’ fear (Shank, 1987). Horror movies such as “Jaws” (by Stephen Spielberg, 1975), which portray waters as unsafe and threatening, seem to have a relevant effect even for swimming in lakes (Cantor, 2004). However, assuming sufficient swimming skills, there are no life-threatening animals or macrophytes in freshwater lakes – at least in Europe. Nevertheless, the fear of these macrophytes can have dramatic consequences.

Touching macrophytes while swimming can trigger life-threatening panic reactions. A swimming accident due to a panic attack triggered by macrophytes in the Bergheim quarry pond near Augsburg, Germany, is just one example (Kinne, 2017). Due to the danger to life posed by such panic reactions, bathing bans are sometimes imposed in the event of excessive growth. However, besides bathing, there are more conflicts of use, such as disruption of boat traffic, fishing activities, or changes of the hydrodynamics in rivers (Verhofstad & Bakker, 2019). As a consequence, different management measures are applied, for example mowing macrophytes (Kuiper et al., 2017).

The occurrence of macrophytes is often misrepresented as “unhealthy for the system” (Oldorff et al., 2017), although they play an important role in the ecology of lakes (Figure 5.1 a). They bind nutrients, stabilise the sediment, and provide shelter and habitat for many animals (Thomaz, 2021). Therefore, the removal of macrophytes has negative effects on those ecosystem services (Thiemer et al., 2021). There are also “dis-services” (the contrary of ecosystem services) of macrophytes (Thomaz, 2021). These dis-services typically occur in reaction to species introductions, eutrophication, or other ecosystem changes (also possible after re-oligotrophication). In order to maintain the balance between the conflicts of use and the functioning of the ecosystem, not just expert knowledge about the linkages within the system is required for lake management. Communicating the importance of macrophytes is essential so that lake management measures taken are accepted by public users of the lakes (bathers, anglers, sailors etc) (Schenk et al., 2007).

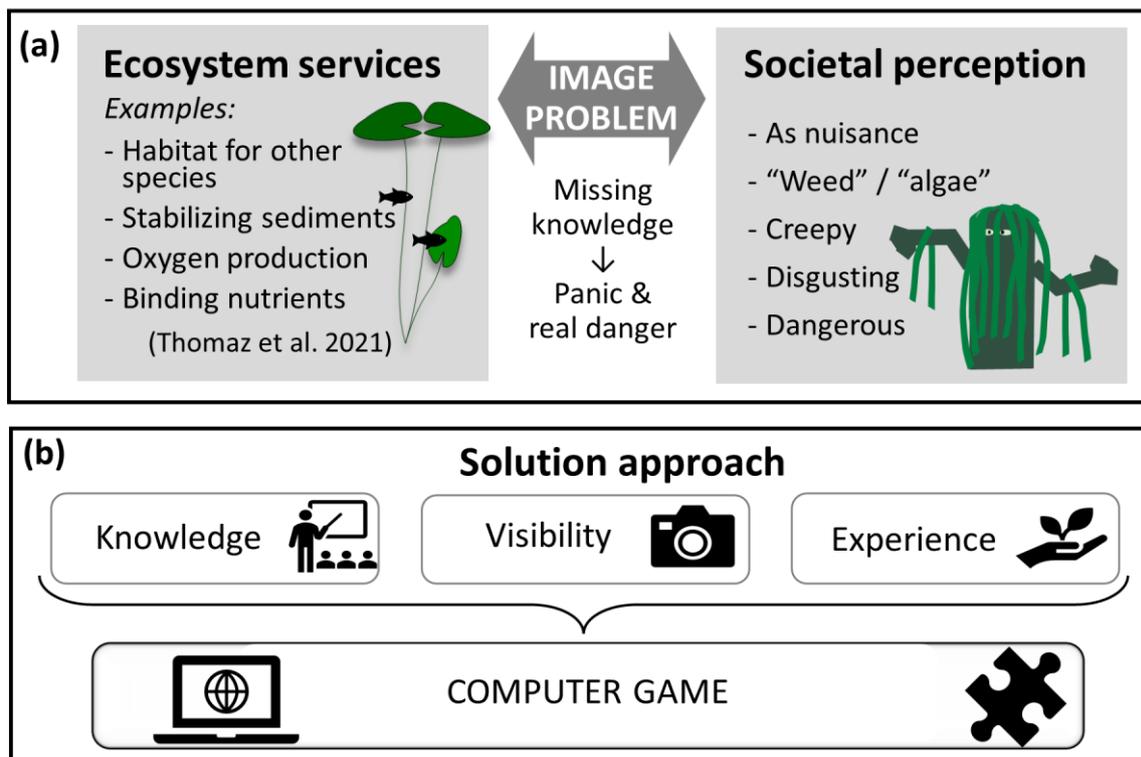


Figure 5.1: The image problem of macrophytes arises from the contrast between societal perception and ecological importance by providing multiple ecosystem services (a). A suggested solution approach to counteract this image problem is transferring knowledge, visibility, and experience by computer games (b).

Approaches to address the fear of macrophytes and their negative image (Figure 5.1 b) include (1) disseminating knowledge – both about the unfounded fear and about their importance in the ecosystem – (2) making them visible, and (3) experienceable.

Systematic desensitisation is a documented method to decrease the fear of swimming (Khatchaturian & Stillwell, 2022). On a small scale, aquariums can also contribute to learning about macrophytes. Most often, these offers are highly theoretical and created for adults. The importance, beauty, and diversity of macrophytes is rarely conveyed. The problem of being overlooked often affects not only macrophytes but all aquatic biodiversity (Kalinkat et al., 2017). One way to learn about the ecosystem and the macrophytes therein is by performing recreational diving, for example as it was done in the award-winning project “Diving for Nature Conservation” of NABU (Nature and Biodiversity Conservation Union of Germany) and VDST (Association of German Recreational Divers). However, the path via recreational diving is a very long one and can therefore not be applied across the board to improve the image of macrophytes.

5.2 Virtual contributions to environmental protection

“Serious game” is a term describing games that are not just for entertainment, but also impart knowledge and skills (de Freitas & Liarokapis, 2011). They offer a methodologically and scientifically sound approach for game-based learning by testing consequences of one’s own actions and learning behavioural patterns and contexts in an intuitive way. The emotional connection of the player to the subject of the game can support the absorption of the content (Wouters et al., 2013) and motivation (Larson, 2020; Subhash & Cudney, 2018; Zhonggen, 2019). The combination of motivation-enhancing elements with knowledge and competence transfer has established itself as a separate research and application field under the term “gamification” (Baptista & Oliveira, 2019; Deterding et al., 2011; Seaborn & Fels, 2015). Serious games have a particularly large potential for communicating nature conservation and sustainability issues, especially to a younger target group (Sandbrook et al., 2015). The use of serious games in the field of sustainability education is increasing, but it is still very complex and expensive, since it demands highly interdisciplinary skills and knowledge of many different areas of expertise ranging from game engineering and game design to ecology and didactics (Stanitsas et al., 2019).

Serious games can be offered on a variety of platforms and are not tied to stationary facilities – compared to elaborate installations in museums, for example in the private sector as well as in schools and libraries. Desktop computers as well as powerful tablets and smartphones can offer sufficient computing power. Content can be made available online with little effort and thus reach a large circle of interested parties. In addition, young formats such as augmented reality (AR) and virtual reality (VR) are increasingly present. Both can serve as a way to make difficult-to-reach places experiential, create immersive experiences, and achieve learning outcomes. VR – the experience of a synthetic, virtual world that engages one’s sensory perception via a display worn on the head, for example – can be used to immerse oneself in an unfamiliar environment (Checa & Bustillo, 2020). This technology can be used, for example, to explore the underwater world of the Baltic Sea, simulating a real-life dive experience (NABU, 2020). Moreover, it can be used to show

the effects of climate change on fish (Pimentel et al., 2019). With AR – the augmentation of the real world with additional information, for example, via the video image of a phone’s camera – one’s own surroundings can be perceived in a different way. “AR butterfly gardens” are an example in which real plants serve as the basis for a simulated ecosystem and virtually displayed caterpillars and butterflies of various species can be studied (Tarng et al., 2015). It has been shown in a study that these AR gardens increase students’ interest and motivation to learn about the ecology and biology of butterflies (Tarng et al., 2015). This is particularly relevant when the cost of a real butterfly garden and the effort required to create and maintain it are too high. However, the majority of serious games still use established formats such as applications for screens on the desktop computer or mobile phone, as this enhances the accessibility.

The technical barriers for the implementation of new virtual products are constantly falling, and with them the costs of the development process. Game engines make it possible to create highly complex virtual worlds with relatively little effort (Epic Inc., 2020; Linietsky & Manzur, 2020; Unity Inc., 2020). Technologies that represent the industry standard are now often available under licences that facilitate their use in the education sector. The now almost universal standardisation of web technologies also makes it possible to develop platform-independent applications for HTML and JavaScript at low cost. Those platforms can be easily accessed in web browsers on a wide variety of devices.

In the context of an interdisciplinary course of the working group *Games Engineering* and the *Center for Computational and Theoretical Biology* of the *University of Würzburg*, a serious game about macrophytes was developed. The goal was to convey knowledge about lake ecosystems and the effects of water quality and climatic conditions on macrophytes to children at the age of 10 – 12 years. The interaction of macrophytes, ecosystems, and the effects of human interventions should be made visible, and the ecological interrelationships should thus be made comprehensible.

5.3 The computer game biodiversity

The developed prototype of bioDIVERsity combines a process-based growth model for macrophytes (Lewerentz et al., 2022) with the virtual underwater world of a lake. The model simulates the life cycle of macrophytes from germination and growth to reproduction, where the growth rate of each individual depends primarily on light availability, nutrient availability, and water temperature. The water temperature follows an annual pattern and is consistent throughout the water column. The available light depends on the particular depth in the lake, the seasonally changing solar radiation, and the turbidity of the water. The model is written in the open-source programming language Julia (Bezanson et al., 2017), which is fast, open-source, and increasingly popular in the field of numerical modelling. The game represents an interactive simulation in which the player can influence the environmental parameters at runtime. Consequently, the effects of environmental changes become more comprehensible. This is an approach that has often been successfully used to make complex systems understandable (Narayanan & Kidambi, 2011).

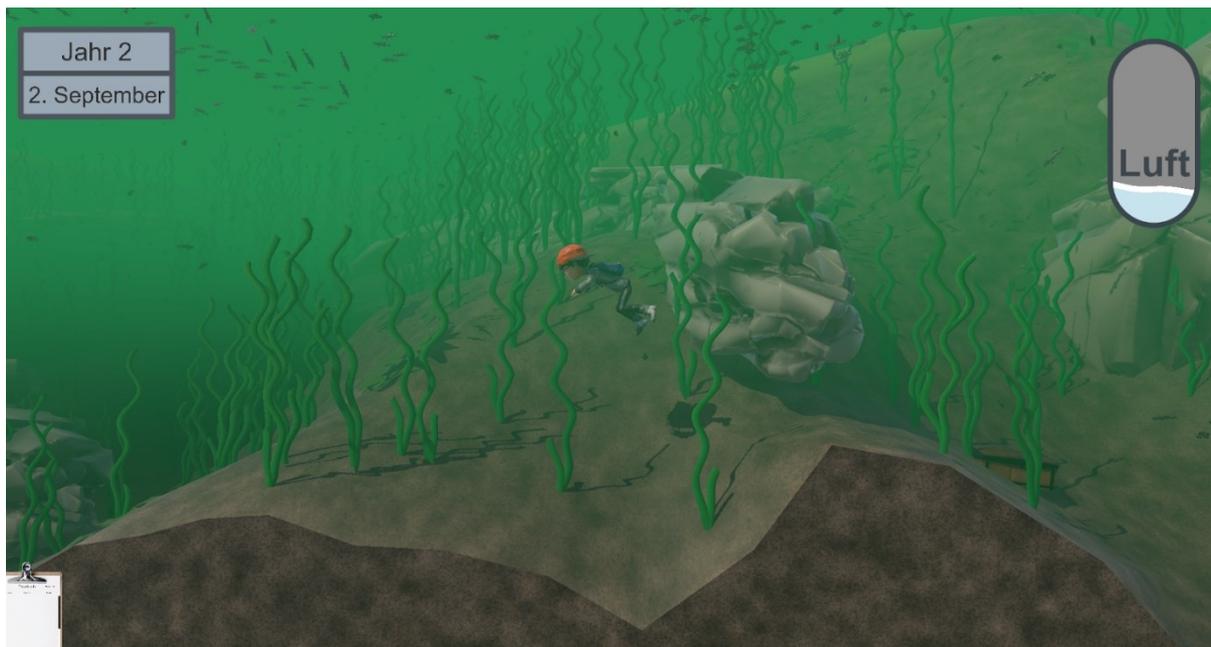


Figure 5.2: The underwater world as displayed in the game with animated growing aquatic macrophytes and schools of fish, the game character (diver, in the centre) and the user interface with date display (top left), air display (top right) and diary (bottom left). The coloration of the water and the visibility in the water change dynamically from light and blue (clear and cold water) to dark and green (turbid and warm water) depending on the water quality.

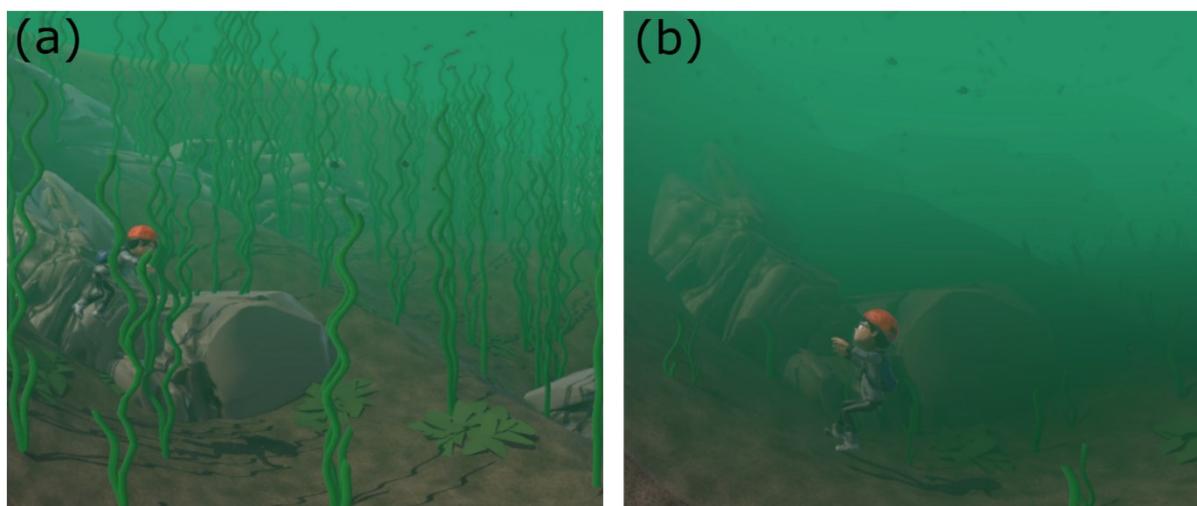


Figure 5.3: Comparison of plant growth on a given day (May 21) in (a) a scenario with clear water and strong plant growth after successfully passing the quiz and (b) a scenario with high turbidity and low plant growth after incorrectly answering the quiz.

The player controls a stylized animated character that swims and dives in a lake. A limited supply of air is available for diving, which must be refilled by emerging (Figure 5.2 and Figure 5.3). Otherwise, the character automatically cannot move anymore and drifts slowly to the water surface. The objective of the game is to correctly answer background questions about the ecosystem of the lake and the macrophytes. After a simulated year in the game, the player is confronted with a quiz (Figure 5.4). Each quiz contains three questions about an overall theme that changes with each

year. The necessary information is obtained during the course of the game by completing a series of mini games (Figure 5.5 a – c). The game character obtains the tasks from another person sitting on a boat. The tasks of the mini games are chosen related to the theme. For example, garbage has to be collected or a pipe that discharges sewage into the lake has to be closed. This motivates the player to remember and apply the knowledge gained, thus reinforcing the learning effect. Further information about the ecosystem is hidden in treasure chests that can be found in each round at different places. Depending on the result of the quiz, the turbidity of the water and thus the growth of the macrophytes is either positively or negatively affected during the following year (Figure 5.3 and Figure 5.4). Since turbid water reduces the visibility of objects under water, this directly affects playability and makes progress more difficult. The knowledge can be acquired within four rounds corresponding to four years, each lasting five minutes. Each round covers one of the following topics: (1) light in the lake; (2) phytoplankton; (3) nutrients in the lake; (4) importance of macrophytes.

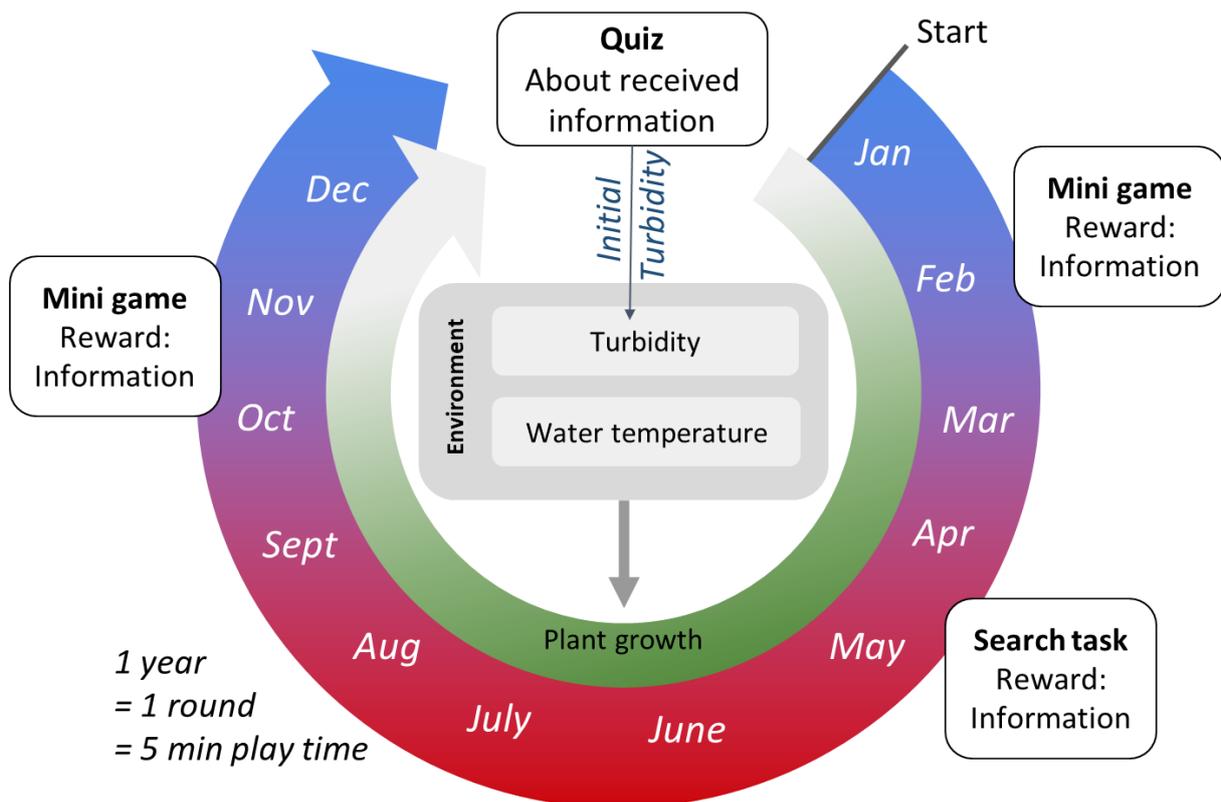


Figure 5.4: Game flow following the annual cycle of plant growth and environmental variables (progress arrows). In the centre is the simulation model in the Julia programming language (grey box), which is parameterized by the results of the quiz (white boxes). Its output, in turn, controls the water quality of the lake and the growth of the plants.

The turbidity and temperature of the water are used as the main factors influencing the growth of macrophytes in the model simulation. The changes in both factors determine the appearance of the water. The water temperature is reflected by the water colour (blue corresponds to cold, green corresponds to warm), the turbidity of the water by its transparency.

During the development of the game, special attention was paid to the aesthetic design of the underwater world: In addition to the representation of the water with dynamic turbidity (Figure 5.3) and a realistic depth-dependent reduction of the light spectrum, fish were added that show lifelike simulated schooling behaviour (Figure 5.5 d). To support the underwater experience, atmospheric background music was used, which changes depending on the season, turbidity, and depth in the lake. In winter, an additional instrument supplements the music to provide an additional stimulus during the season when vegetation is scarce. With increasing turbidity and depth in the water, higher sound frequencies are cut off to emphasise the immersion in the water. Sound effects, such as the creaking when chests are opened, increase the immersion effect while playing the game.

In total, bioDIVERSity tries to increase the user's motivation and to focus his or her attention on the lake's ecosystem by setting incentives inspired by games (e.g., challenges and rewards) and by offering an experienceable environment. The aim of the game is to put the lake into a good ecological state. This approach connects scientific facts in the form of a mechanistic model with success and positive emotions during the game play.

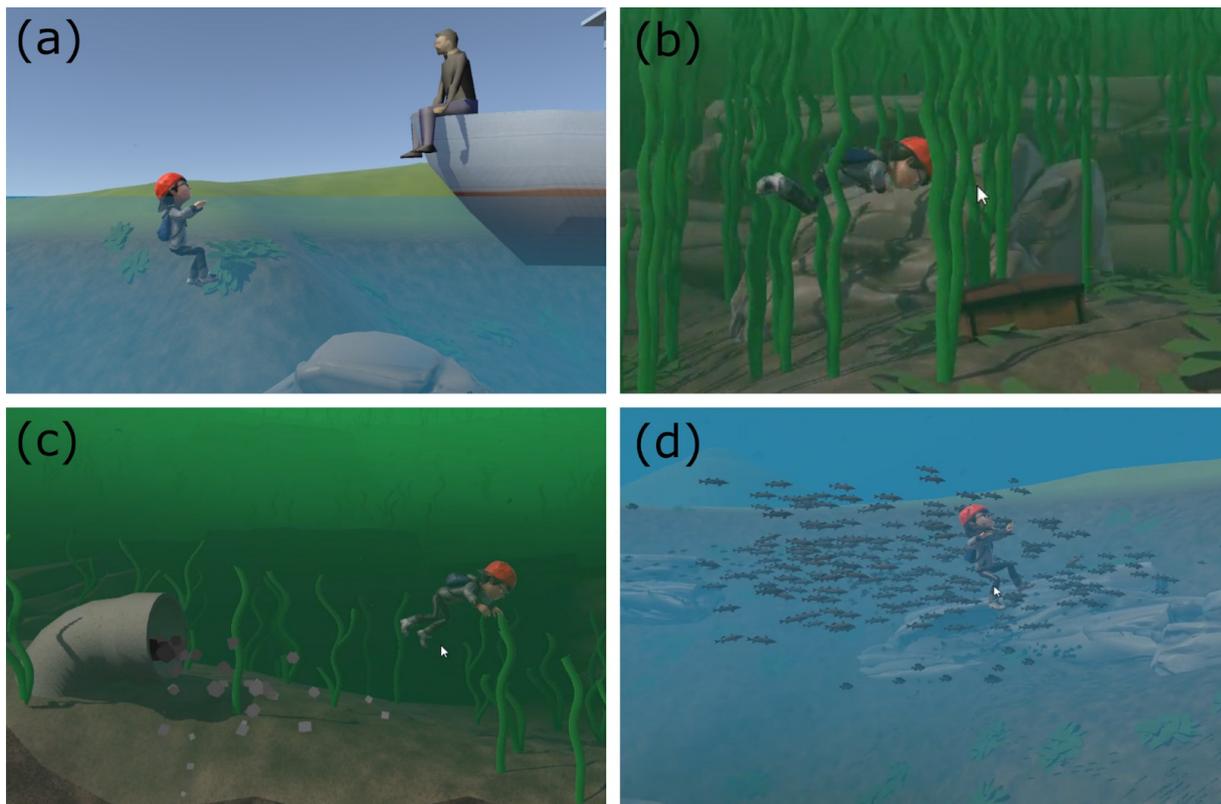


Figure 5.5: Design of the underwater world and the game elements: The game character obtains tasks from another person sitting on a boat (a). One task is to find treasure chests (b), another is to close drainage pipes with a stone (c). To make the underwater world look more alive, there are different schools of fish and single fish (d). The water temperature is reflected in the representation of the water: In winter, the water is cold and therefore blue (a, d), while in the warmer summer (b, c) it is shown in green.

5.4 Next steps

The next step in the game development process would be an evaluation and test phase with the target group. With this, we would aim to figure out the degree to which the formulated goals of knowledge transfer, experientiality, and visibility are achieved with the game. In order to obtain representative data from which meaningful conclusions can be drawn, the evaluation must also inquire about the prior knowledge of the children playing the game. The initial knowledge about macrophytes, the attitudes toward them, and the previous experiences with other games may have a significant impact on the children's experience with the game. After playing bioDIVERSity, children's knowledge of macrophytes would be re-surveyed along with their experience with the game (fun, immersion, etc.) to determine the increase in knowledge and compare it to a control group that did not play the game. On the basis of the evaluation results, the game could be improved afterwards.

In addition, the project could be developed further in a variety of ways. So far, only one aquatic plant species has been simulated. However, in order to live up to the title of the game, bioDIVERSity, it would be desirable to add more species to the simulation. Furthermore, more possibilities to interact with the environment, such as ways to influence the water temperature or the water level through interactions, could help to increase the learning effect with regard to multiple environmental drivers and their interactions. A larger underwater world, possibly also designed as levels to be unlocked, would increase the attractiveness of the game. Another idea is to develop the game further in order to make it suitable to other age levels, e.g. with a focus on the knowledge of macrophyte species. Furthermore, further consideration should be given on how precisely prejudices and media-facilitated misconceptions can be eliminated more directly while playing. However, a requirement to further develop the project is to improve the connection between the model language (Julia) and the game engine (Unity) to achieve more stable and flexible interaction possibilities. The first steps to develop a Julia plugin for Unity have already been taken.

Finally, it would be desirable to make the game accessible to a broader audience. The game could be used at home by children with an interest in the topic; it could also be integrated into the school curriculum; and it could be used in educational institutions like museums, or at research events for children such as girls' days or open house days of research institutions. Testing with different target groups, fine-tuning the level of difficulty, and finally publishing the game for widespread devices such as smartphones would be necessary in order to achieve this goal.

5.5 Conclusion

BioDIVERSity is a prototype of a computer game that provides young people an easy access to the underwater world of lakes. The aim is to raise interest and curiosity, and to impart knowledge at the same time. The knowledge transfer is embedded in an alternating playful and challenging sequence, which is intended to increase motivation and knowledge retention. Although the game does not explicitly aim to reduce overcoming phobias towards macrophytes, imparting knowledge about the underwater ecosystem could lower the hurdle for a casual contact with macrophytes.

Nevertheless, this cannot replace real contact with nature, but should be seen as a supplement and extension of real nature experience. In the best case it can serve as an encouragement to go into nature with more open eyes and an increased interest. Children who have an affinity for computer games and have little contact with nature are taught about ecology and thereby gain a better understanding of processes in nature.

If the game can help to decrease the image problem of macrophytes still must be tested. We hypothesise that an increase in knowledge about macrophytes and the virtual contact with the species already helps to decrease the fear of the unknown. In the future, more games, but also VR and AR applications could be used to help the frequently overlooked biodiversity in freshwater to be more noticed, appreciated, and consequently also protected.

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Further material – The prototype of the game can be tested upon request. Videos (German / English) introducing the game, explaining the game mechanics, and visualising the underwater experience can be found on the project website: <http://bayklif-bliz.de/de/2020/09/14/computerspiel-wasserpflanzen-2/>

Part III
General discussion



Chapter 6

Empirical and modelling insights into changing macrophyte species richness in space and time

In the previous chapters, I took several steps to study the spatiotemporal dynamics of freshwater macrophytes in Bavarian lakes under environmental change by following multiple circuits within the coupled empirical and modelling cycles (Figure 6.1 a). The study questions, results, and conclusions of each step are summarised in brief in Figure 6.1 b. I started with a data analysis of empirical field observations (Chapter 2). The aim was to obtain a general overview of species richness and drivers of submerged and emergent species richness in natural and artificial lakes within Bavaria. I found a higher species richness of submerged macrophytes in natural lakes than in artificial lakes and that the richness of submerged species is better explained by physio-chemical lake parameters than the richness of emergent species. Based on the determined environmental drivers identified in the data, I formulated hypotheses about the arising influences of future climate and land-use changes on the future species richness of submerged macrophytes. Following that, I started a second empirical cycle. I studied the species richness distribution of submerged macrophytes along the depth gradient of natural lakes and its environmental drivers and recent shifts of the distribution pattern (Chapter 3). This study is the first comparative assessment of the depth diversity gradient (DDG) of macrophytes showing that this short-scale gradient within freshwater lakes reveals detailed information about influencing factors on species richness. I did not find a general trend of the hump-shaped DDG within recent years, but single lakes showed trends in different directions. Next, I used a mechanistic, eco-physiological Macrophyte Growth Model to verify the explainability of the observed patterns by modelling eco-physiological processes (Chapter 4) following the modelling cycle. Furthermore, I explored changes of the potential species richness of macrophytes under different environmental change scenarios. I verified the observed species richness patterns and identified that turbidity and nutrient changes (-25% / +25%) have a higher impact on the potential species richness of submerged macrophytes than the selected temperature increase (+1.5 °C / +3.0 °C). These changes are depth dependent and lake type specific. Moreover, I identified species traits that make the species “winners” or “losers” within a scenario. Finally, I described the image problem of macrophytes and used the eco-physiological macrophyte growth model to develop an interactive computer game (Chapter 5). The aim of the game is to make the underwater world of lakes experienceable and to share knowledge on macrophytes to children. This interactive tool is a way to communicate the model as part of the modelling cycle (Figure 6.1 a).

In the following sections, I will discuss implications of these studies for ecological theory and for conservation practices. Finally, I will give an overview of open research questions that arise from these studies.

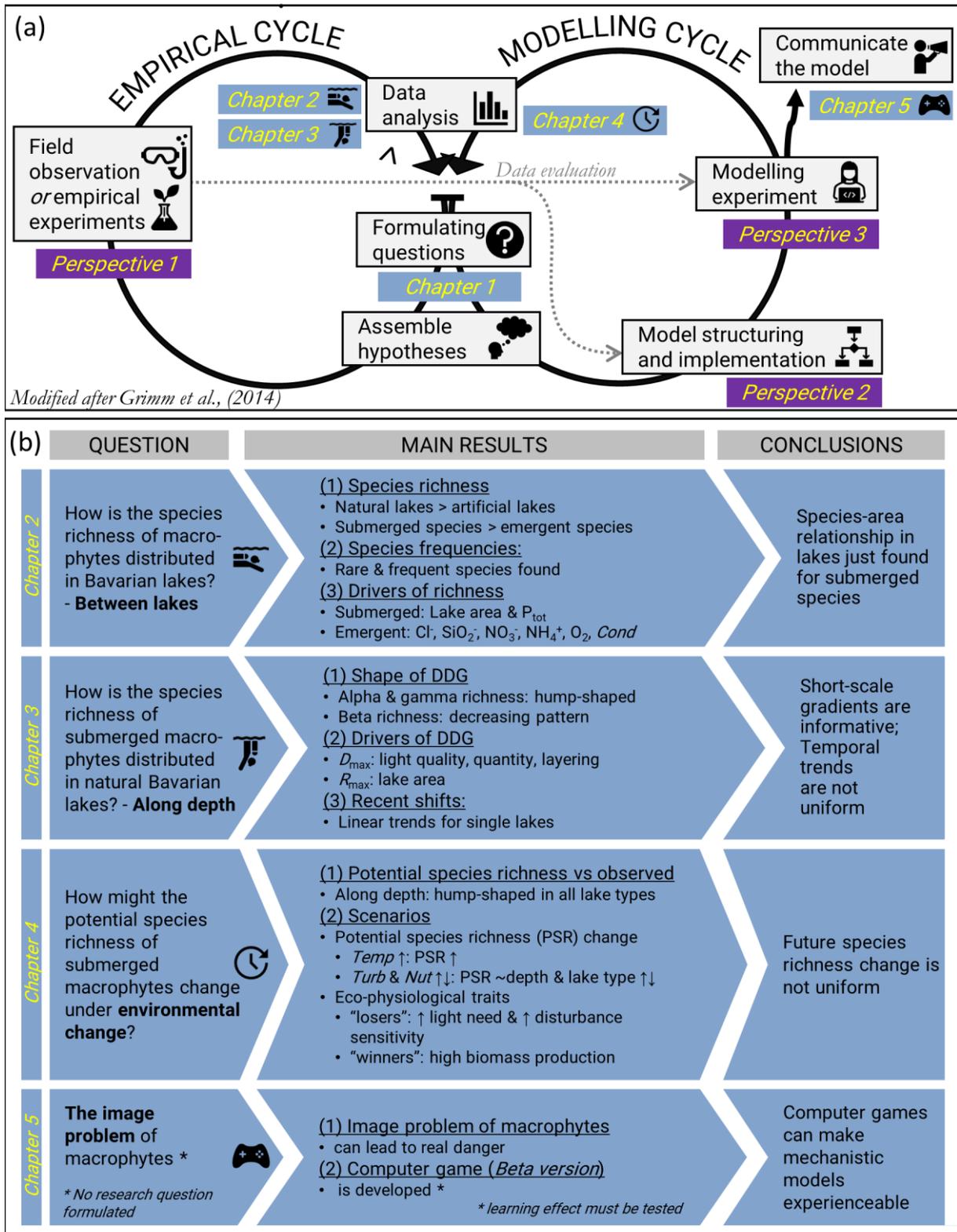


Figure 6.1: Chapters of the thesis and discussed perspectives located within the coupled empirical and modelling cycles, modified after (Grimm et al., 2014) (a). Summary of the main questions, results, and conclusions of the chapters 2 – 5 (b). Abbreviations / symbols: P_{tot} (total phosphorus), Cl^- (chloride), SiO_2 (silicon dioxide), NO_3^- (nitrate), NH_4^+ (ammonium), O_2 (dissolved dioxygen), $Cond$ (conductivity), DDG (depth diversity gradient), D_{max} (depth of the maximum richness), R_{max} (maximum alpha richness within the depth gradient), PSR (Potential species richness), $Temp$ (water temperature), $Turb$ (turbidity), and Nut (limiting nutrient content).

6.1 Implications for ecological theory

Understanding biodiversity patterns across space and time is a central task of biogeography. It builds a crucial basis for being able to warn of potential threats for biodiversity. Especially in freshwater biodiversity research there are various knowledge gaps concerning the response of biodiversity to multiple stressors (Maasri et al., 2022). However, predicting species ranges and species richness is a challenging task as it includes different species, dimensions, and components (Evans et al., 2016).

6.1.1 Modelling macrophytes

In Chapter 2 and Chapter 3, I used statistical models to identify drivers of species richness. By applying the space-for-time substitution approach which assumes that spatial and temporal variation are equivalent (Blois et al., 2013; Pickett, 1989), the findings can help to formulate hypotheses about future changes dependent on the changes of the input drivers. However, the space-for-time substitution approach is criticised for underestimating species loss (França et al., 2016), e.g. because more than one process could be the reason for the observed patterns (Damgaard, 2019; De Palma et al., 2018). Furthermore, not all temporal processes can be replaced by space: changes in the environment can lead to delayed ecosystematic reactions such as extinction debts (Figueiredo et al., 2019). Correlative species distribution models are subject to the same challenges (Zurell et al., 2016), since they also obtain their information from correlations in space and predict into the future. Especially if the future environmental conditions are beyond the studied conditions, the space-for-time substitution approaches cannot be applied.

By contrast, mechanistic models reproduce processes instead of correlations. Therefore, they can help to understand biodiversity patterns across both space and time (Cabral et al., 2017). In particular, the effects of new conditions and multiple drivers can be investigated. However, most data-driven, process-based range models require long computational runtimes and detailed information for each species, which are often not available for a broad range of species, and always have to balance the trade-off between simplification and complexity (Evans et al., 2016; Zurell et al., 2016). Therefore, an often-used approach is to simulate selected characteristic species representing functional groups and to draw proxy conclusions about biodiversity based on them. To overcome the data-availability problem, I chose to simulate random species combinations within different functional groups that were defined on the basis of expert knowledge (Chapter 4). I could show that combining a data-driven model with a theoretical framework can yield valuable insights which will be discussed in the following sections.

6.1.2 Macroecological pattern of macrophytes

One concept to explain distribution of species richness in space is the species-area relationship (Arrhenius, 1921). It states that the number of species increases with increasing areas. Like several studies before (Alahuhta et al., 2017; Søndergaard et al., 2005), I confirmed that area can be a main explanatory driver of macrophyte species richness, but only for submerged species (Chapter 2). It not just influences the general gamma richness (Chapter 2), I could also show that it has a major impact on the height of the DDG peak along depth. Furthermore, I showed that macrophyte

species richness responds to resource availability. The main resources for macrophyte growth are light availability, which is depth dependent, and nutrient availability. In Chapter 2, I found phosphorus as a limiting factor of species richness, while in Chapter 3 light quality, light quantity, and layering depth turned out to determine the depth of the peak of diversity. However, all three factors correlate with each other (Chapter 2). If nutrient availability is high, this leads via increased algae growth to a decrease of light availability. Moreover, high water temperature can result in high nutrient levels as a consequence of resuspension processes. Due to these connections, it is hard to disentangle the mechanisms via statistical models (Chapter 2, 3). Therefore, I used a mechanistic model to test the influence of the drivers on macrophyte growth (Chapter 4). The potential species richness was maximal under intermediate lake conditions. This might support at first look the intermediate productivity hypothesis (Grime, 1973a, 1973b), but the reason seems not to be the competition at high resource availability, but rather the availability of antagonistic resources itself. In general, this approach shows that mechanistic models can help to understand macroecological patterns of macrophyte species richness.

Macrophyte species richness is changing in time. As the study on the depth diversity gradient could show (Chapter 3), the pattern is quite stable within most of the lakes during the last years. However, for single lakes, a significant trend towards more species in either shallower or deeper water was found. This indicates that at this short time scale, no general influence of climate change on submerged macrophyte species richness can be observed. Despite this lack of a general trend, local changes within individual water bodies were indeed detected. However, by studying scenarios of potential changes of environmental drivers (Chapter 4) and testing the direct effects of environmental drivers (expectations formulated in Chapter 2), it became clear that the direction of change (increase or decrease of species richness) not just depends on the direction of the driver but also on the initial situation within the lake. In general, I could confirm the expectation of better growth under increased water temperature, enhanced nutrient supply and under decreased turbidity (Chapter 2). However, while macrophyte growth in clear lakes could profit from increased nutrient supply and is less affected by simultaneously increased turbidity, macrophyte growth in turbid lakes decreased under the same environmental scenario. Therefore, approaches to identify general trends of species richness changes within multiple lakes can be insufficient, as the reactions can be lake type specific and depth dependent.

6.1.3 Eco-physiology of macrophytes

In Chapter 5, I applied a Macrophyte Growth Model (MGM) to study the shifts of eco-physiological traits. I could identify that species have a disadvantage under increased turbidity if they germinate later than others. This might be due to the higher water temperatures, which increase respiration costs, in addition to the reduced photosynthesis rate caused by the turbidity. A negative net primary production under increased water temperature is e.g. also reported for marine macrophytes such as *Zostera marina* L. beyond 30 °C (Hammer et al., 2018; Marsh et al., 1986), or for microalgae (Huesemann et al., 2016). Besides that, I could mechanistically show the negative effect of wave disturbance sensitivity under increased turbidity, since even though shallow areas in the lake offer enough light, they do not provide a stable habitat. That different macrophyte species

have a different sensitivity towards wave disturbance has already been shown in a mesocosm study (Van Zuidam & Peeters, 2015), where, besides the mechanical disturbance, the waves also induced higher turbidity. These findings suggest that reducing mechanical stress from large ships or the creation of wind shadows e.g. through afforestation would help to protect submerged macrophytes in shallower areas of lakes. However, how future climate change will change wind-driven wave heights and frequencies in lakes is not yet clear. In general, I was able to show how mechanistic models can help to gain insight into macrophyte traits and to assist the development of conservation measures.

6.2 Implications for conservation practices

There is no doubt that macrophyte species are a key element in the functioning and richness of freshwater systems (Bornette & Puijalon, 2011). In global studies, freshwater diversity was found to be highly threatened (Williams-Subiza & Epele, 2021). In Germany, water quality is, on the one hand, improving due to political requirements (F. Murphy et al., 2018), but on the other hand, lakes are already affected by a changing climate (Arvola et al., 2010; Dokulil et al., 2010; George, 2010).

I showed that among both emergent and submerged species there is a high percentage of rare species in Bavaria's large lakes (Chapter 2). Moreover, under changing environmental conditions lakes can lose species (Chapter 4). The key drivers of species richness between lakes and along depth in both the empirical and the modelling study were phosphorus content as well as light quality and quantity (Chapter 2, 3, 4). This confirms the importance of reducing nutrient input for species conservation. However, the observed and predicted trends varied for different lake types and depths (Chapter 3, 4). Therefore, conservation measures at regional and local scale are necessary, as lakes can react very differently. These measures can e.g. include improvement of wastewater treatment systems or reduction of fertilisation in agriculture. The concept of protected areas – preserving distinct parts of a lake from human use – is not sufficient in preventing lakes from human pressures, since they are connected with the surrounding areas via inflows (Mammides, 2020). Therefore, a holistic view of monitoring on the landscape level, as the European Water Framework Directive (EU-WFD) demands, must be combined with individual measures for each lake. However, just 2.8% of all lakes within Germany are monitored within the EU-WFD (Meunier, 2016). Information about small lakes is missing although they are in general at higher risk for changes (Williams et al., 2004). Still, the EU-WFD monitoring has a great potential to be the base of scientific studies about biodiversity.

To stop the global decline of biodiversity, societal awareness leading to political action is needed. The global decline of biodiversity is much less communicated in the media than climate change although both topics are just as thoroughly investigated (Legagneux et al., 2018). Therefore, outreach of scientific findings on all levels, but especially to the general public, media, policy makers, and schools, must be strengthened and valued more highly as part of science (Bickford et al., 2012). As I showed in Chapter 5, macrophytes, their functioning within the ecosystem, and their diversity are so little known or even perceived as negative. Therefore, I suggest that communication about macrophytes must start with basic knowledge. Future possible changes in species composition and

biomass production (Chapter 4) could lead to further conflicts, often also based on misunderstandings and ignorance. To prevent this, education and communication on the topic is crucial. Mechanistic models can be a promising tool in environmental education to make processes and consequences of action comprehensible via ecological serious games or applications like shiny apps to interactively explore consequences of global change (see links to online resources in Appendix A).

6.3 Perspectives

In the previous chapters, I followed the empirical and modelling cycles by combining analysis of field data and data-driven mechanistic models to obtain an overview of the distribution dynamics of macrophyte species richness in space and time (Figure 6.1 a). These analyses raise new questions that could be answered in new empirical and modelling circuits.

6.3.1 Emerging empirical studies

In the modelling study (Chapter 4), I identified loser and winner traits of macrophytes under changing nutrient and turbidity conditions. These findings could be used as a basis for further empirical studies. For example, after identifying real macrophyte species, the values of their respective winner and loser traits could be measured in mesocosm experiments. By exploring which real species match the determined loser traits, one can then identify respective loser species that are especially threatened under changing environmental conditions. This could help to determine thresholds of environmental variables for species win or loss.

In general, identifying parameters that are sensitive to environmental change from a perspective of ecophysiology helps to minimise further experimental expenditures for empiricists.

6.3.2 Emerging model extensions

This thesis has shown the influence of phenology on which macrophytes are winner or loser species. However, within the MGM the whole phenology of the species is set along fixed dates, although studies show that the phenology of macrophytes is influenced by environmental factors such as light, water level fluctuation, or temperature (Calero & Rodrigo, 2019; Holzhausen et al., 2018; Torso et al., 2020). Integrating these processes into the MGM would start another modelling cycle (Perspective 2, Figure 6.1 a). To that end, more information about the mechanisms that trigger e.g. timing of germination or seed production would be necessary. It is not yet clear if germination of macrophytes depends on a fixed date, or if it is triggered by environmental variables such as light or temperature. This information could be retrieved with field observations or mesocosm studies. Subsequently, the influence of multiple climate and water quality change drivers on the annual life cycle could be tested in new modelling experiments. This broadened knowledge about macrophyte phenology could help to understand the consequences of the interaction of multiple drivers for macrophyte growth and distribution, which are not yet disentangled.

When focusing on water temperature, nutrient content, and turbidity, I found a depth- and lake type-dependent effect of coupled nutrient and turbidity changes on submerged macrophyte species richness (Chapter 4). However, global change evokes more influences on lake ecosystems that

might affect macrophytes (Adrian et al., 2009; Kraemer et al., 2021; Lind et al., 2022; Moss et al., 2011; Whitehead et al., 2009; Woolway et al., 2020). In Chapter 3, I showed that besides light quantity, light quality also influences the pattern of the depth diversity gradient. Humic substances in freshwater affect light quality and are accumulating due to global change (Reitsema et al., 2018). In mesocosm experiments, this so-called brownification of lakes, when combined with warming, leads at low levels to a better growth, but at high levels to a collapse of charophytes (Choudhury et al., 2019). By implementing the different influences of wavelengths on macrophyte growth and photoinhibition into the MGM as a new modelling cycle (Perspective 3, Figure 6.1 a), the non-linear reactions of brownification on macrophyte growth could be determined. In general, climate and water-quality change have multiple direct and indirect effects on aquatic systems that are highly correlated. Integration of different models such as lake models (including lake physics, e.g. stratification), land-use models, food-web models (including pressures of herbivory on macrophyte growth), or substance emission models on catchment scale (including nutrient and sediment input in lakes dependent on land-use change) with the Macrophyte Growth Model could enable a more holistic insight into the changes of macrophyte growth and communities (Cabral et al., 2022).

6.3.3 Emerging modelling experiments

I showed in Chapter 4 how the potential species richness of theoretical species – i.e. random species trait combinations within expert-derived trait ranges for oligotraphentic, mesotraphentic, and eutraphentic species groups – would react to changing environmental drivers. It remains an open question whether the observed species are covered within these theoretical ones and if they would react in the same way. Therefore, a next step would be to parameterise the model for the observed species. As trait databases of macrophytes are still lacking or under initial construction (Dalla Vecchia et al., 2020; Iversen et al., 2022), other methods to optimise the model based on the observed species distributions to inversely estimate the parameters could be a solution (Evans et al., 2016). However, methods to iteratively test solutions of the model, comparing the output with the desired distribution such as Differential Evolution (Storn, 1996; Storn & Price, 1997) can be time consuming, since complex mechanistic models can have runtimes ranging between seconds and minutes, which, when multiplied by thousands to hundreds of thousands repetitions, result in long computing times. One method to shorten the model runtime could be to first emulate the model with a faster model, e.g. by training a Deep Neural Network (DNN) with previously generated input and output data of the ecological model (Lim & Wang, 2022; S. Wang et al., 2019). The trained DNN could then be used for optimisation to try out more parameter combinations more quickly. First attempts to emulate the MGM with a DNN look promising (unpublished results). Alternatively, a DNN could also serve as an inverse estimator of parameters, if trained to predict the model input parameters from distribution and environmental data. This idea is already successfully applied in various other fields (Mitra et al., 2020; Xiao et al., 2021). As deep learning becomes increasingly important in ecology research (Pichler & Hartig, 2022), this might be a promising approach for multi-species optimising of mechanistic models.

Even without implementing the above-mentioned improvements to the model, further questions could be tackled with the current version of MGM. Examples for such questions are:

1. How might a future increase of water level fluctuations due to the changing climate influence the growth and species richness of submerged macrophytes?
2. Will the biomass production of submerged macrophytes increase or decrease under changing environmental conditions?

In this thesis, I studied in depth the regional distribution of submerged macrophytes in Bavaria partly because a sound database of the macrophyte distribution is already available for that area, which is a prerequisite for data-driven models. However, in many other regions human pressure on lakes is increasing more rapidly (Mammides, 2020) and the so-called “megadiverse” countries of freshwater richness in the tropics are less studied (Williams-Subiza & Epele, 2021). The MGM could also be applied to other regions. This might help to better understand and assess the consequences of increasing human pressures on a global level.

6.4 Conclusion

Bavaria’s freshwater lakes are undergoing a transformation: on the one hand, water quality is improving due to the implementation of political decisions, but on the other hand, these lakes face a climate that is already changing. In this thesis, I have provided focused insights into the status of their submerged species richness and model-based hypotheses for future changes by combining empirical research with mechanistic modelling (Figure 6.1). In particular, I have shown that Bavaria’s large lakes host a high species richness of macrophytes that is driven by lake area and phosphorus content. To emergent macrophytes in those large lakes, the species-area relationship is not applicable. The depth distribution of macrophyte species richness is hump-shaped and does not show a general trend within recent years. However, I have confirmed with a process-based model that mainly changes in water turbidity and nutrient availability can have a non-uniform depth and lake-type dependent effect on species richness. Besides providing insights into changes and processes of species richness, the developed serious game shows that eco-physiological models can be made useful for outreach and immersing experience.

Macrophyte species richness is crucial for freshwater ecosystems, and the findings of my study promote a better spatial and temporal understanding of the distribution of species richness along different scales and through multiple drivers. The coupling of empirical studies and process-based simulation modelling contributes to ecological theory of diversity gradients and conservation efforts under future environmental changes.

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Appendices



Appendix A – Online resources

This is a collection of all open-access online resources that complement the thesis. The resources are assigned to the individual chapters of the thesis.

Chapter 2

Processed data and code of data analysis are provided online as research compendium, structured as R package:

- https://github.com/AnneLew/LewerentzCabral_Macrophytes-Bavaria

Chapter 3

Processed data and code of data analysis are provided online as research compendium, structured as R package:

- Published version: DOI: 10.5281/zenodo.5255571
- On github: https://github.com/AnneLew/Lewerentz-etal_2021_Macrophytes-DDG

Chapter 4

As additional resources, the model code, data analysis and a shiny app for interactively exploring the results are provided:

- Model code: <https://github.com/AnneLew/MGM>
- Experiment setup files and data analysis as research compendium: <https://github.com/AnneLew/LewerentzEtAl2022>
- Shiny App: https://annelew.shinyapps.io/mgm_macrophytes_scenarios/

Chapter 5

Videos showing the game design and dynamics can be found on the project website:

- German: <http://bayklif-bliz.de/de/2020/09/14/computerspiel-wasserpflanzen-2/>
- English: <http://bayklif-bliz.de/2020/09/14/computerspiel-wasserpflanzen/>

Appendix B – Depth diversity gradients of macrophytes

General information

Lake morphology

Table B.1: Morphology of studied lakes: Lake surface area (*Area*) and depths of deepest point of the lake (*max. depth*).

| Lake | Area (ha) | Max. depth (m) |
|------------------------|-----------|----------------|
| Chiemsee | 7990.00 | 73.4 |
| Lake Starnberger | 5636.20 | 127.8 |
| Ammersee | 4700.00 | 81.0 |
| Tegernsee | 893.40 | 72.2 |
| Staffelsee | 800.00 | 39.0 |
| Lake Waginger | 661.00 | 27.0 |
| Simssee | 649.00 | 22.5 |
| Kochelsee | 600.00 | 66.0 |
| Koenigssee | 500.00 | 190.0 |
| Woerthsee | 433.90 | 34.0 |
| Gr. Alpsee | 247.30 | 22.7 |
| Lake Tachinger | 236.00 | 16.5 |
| Bannwaldsee | 228.00 | 12.0 |
| Schliersee | 222.00 | 40.3 |
| Pilsensee | 194.57 | 17.1 |
| Hopfensee | 194.00 | 10.4 |
| Riegsee | 188.47 | 15.4 |
| Grosser Ostersee | 177.63 | 29.7 |
| Eibsee | 177.00 | 36.0 |
| Lake Niedersonthofener | 135.50 | 21.3 |
| Weissensee | 134.65 | 24.7 |
| Lake Langbuergener | 104.00 | 37.3 |
| Alpsee bei Schwangau | 88.00 | 62.0 |
| Hartsee | 86.64 | 39.1 |
| Lake Abtsdorfer | 84.04 | 20.0 |
| Lake Pelhamer | 77.90 | 21.3 |
| Obersee | 57.00 | 51.0 |

Depth diversity gradients (DDG) of macrophytes: shape

Correlations between richness components

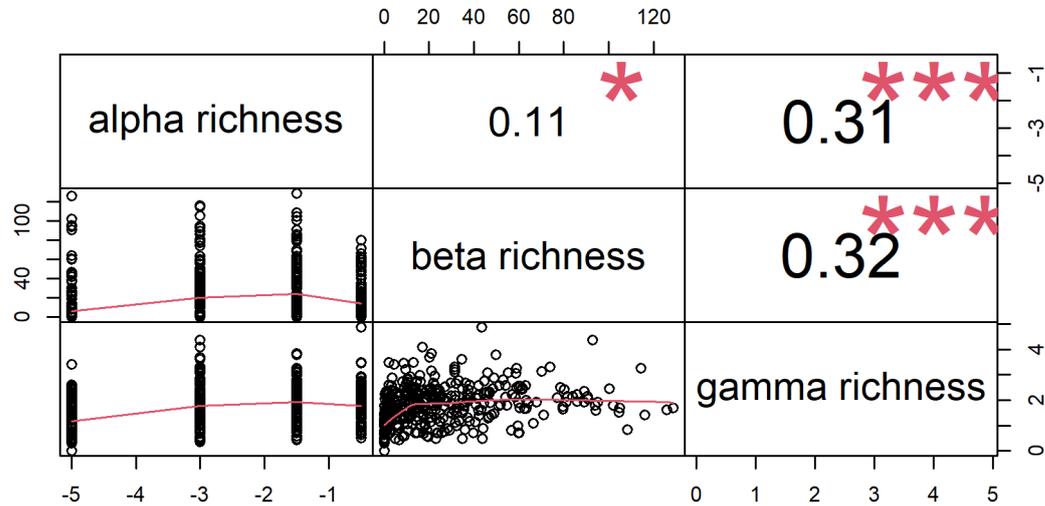


Figure B.1: Correlations between diversity metrics (method = pearson). Significance levels of p -values: * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$

DDG of all field campaigns

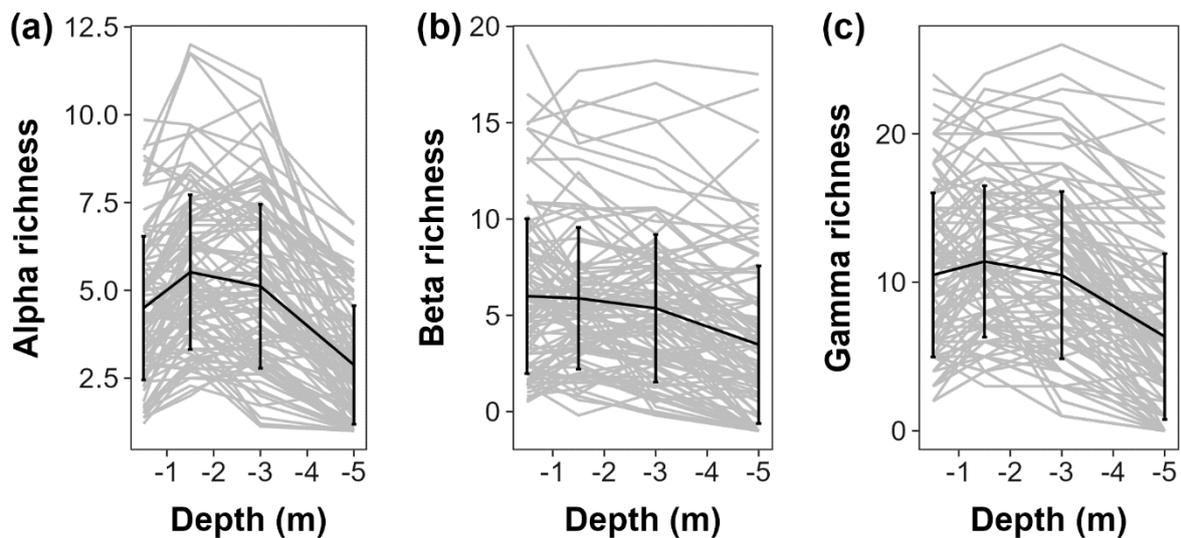


Figure B.2: Depth diversity gradients (DDG) of macrophytes for alpha (a), beta (b), and gamma richness (c) with mean as black line and SD as black bars. Each single grey line is one field campaign (lake*year).

DDG per lake

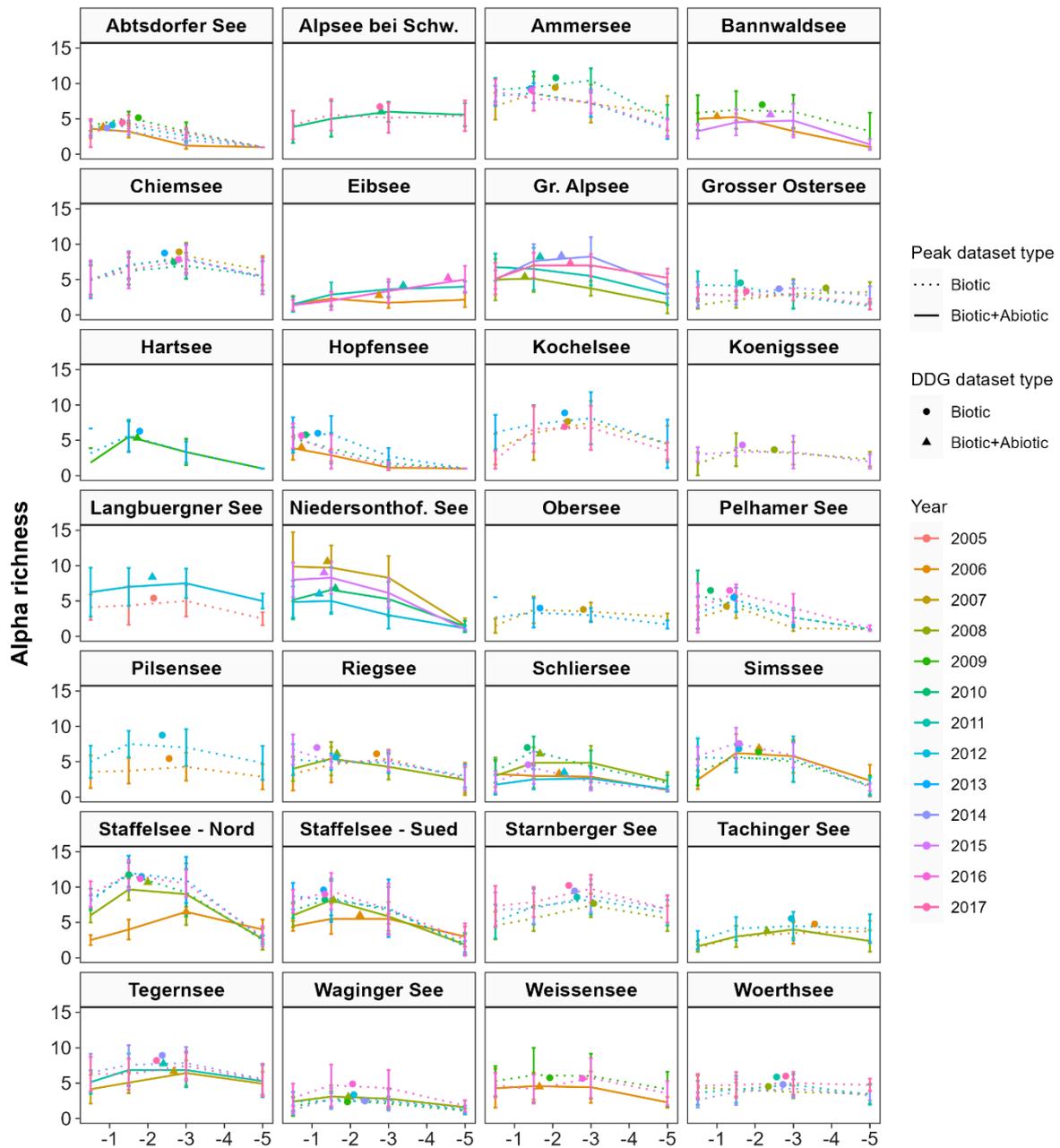


Figure B.3: DDG of submerged macrophytes for alpha richness. Lines show the mean alpha richness per lake and year with their corresponding standard deviation; the single richness peaks (= DGG measures) are depicted as points. The different dataset levels can be distinguished by line type and point shape. Points and dashed line: Biotic dataset of all available macrophyte mapping (biodiversity dataset); triangles and solid line: subset of biotic dataset, where also abiotic data is available (environmental & biodiversity dataset).

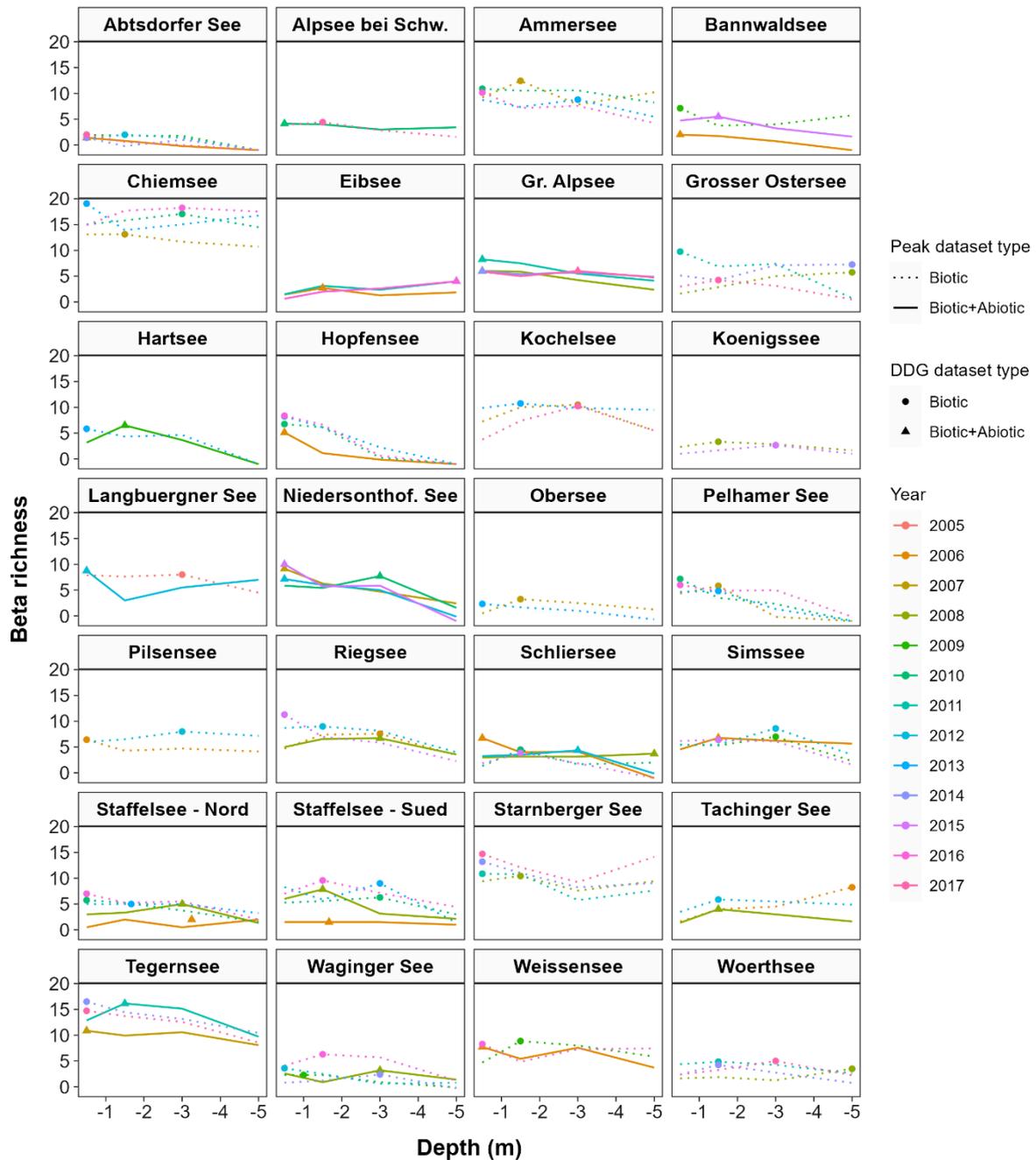


Figure B.4: DDG of submerged macrophytes for beta richness. Lines show the beta richness per lake and year; the single richness peaks (= DGG measures) are depicted as points. The different dataset levels can be distinguished by line type and point shape. Points and dashed line: Biotic dataset of all available macrophyte mapping (biodiversity dataset); triangles and solid line: subset of biotic dataset, where also abiotic data is available (environmental & biodiversity dataset).

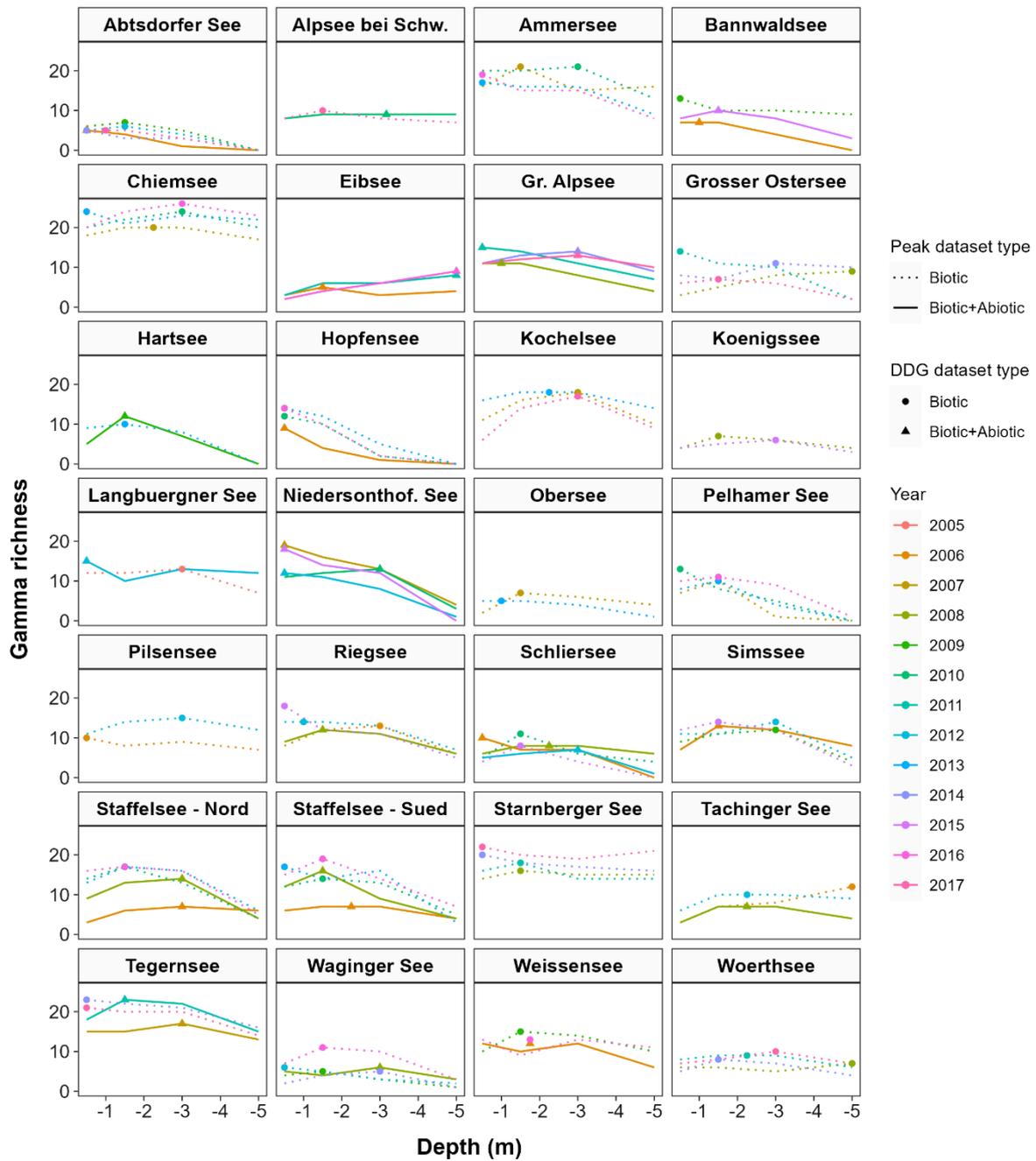


Figure B.5: DDG of submerged macrophytes for gamma richness. Lines show the gamma richness per lake and year; the single richness peaks (= DGG measures) are depicted as points. The different dataset levels can be distinguished by line type and point shape. Points and dashed line: Biotic dataset of all available macrophyte mapping (biodiversity dataset); triangles and solid line: subset of biotic dataset, where also abiotic data is available (environmental & biodiversity dataset).

Herberich test

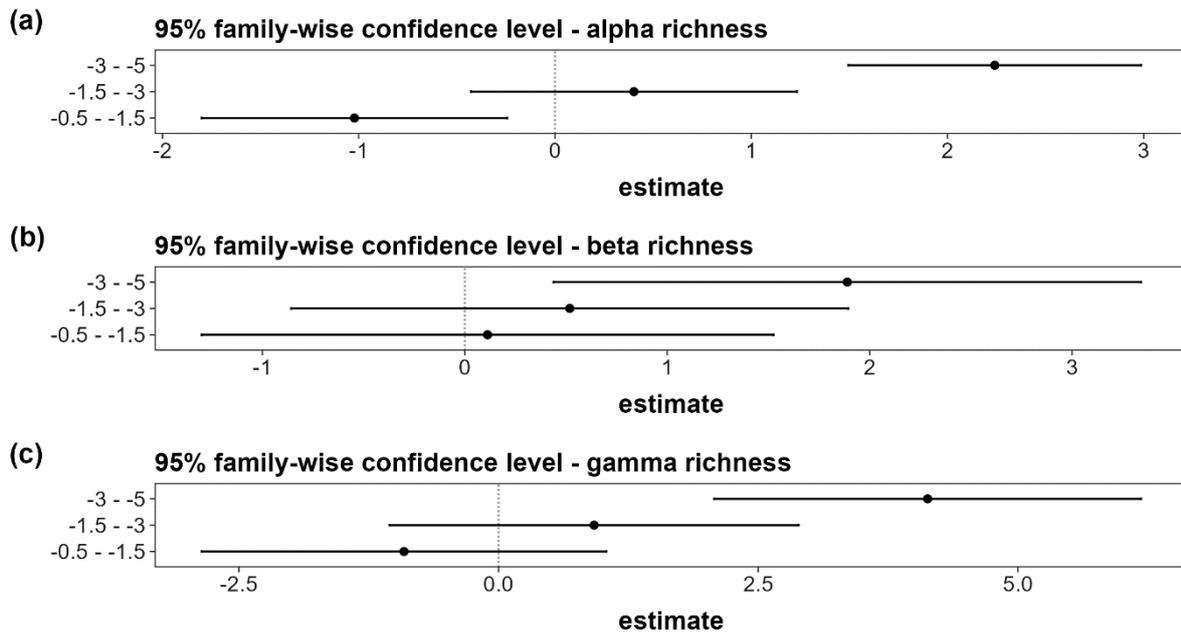


Figure B.6: Simultaneous tests for linear models with multiple comparisons of means using Tukey contrasts that are robust under non-normality, heteroscedasticity and variable sample size (Herberich et al., 2010) to check significant differences between depths within richness components. Results are plotted for alpha richness (a), beta richness (b) and gamma richness(c).

DDG pattern types

Table B.2: Overview about DDG patterns of decreasing curves, hump-shaped curves (different peak depths) and increasing curves. Number of field campaigns (lake*year) showing a distinct depth pattern for each richness component.

| | Decreasing curve (Peak: > -1 m) | Hump-shaped (Peak: -1 – -2 m) | Hump-shaped (Peak: -2 – -4 m) | Increasing curve (Peak: < -4 m) |
|----------------|---------------------------------------|----------------------------------|----------------------------------|------------------------------------|
| Alpha richness | 6 | 41 | 52 | 1 |
| Beta richness | 40 | 31 | 22 | 7 |
| Gamma richness | 26 | 39 | 30 | 5 |

Correlations between DDG metrics

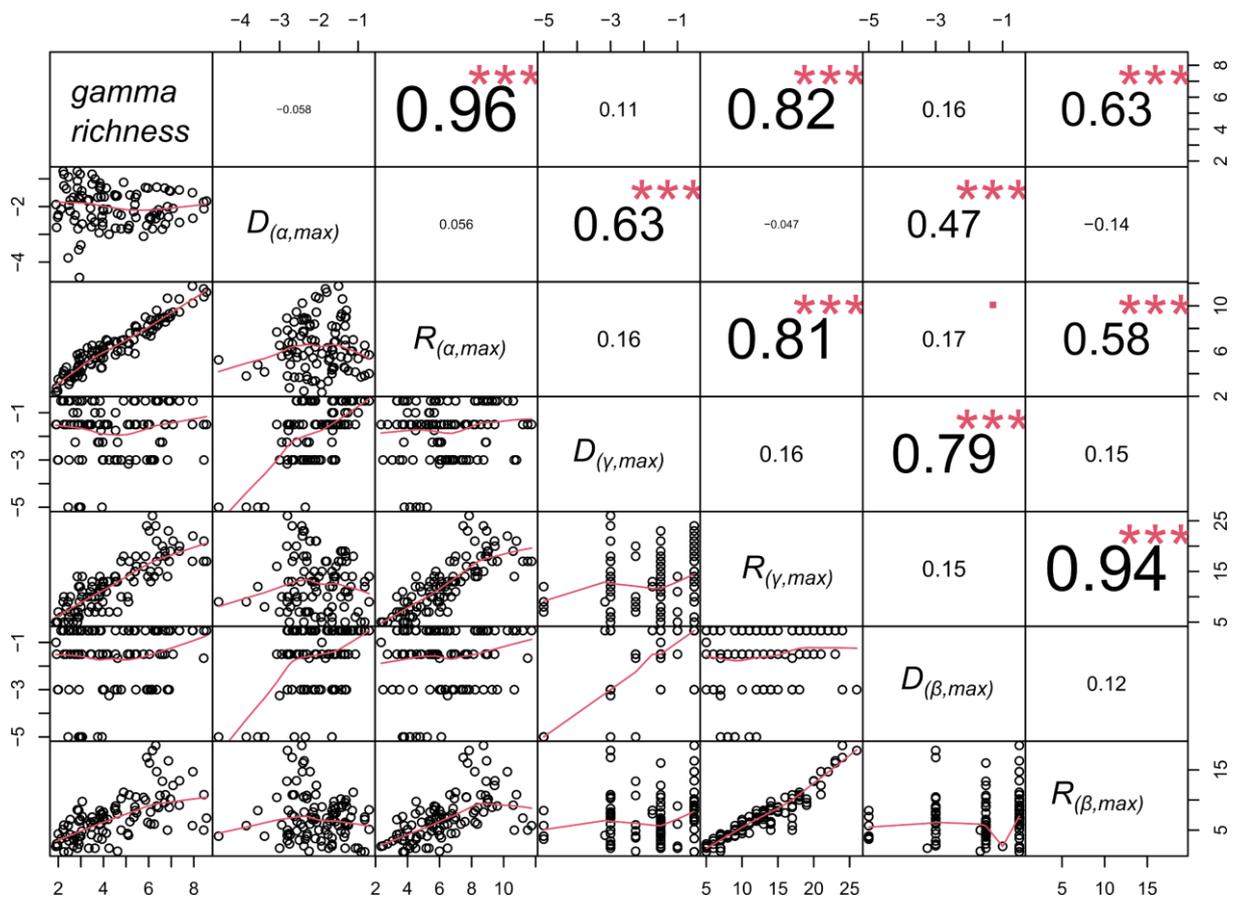


Figure B.7: Pearson correlations between DDG measures of different species richness components. Significance levels of p -values: * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$

Chi-square test of DDG pattern

Chi-square is done to see significant differences in frequency among the DDG pattern types (Table B.2) to see if they are significantly different for each richness component.

```
##
## Pearson's Chi-squared test with simulated p-value (based on 2000
## replicates)
##
## data: PEAKCLASS
## X-squared = 44.078, df = NA, p-value = 0.0004998
```

Depth diversity gradients of macrophytes: drivers

Data representativeness of nested subsets

To show that the diversity metrics of the environmental & biodiversity dataset are representative for the diversity metrics of biodiversity dataset we applied the PERMANOVA test `adonis2`, using the R package ‘`vegan`’ which compares centroids and the variance (Oksanen et al., 2019). A non-significant result ($p > 0.05$) confirms that centroids and variance of two groups are not different. The results show that the *Environmental & biodiversity dataset* ($n = 27$) is representative for the *Biodiversity dataset* ($n = 100$).

```
## Permutation test for adonis under reduced model
## Permutation: free
## Number of permutations: 999
##
## adonis2(formula = PEAK[, c(3, 5)] ~ datasettotalsimpl, data = PEAK, by = NULL)
##      Df SumOfSqs   R2    F Pr(>F)
## Model  1 -25.160 -0.36115 -26.002 0.746
## Residual 98  94.827  1.36115
## Total  99  69.667  1.00000

## Permutation test for adonis under reduced model
## Permutation: free
## Number of permutations: 999
##
## adonis2(formula = (PEAK[, c(14, 15)]) ~ datasettotalsimpl, data = PEAK, by = NULL)
##      Df SumOfSqs   R2    F Pr(>F)
## Model  1  0.1690 0.02018 2.0189 0.128
## Residual 98  8.2047 0.97982
## Total  99  8.3738 1.00000

## Permutation test for adonis under reduced model
## Permutation: free
## Number of permutations: 999
##
## adonis2(formula = scale(PEAK[, c(16, 17)]) ~ datasettotalsimpl, data = PEAK, by = NULL)
##      Df SumOfSqs   R2    F Pr(>F)
## Model  1 -45388 -0.26182 -20.335 0.649
## Residual 98 218744  1.26182
## Total  99 173355  1.00000
```

Correlations between drivers

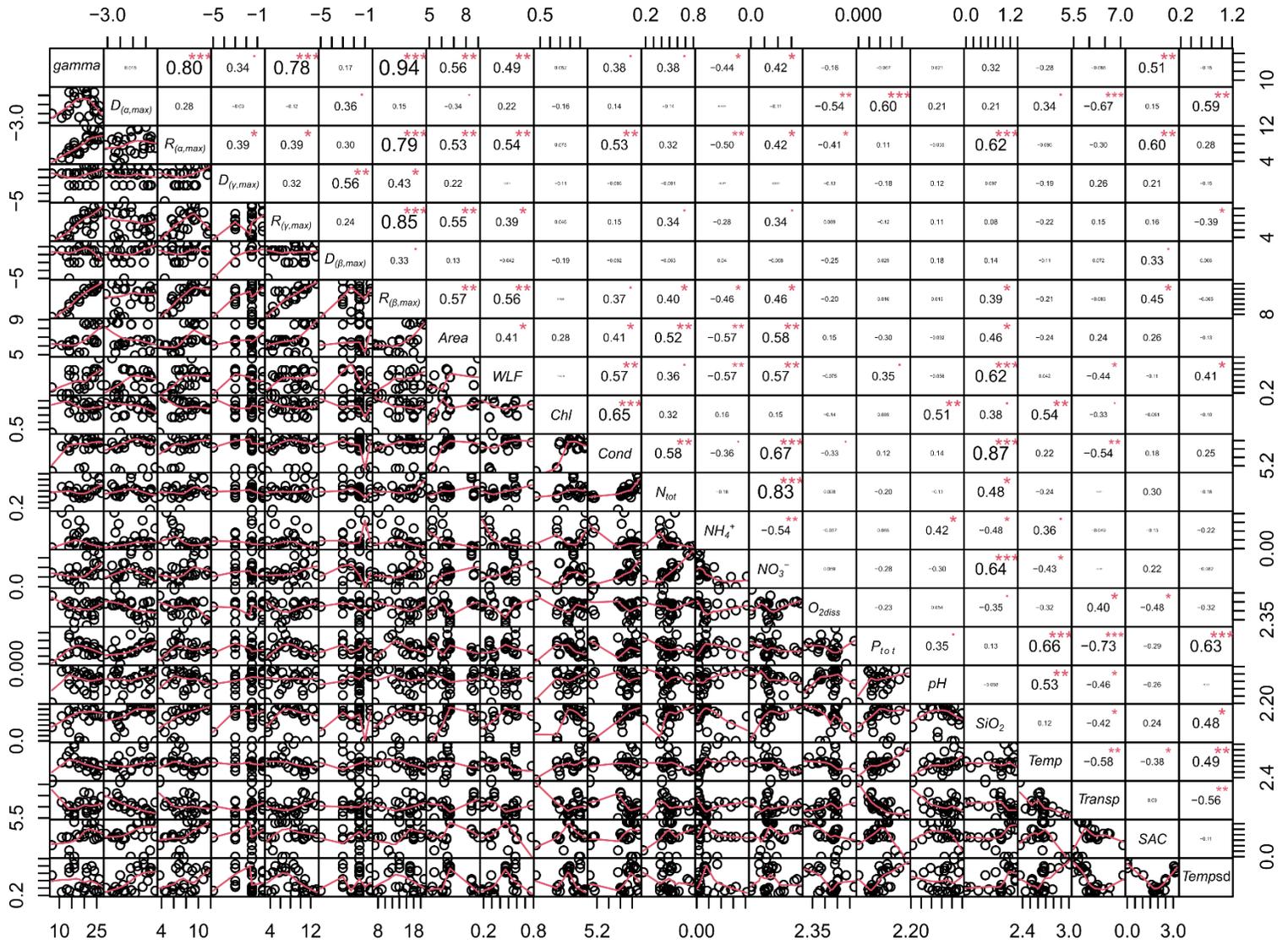


Figure B.8: Pearson correlation between normalized chemical-physical values and DDG measures for all richness components. Environmental and biodiversity dataset is used. Significance levels of p -values: * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$

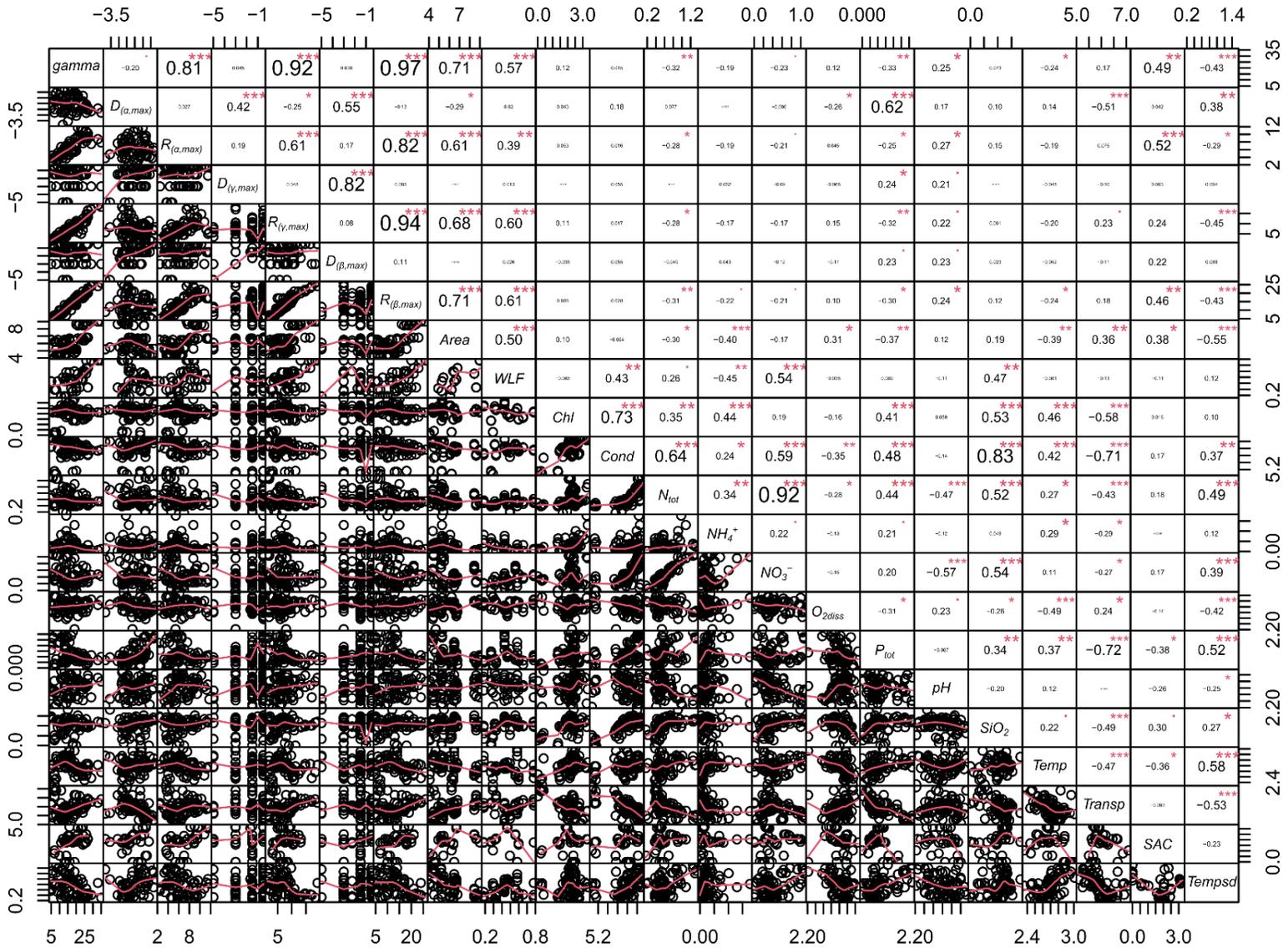


Figure B.9: Pearson correlation between normalized chemical-physical values and DDG measures for all richness components. Biodiversity dataset is used, zero values are ignored. Significance levels of p -values: * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$

Alternative GAMM with parameters selected on expert knowledge

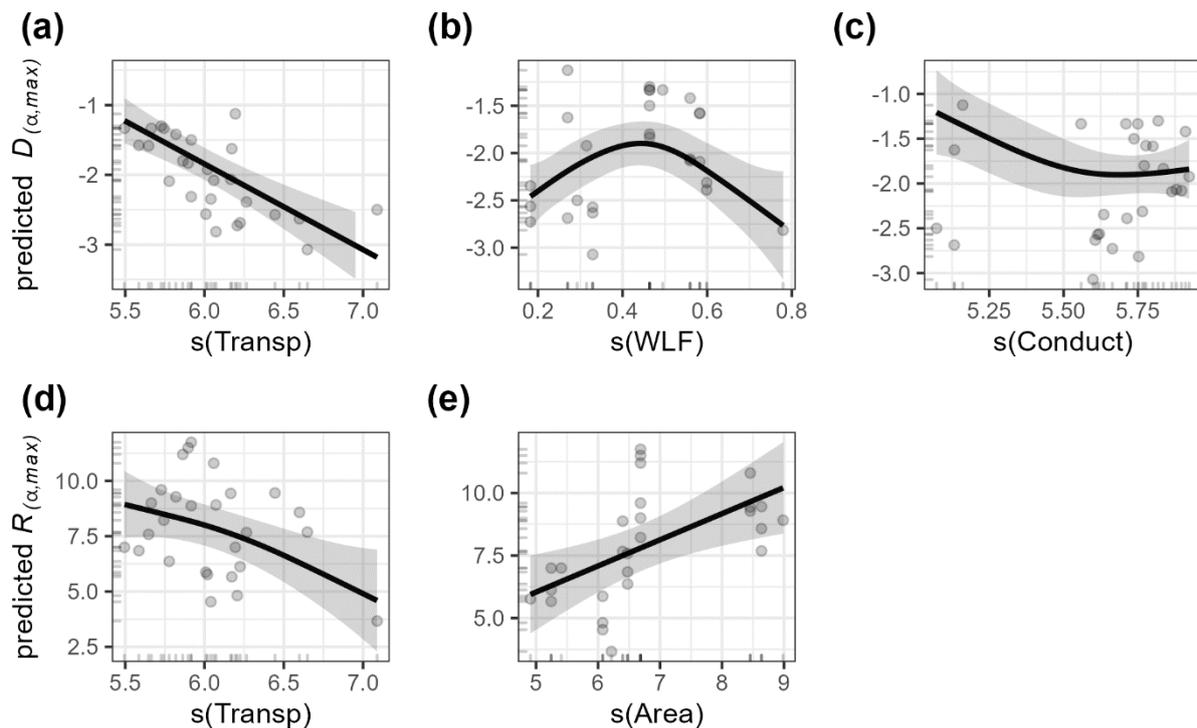


Figure B.12: Alternative GAMMs without PCA for selected parameters. The selection was based on expert knowledge on highly likely influencing factors and excluding high correlations (see Figure 6 and 7). We selected *Cond* (representative for Cl^-), N_{tot} (representative for NH_4^+ and NO_3^-), P_{tot} , *Temp* (representative for *Tempsd*), *Transp* (representative for *SAC*), *Area* and *WLF*. We excluded pH , $\text{O}_{2\text{diss}}$, and SiO_2 . The resulting GAMM for $D_{(\alpha, \max)}$ (a–c) has a R^2 lower ($R^2 = 0.697$) than in the analysis using the PCA axes as variables ($R^2 = 0.73$). GAMM for $R_{(\alpha, \max)}$ (d–f) shows also a slightly lower R^2 ($R^2 = 0.432$) than in the analysis using the PCA axes as variables ($R^2 = 0.44$).

Depth diversity gradients of macrophytes: recent shifts

Invariability analysis

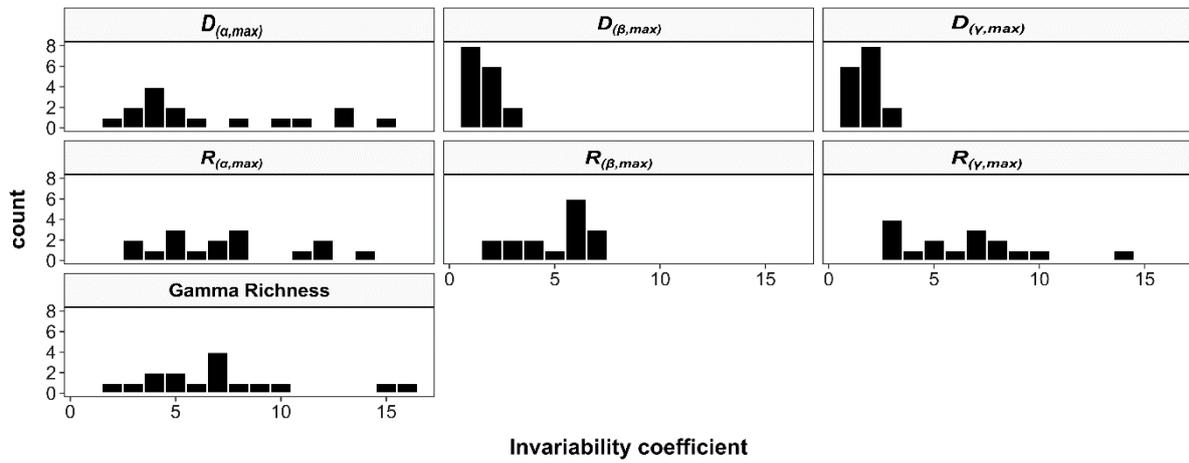


Figure B.13: Histograms for Invariability coefficients for single DDG measures (D_{max} and R_{max} of alpha, beta, and gamma richness) and gamma richness for the biodiversity timeseries dataset. High invariability means a high stability within the timeseries.

Temporal trend of gamma richness

General

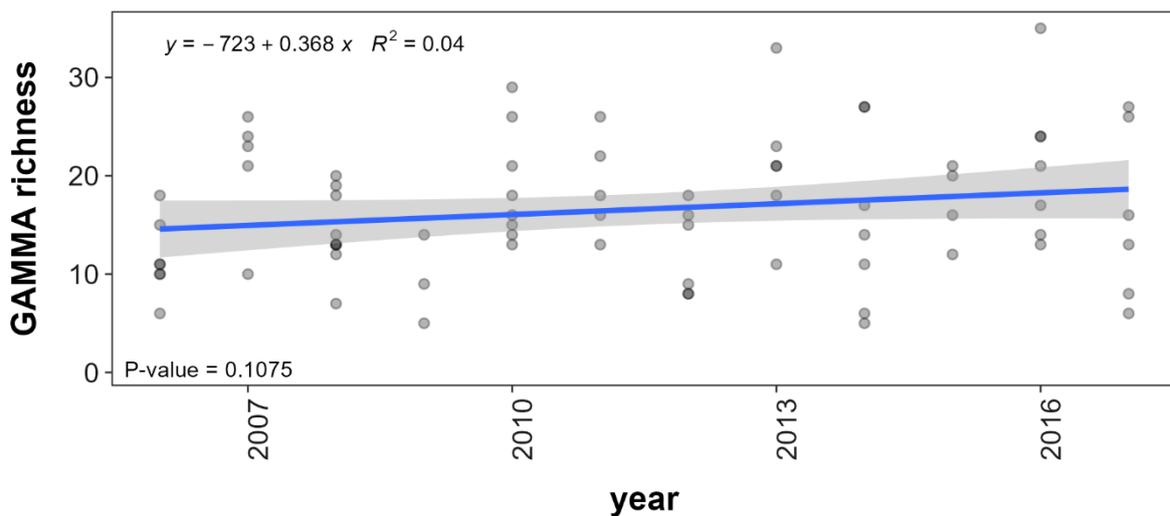


Figure B.14: Temporal change of gamma richness from biodiversity time series dataset for all lakes together. Points show individual values, and the blue line is a linear model.

Individual lakes

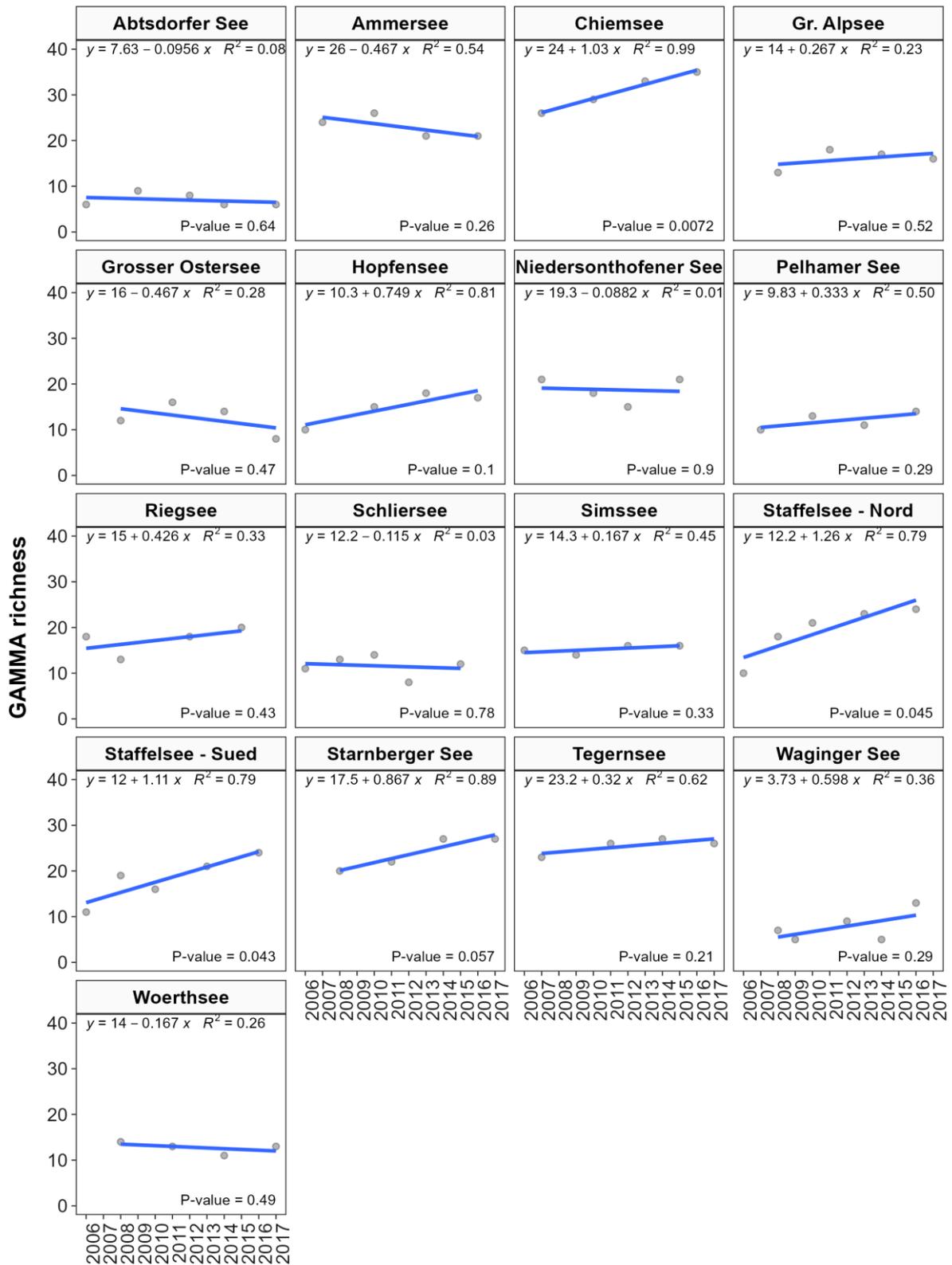


Figure B.15: Temporal change of gamma richness from biodiversity time series dataset for all individual lakes. Points show single values, and the blue line is a linear model per lake.

Temporal trend of DDG measures

General

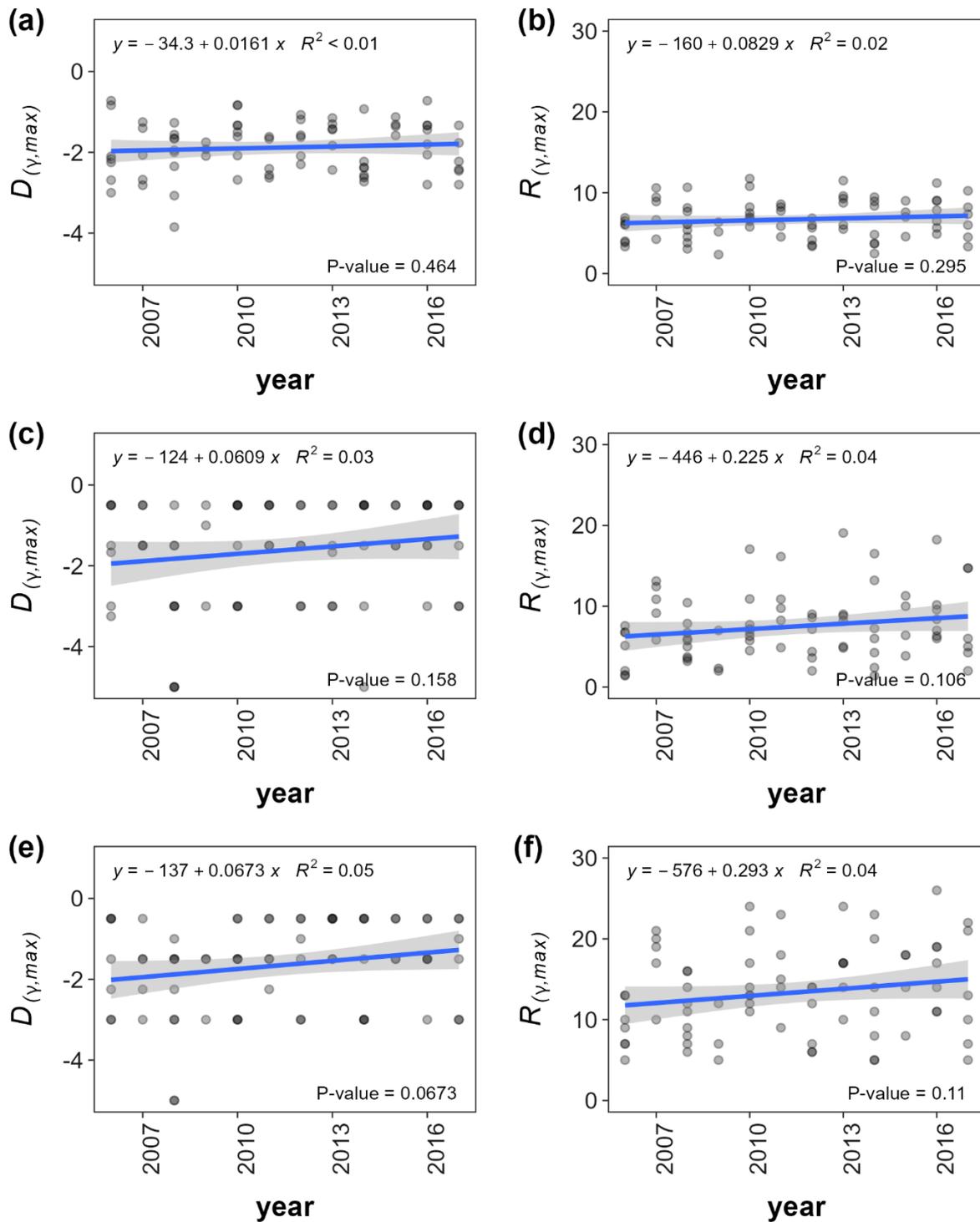


Figure B.16: Temporal change of DDG metrics from biodiversity time series dataset for all lakes at once. Points show single values, and the blue line is a linear model. In panel (a, c, e) temporal change of $D_{(max)}$ is shown and in panel (b, d, f) the corresponding course of $R_{(max)}$ is depicted.

Individual lakes

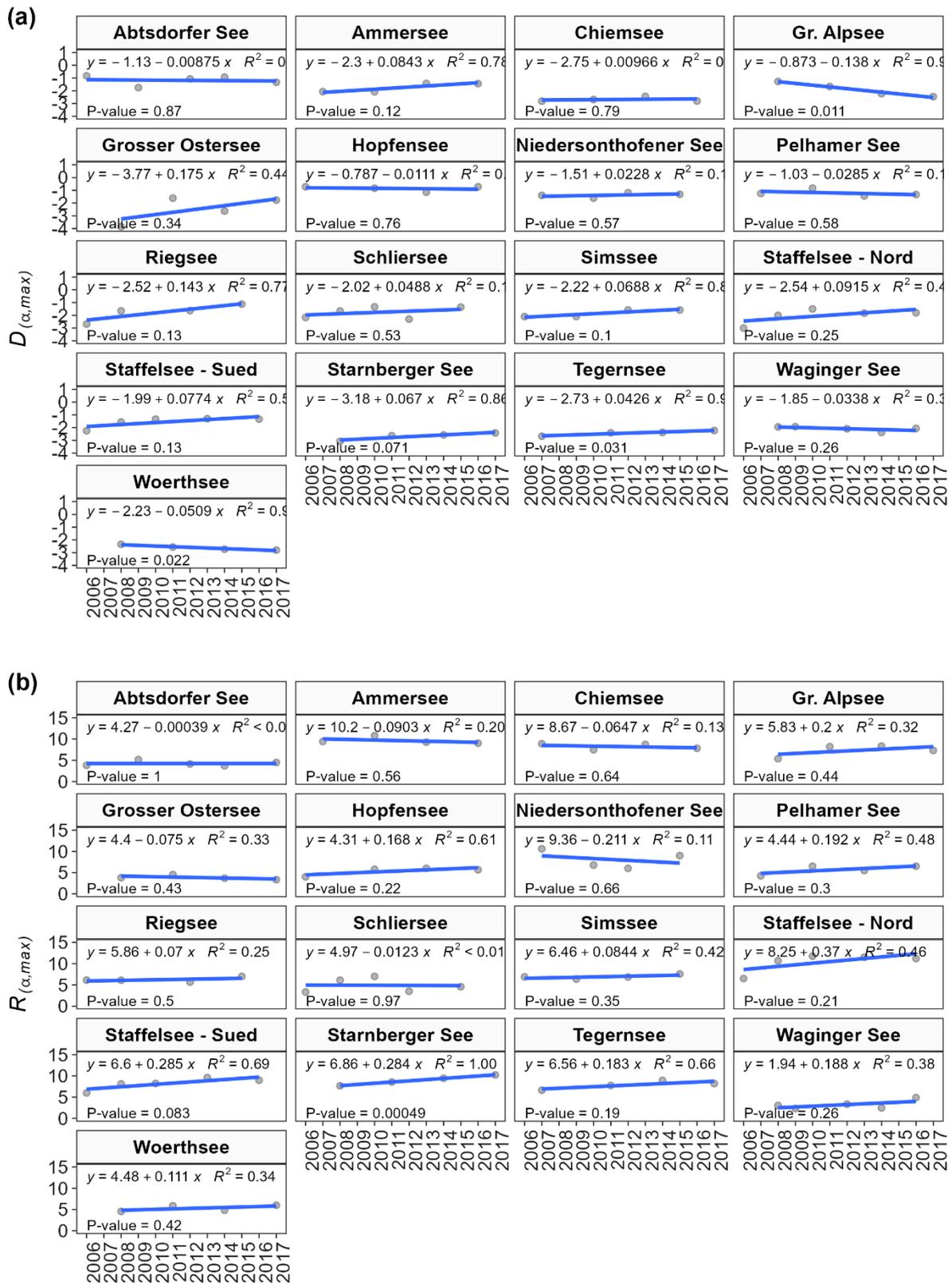


Figure B.17: Temporal change of DDG metrics from biodiversity time series dataset for all lakes. Points show annual values, and the blue line is a linear model. In panel (a) temporal change of $D_{(a,max)}$ is shown for all lakes and in panel (b) the corresponding course of $R_{(a,max)}$ is depicted.

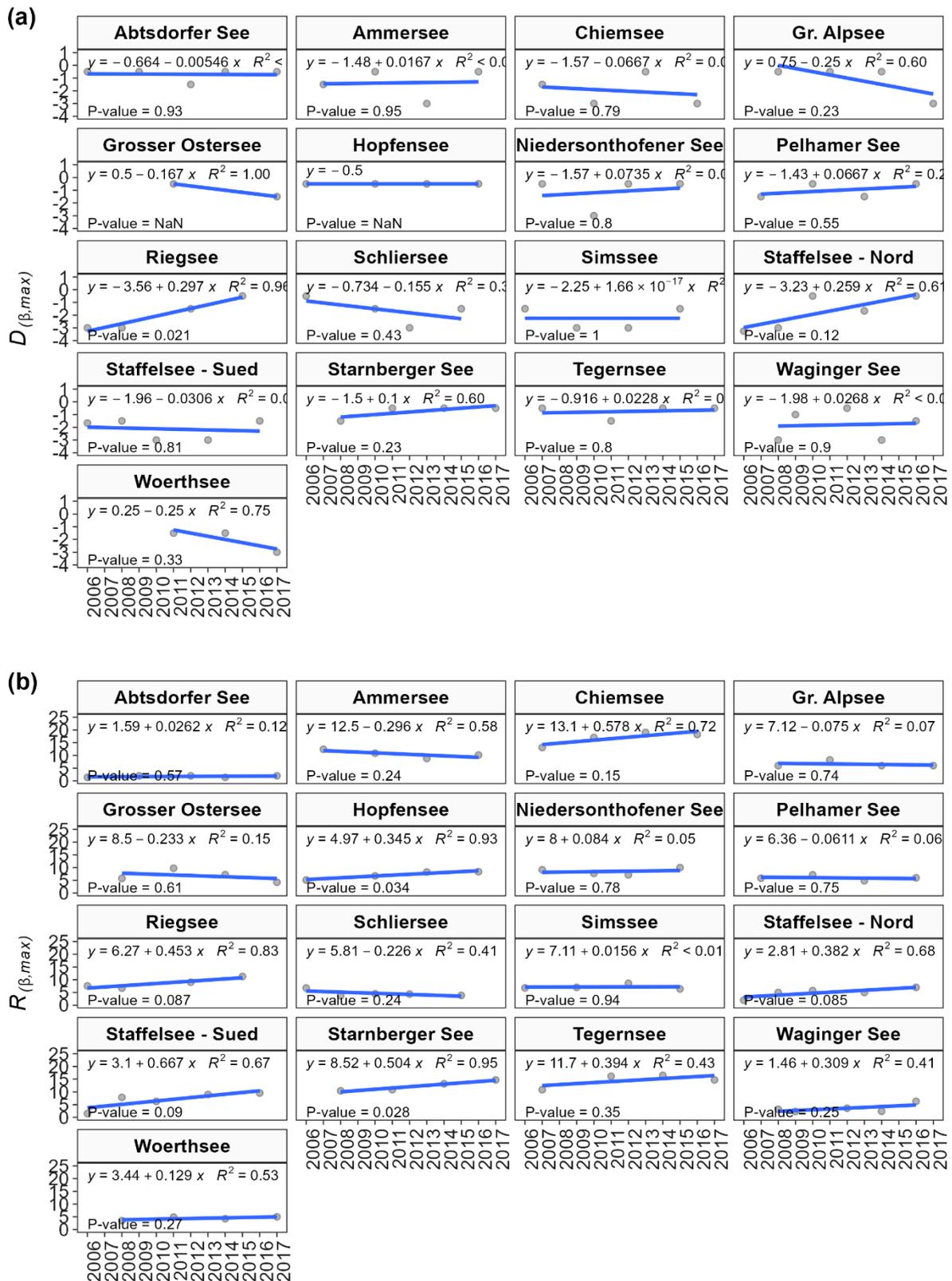


Figure B.18: Temporal change of DDG metrics from biodiversity time series dataset for all lakes. Points show annual values, and the blue line is a linear model. In panel (a) temporal change of $D_{(\beta,max)}$ is shown for all lakes and in panel (b) the corresponding course of $R_{(\beta,max)}$ is depicted.

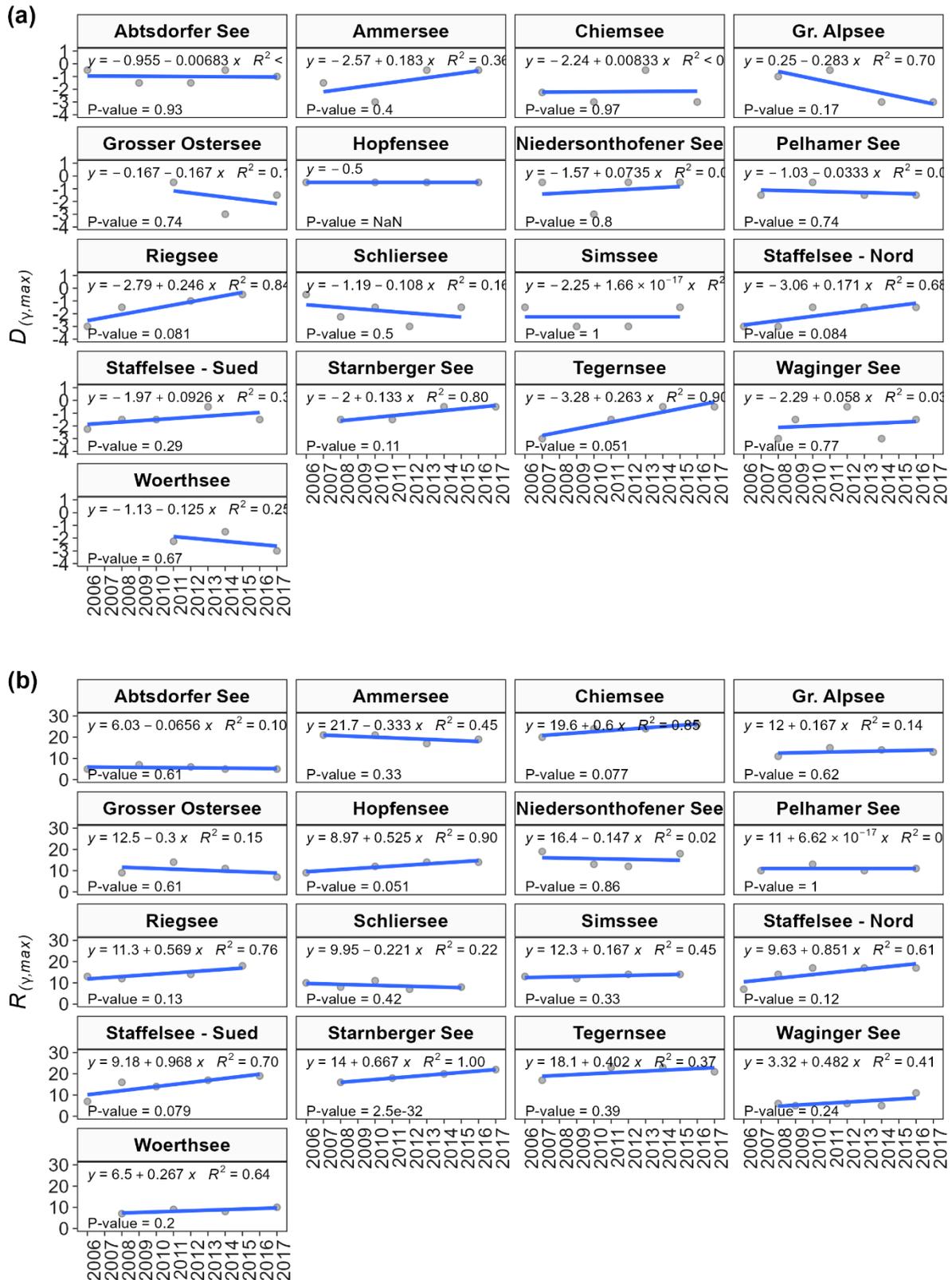


Figure B.19: Temporal change of DDG metrics from biodiversity time series dataset for all lakes. Points show annual values, and the blue line is a linear model. In panel (a) temporal change of $D_{(y,max)}$ is shown for all lakes and in panel (b) the corresponding course of $R_{(y,max)}$ is depicted.

Appendix C – Potential changes of macrophyte species richness

Overview about lake parameters

Table C.1: Overview about lake parameters.

| Parameter | Unit | Description | Value (range or fixed) | Data source |
|------------------------|------------------------------------|--|---------------------------|-----------------------|
| <i>fracReflected</i> | - | Light reflection at the water surface | 0.1 | van Nes et al. (2003) |
| <i>iDelay</i> | d | Days after 1st of January where I is minimal | -9 | StMWi (2019) |
| <i>iDev</i> | - | Deviation factor to change total irradiation | 1 | StMWi (2019) |
| <i>latitude</i> | ° | Latitude of corresponding lake | 47.45 – 48.06 | GKD (2022) |
| <i>maxI</i> | $\mu\text{E m}^{-2} \text{s}^{-1}$ | Maximal Irradiance | 1575 | StMWi (2019) |
| <i>minI</i> | $\mu\text{E m}^{-2} \text{s}^{-1}$ | Minimal Irradiance | 32 | StMWi (2019) |
| <i>parFactor</i> | - | Fraction of total irradiation that is PAR | 0.5 | van Nes et al. (2003) |
| <i>maxNutrient</i> | mg l^{-1} | Concentration of limiting nutrient in water | 0.0026 – 0.045 | GKD (2022) |
| <i>maxTemp</i> | °C | Max. mean daily temperature of a year | 16.7 – 27.3 | GKD (2022) |
| <i>minTemp</i> | °C | Min. mean daily temperature of a year | 4 | <i>simplification</i> |
| <i>tempDelay</i> | d | Days after 1st of January where Temp is minimal | 19 | GKD (2022) |
| <i>tempDev</i> | - | Deviation factor, a factor between 0 and 1 to change the whole temperature range | 1 | van Nes et al. (2003) |
| <i>backgrKd</i> | m^{-1} | Background light attenuation of water (Vertical light attenuation, turbidity) | 1 | van Nes et al. (2003) |
| <i>kdDelay</i> | d | Delay, the day number with the minimal light attenuation coefficient | 0 | <i>simplification</i> |
| <i>kdDev</i> | - | Deviation factor, a factor between 0 and 1 to change the whole light attenuation range | 1 | van Nes et al. (2003) |
| <i>maxKd</i> | m^{-1} | Maximum light attenuation coefficient | 0.13 – 0.91 | GKD (2022) |
| <i>minKd</i> | m^{-1} | Minimum light attenuation coefficient | 0.13 – 0.91 | GKD (2022) |
| <i>levelCorrection</i> | m | Correction for reference level (MWL) | 0 | <i>simplification</i> |
| <i>maxW</i> | m | Maximal water level above MWL | 0 | <i>simplification</i> |
| <i>minW</i> | m | Minimal water level below MWL | 0 | <i>simplification</i> |
| <i>wDelay</i> | m | Delay of cosine of water level | 0 | <i>simplification</i> |

Base scenario

To validate the model, the modelled potential and the observed realised species richness was compared. A lake-wise comparison for eutrophic, mesotrophic and oligotrophic species richness along depth is shown in Figures C.1 – C.10.

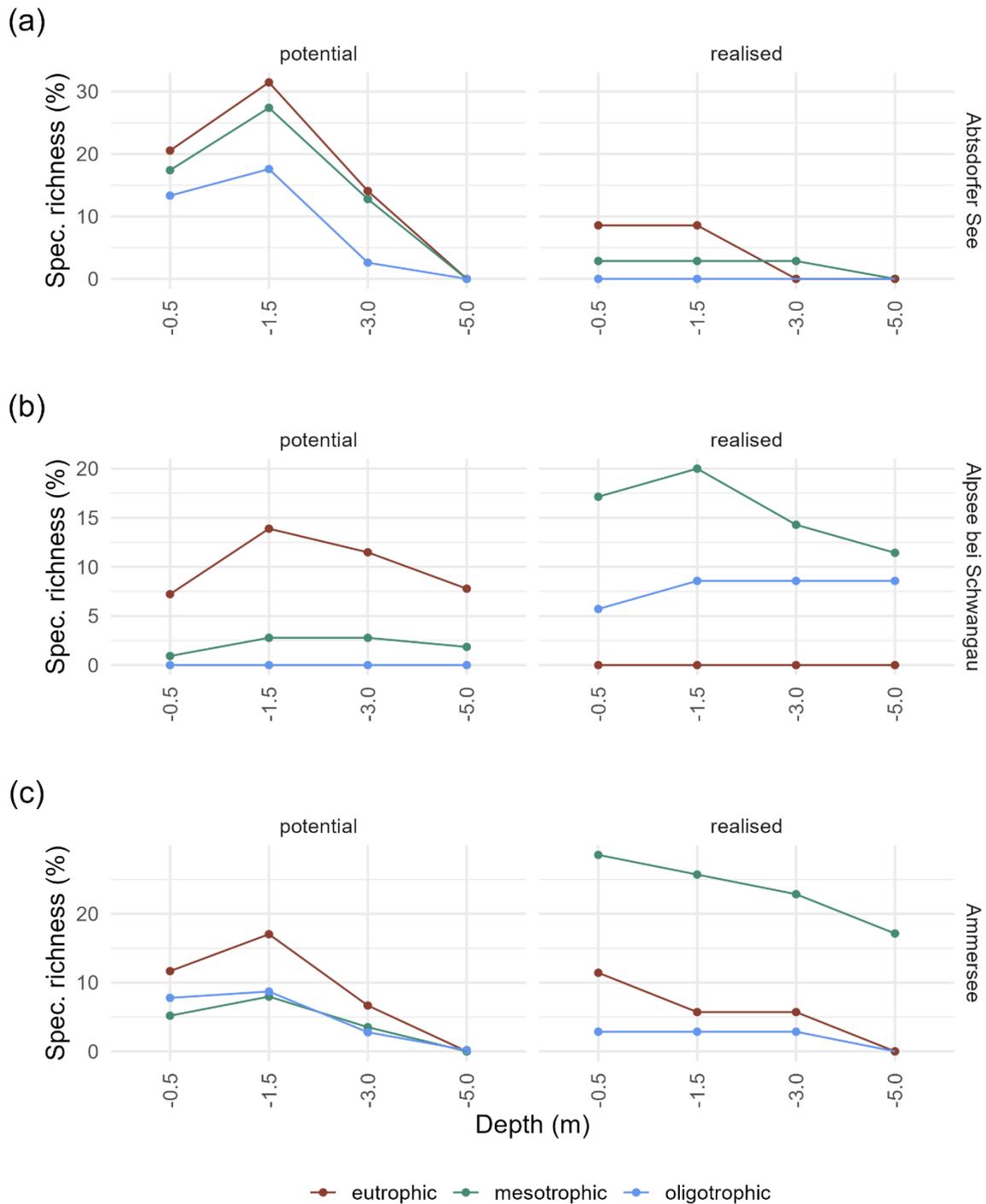


Figure C.1: Comparison of potential and realised species richness for Lake Abtsdorfer (a), Alpee bei Schwangau (b), and Ammersee (c).

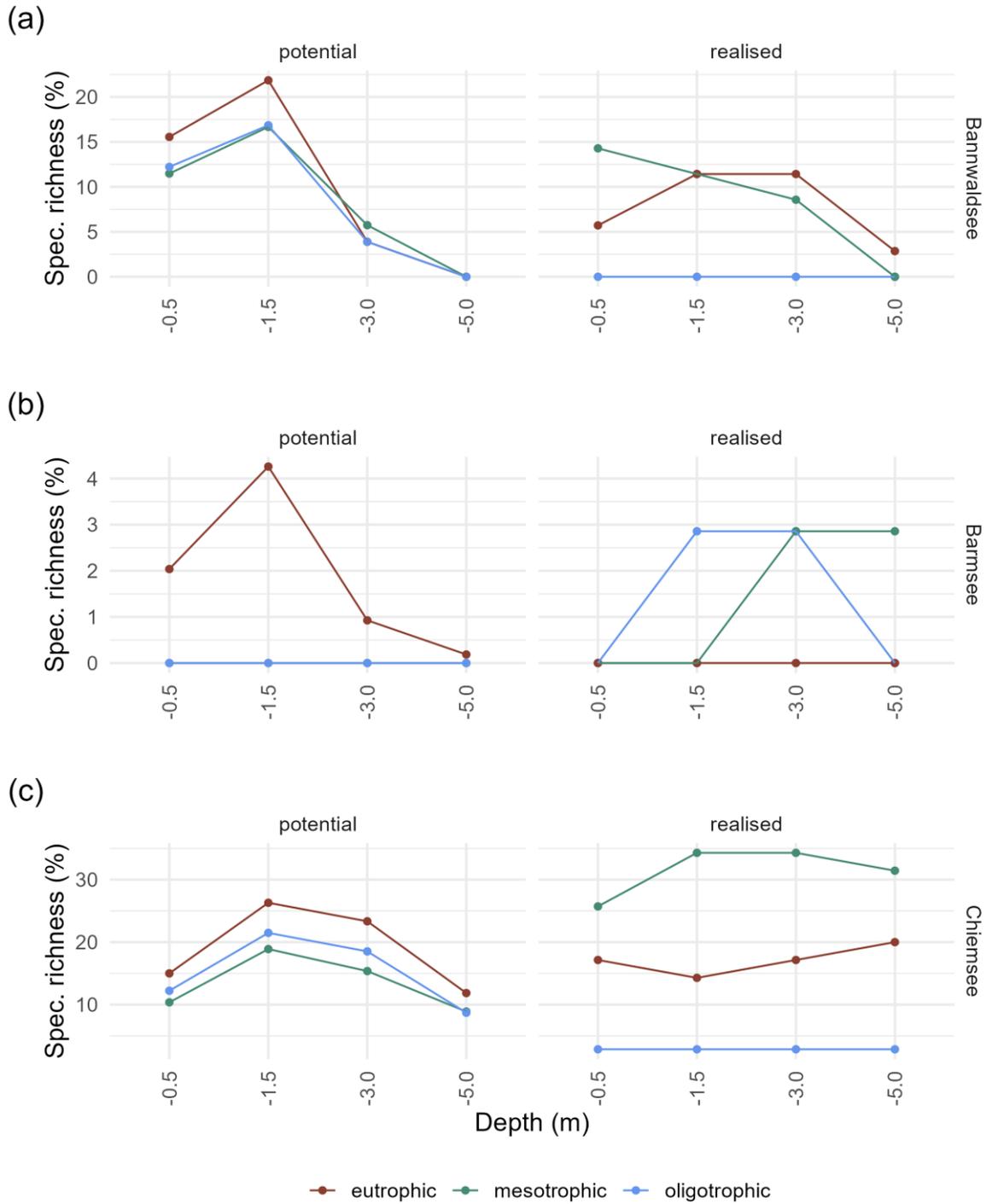


Figure C.2: Comparison of potential and realised species richness for Bannwaldsee (a), Barmsee (b), and Chiemsee (c).

Appendix C – Potential changes of macrophyte species richness

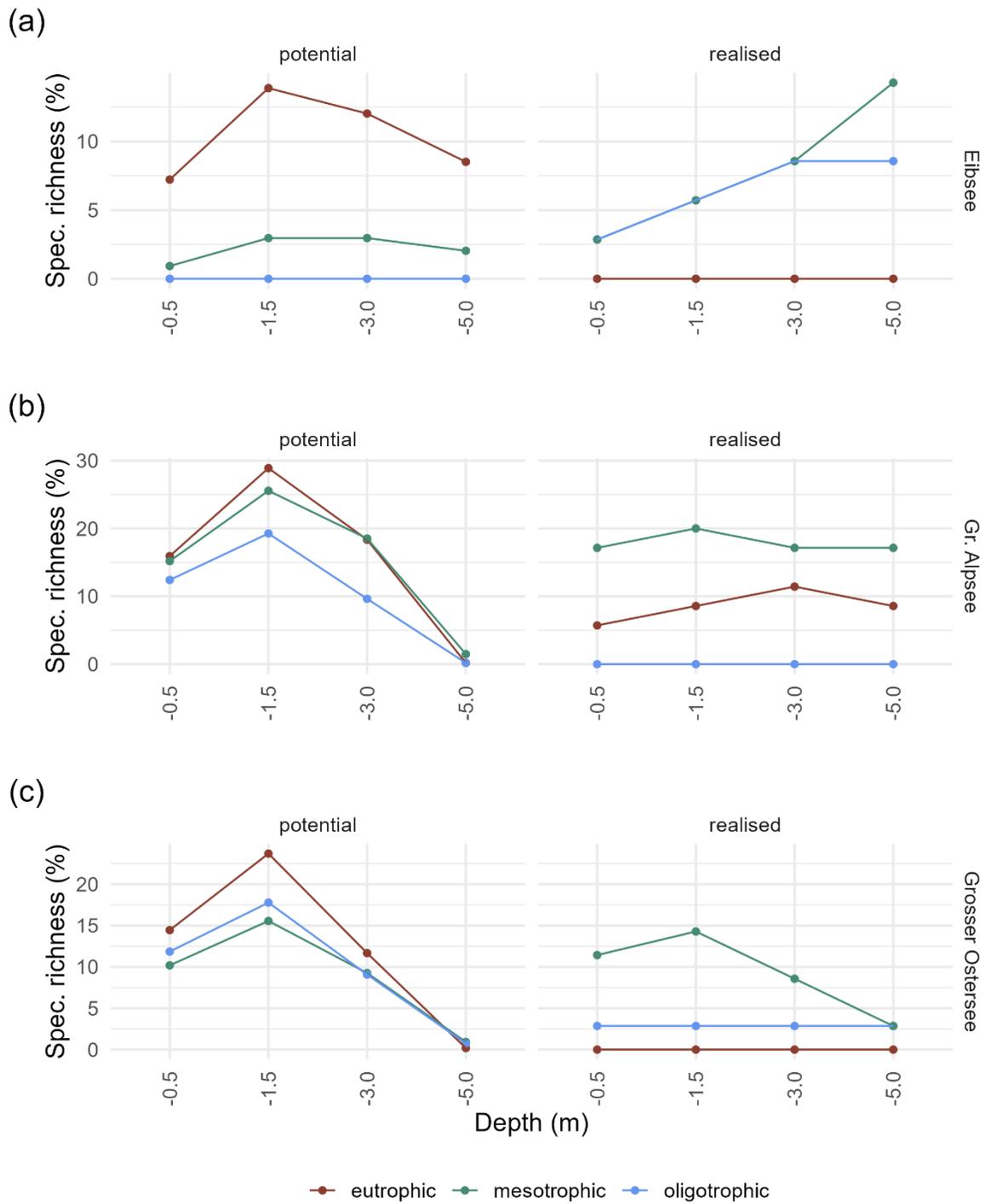


Figure C.3: Comparison of potential and realised species richness for Eibsee (a), Großer Alpsee (b), and Grosser Ostersee (c).

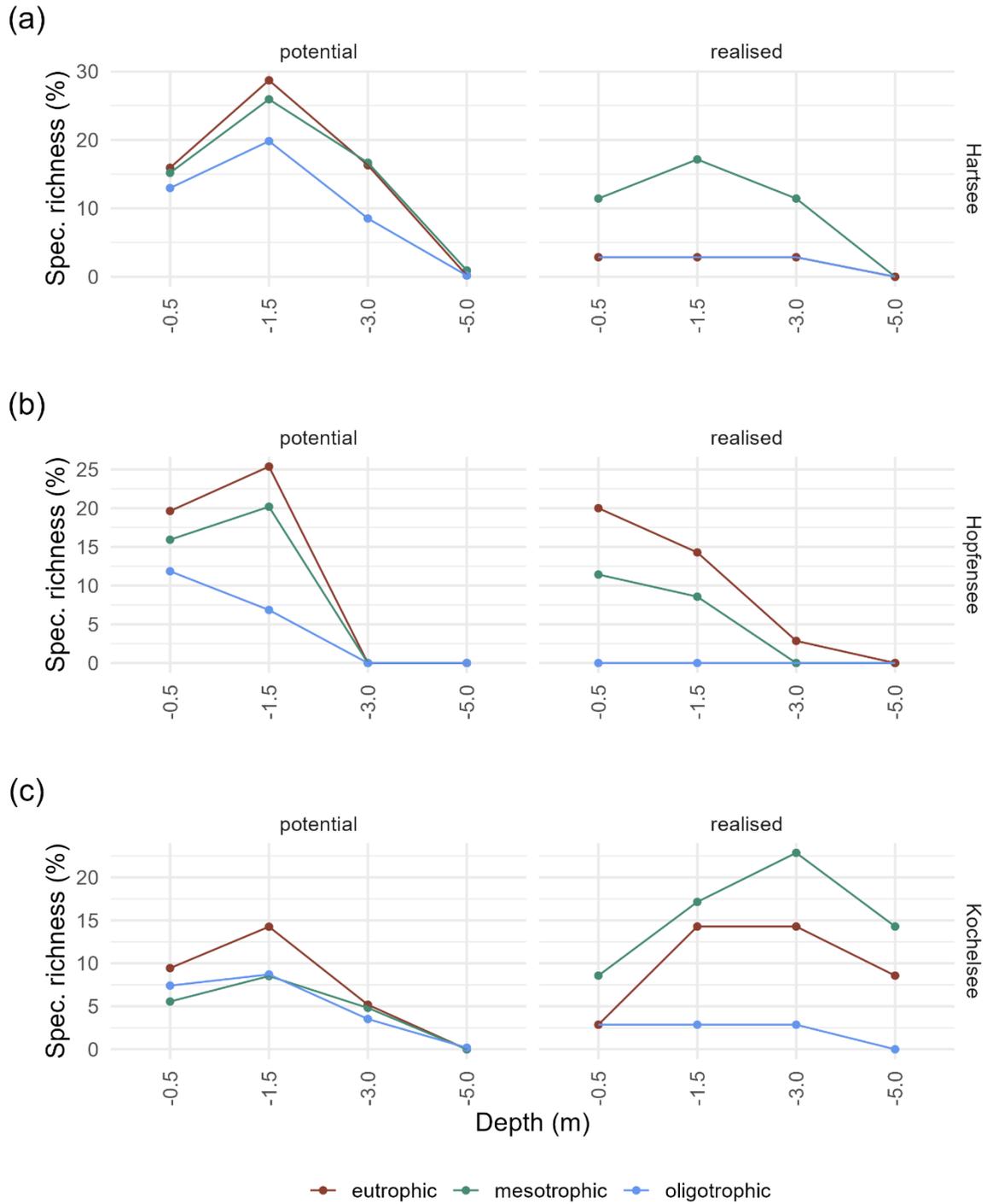


Figure C.4: Comparison of potential and realised species richness for Hartsee (a), Hopfensee (b), and Kochelsee (c).

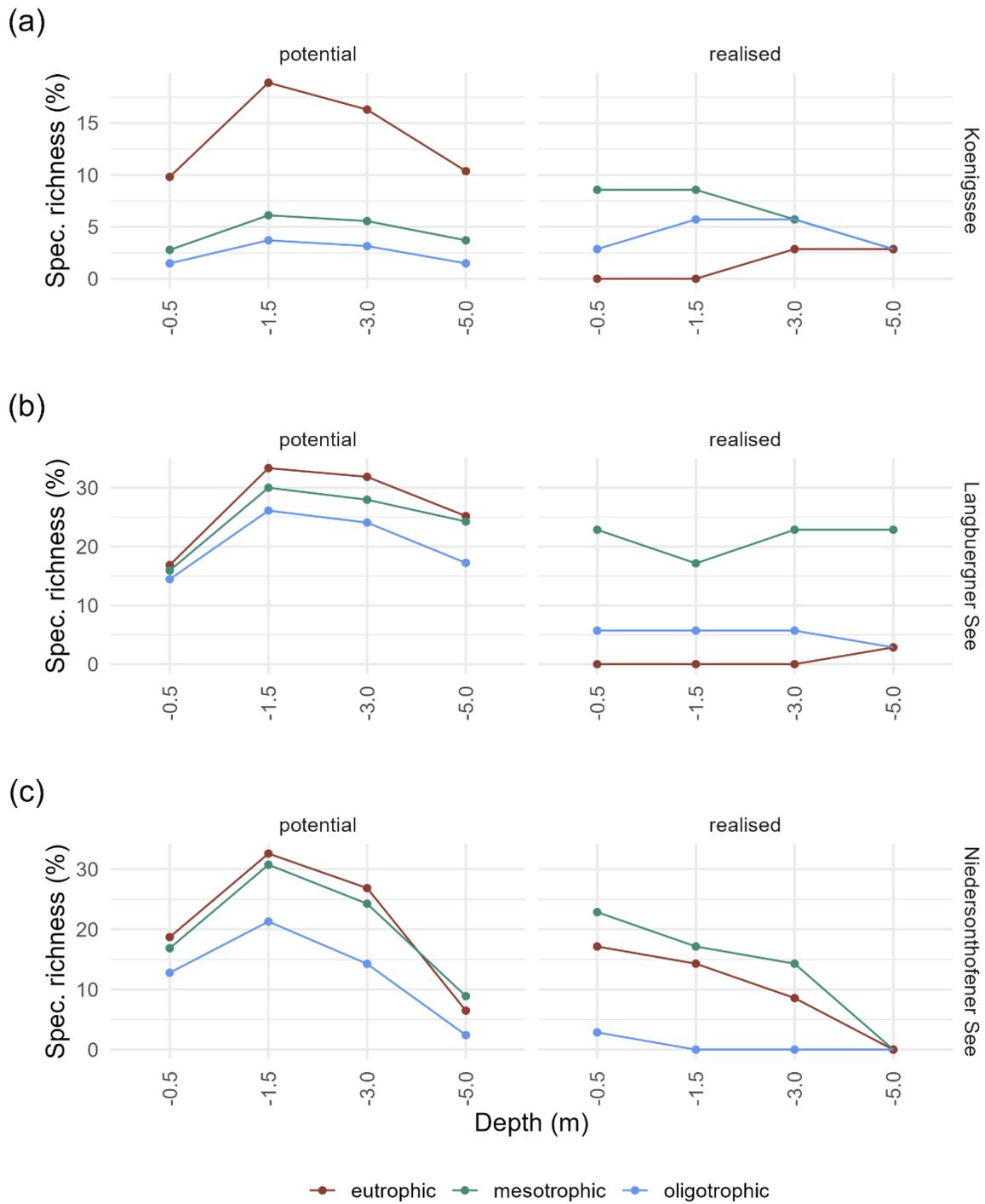


Figure C.5: Comparison of potential and realised species richness for Koenigssee (a), Lake Langbürgner (b), and Lake Niedersonthofener (c).

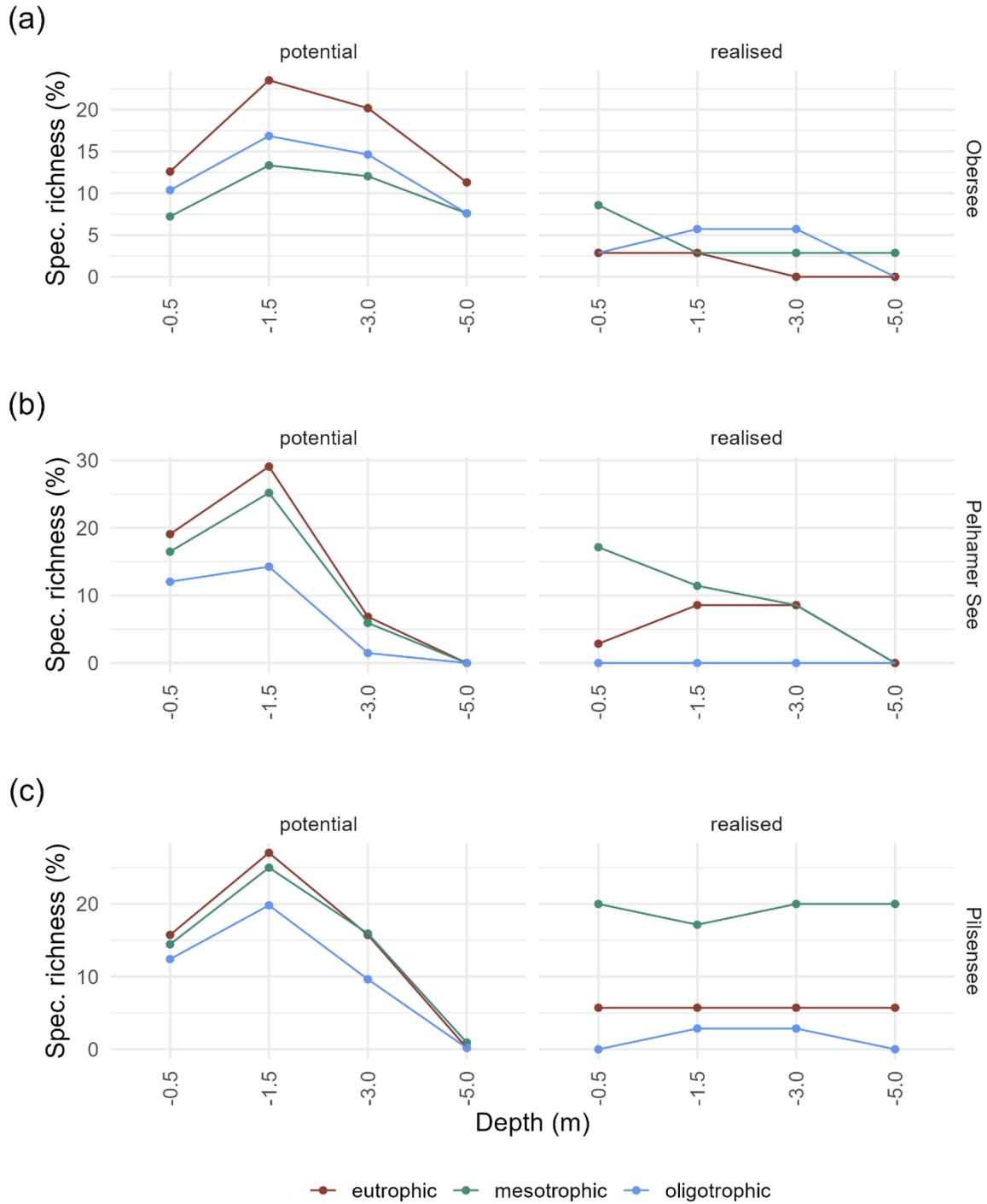


Figure C.6: Comparison of potential and realised species richness for Obersee (a), Lake Pelhamer (b), and Pilsensee (c).

Appendix C – Potential changes of macrophyte species richness

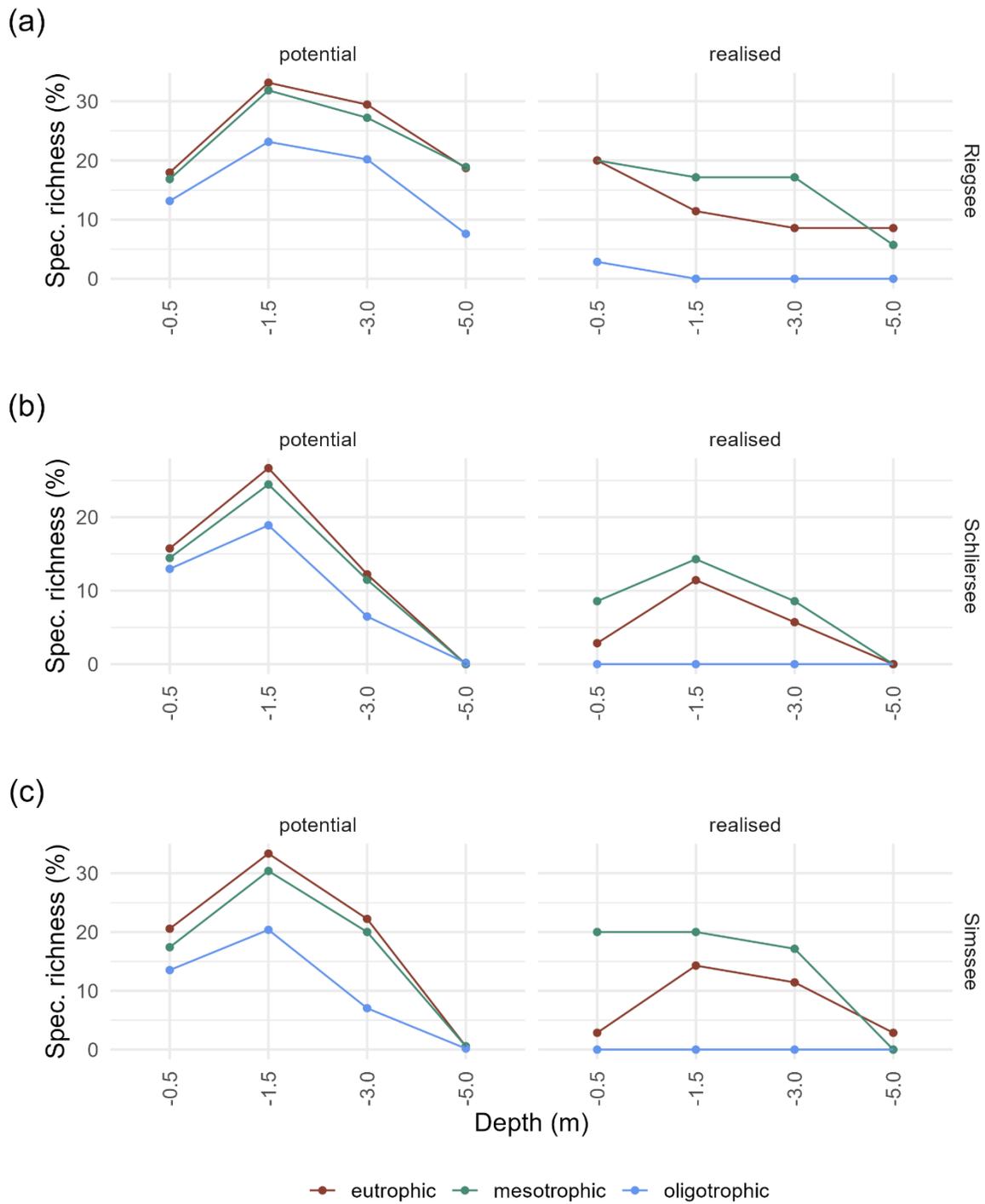


Figure C.7: Comparison of potential and realised species richness for Riegsee (a), Schliersee (b), and Simssee (c).

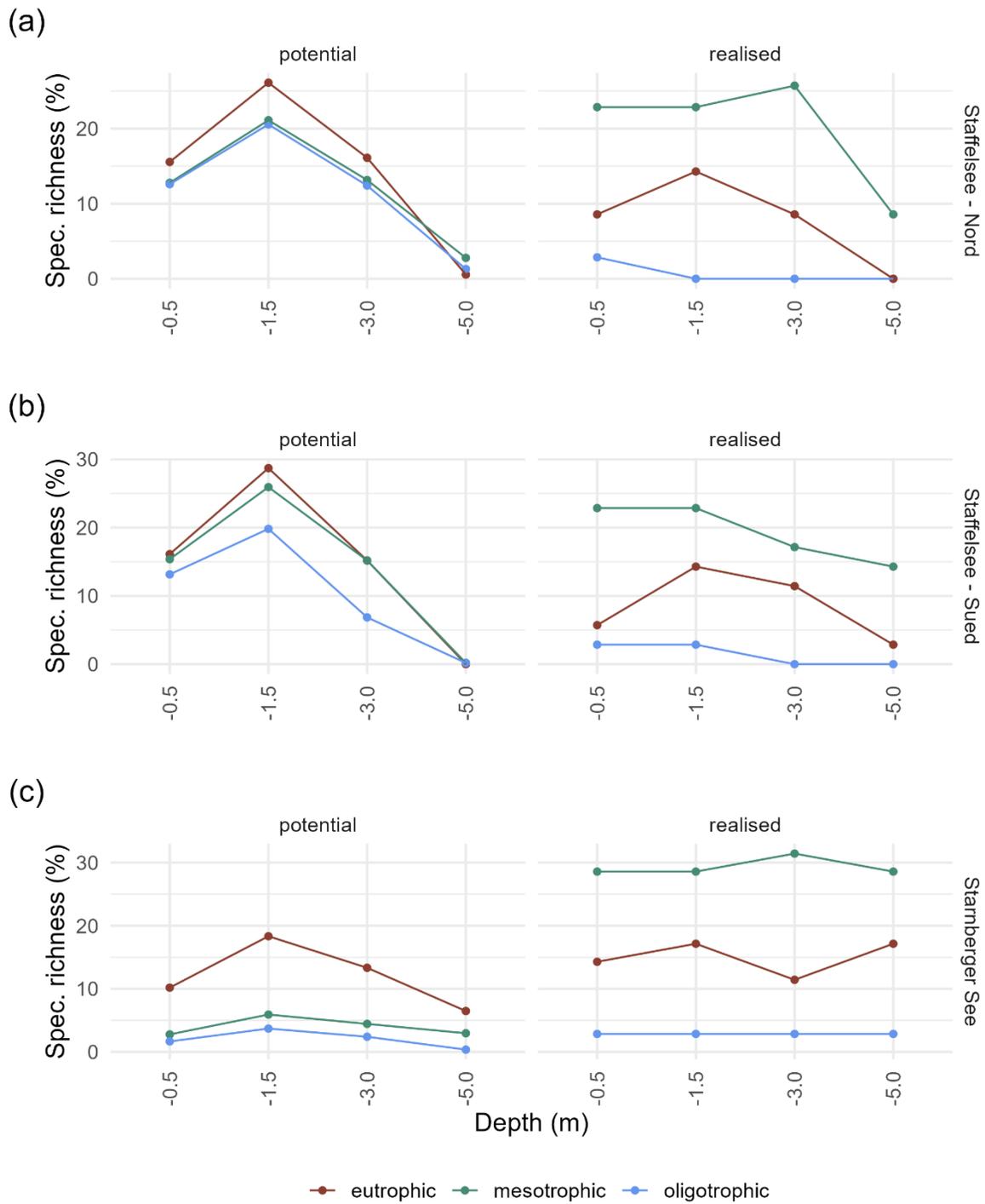


Figure C.8: Comparison of potential and realised species richness for Staffelsee Nord (a), Staffelsee Sued (b), and Lake Starnberger (c).

Appendix C – Potential changes of macrophyte species richness

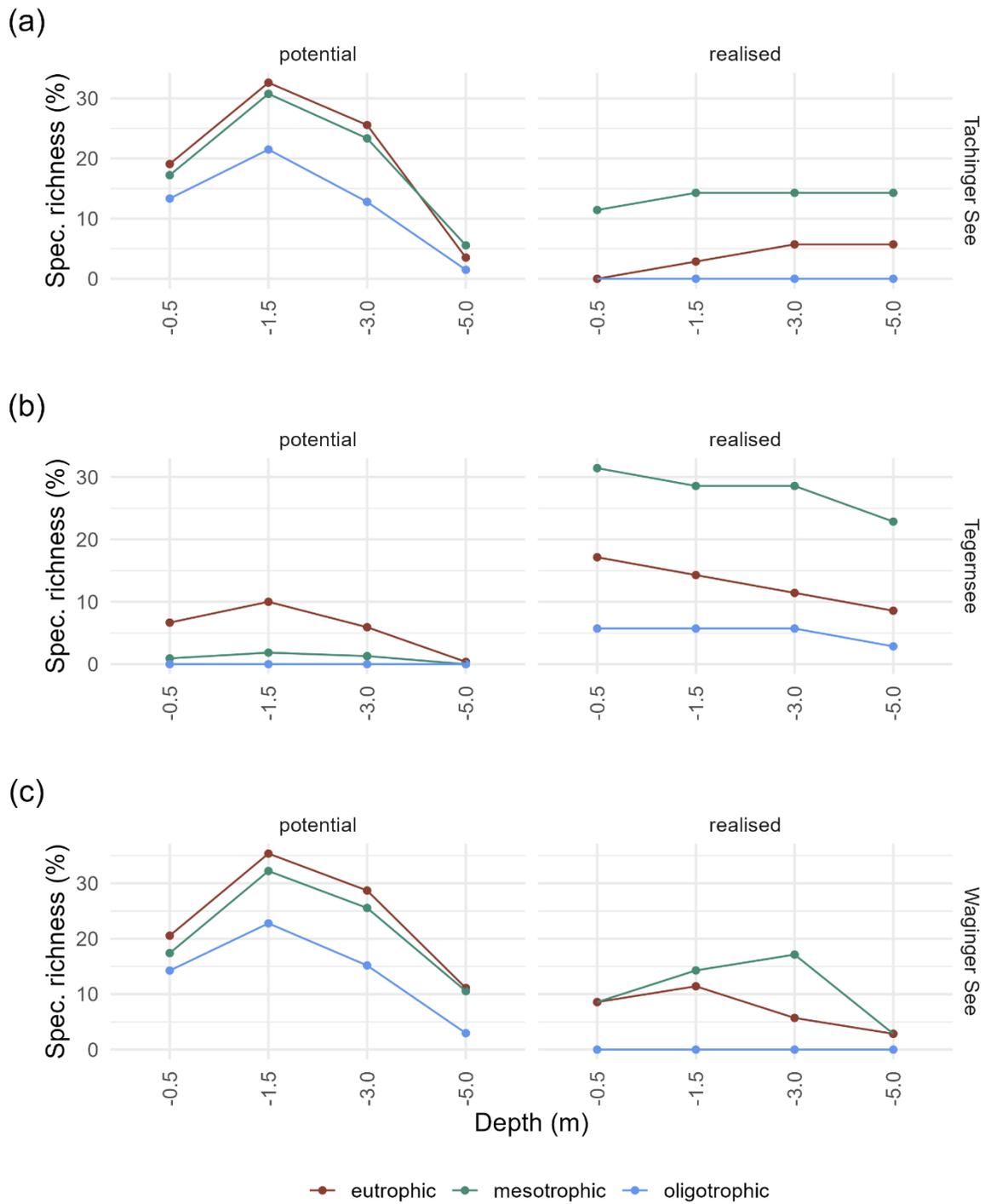


Figure C.9: Comparison of potential and realised species richness for Lake Tachinger (a), Tegernsee (b), and Lake Waginger (c).

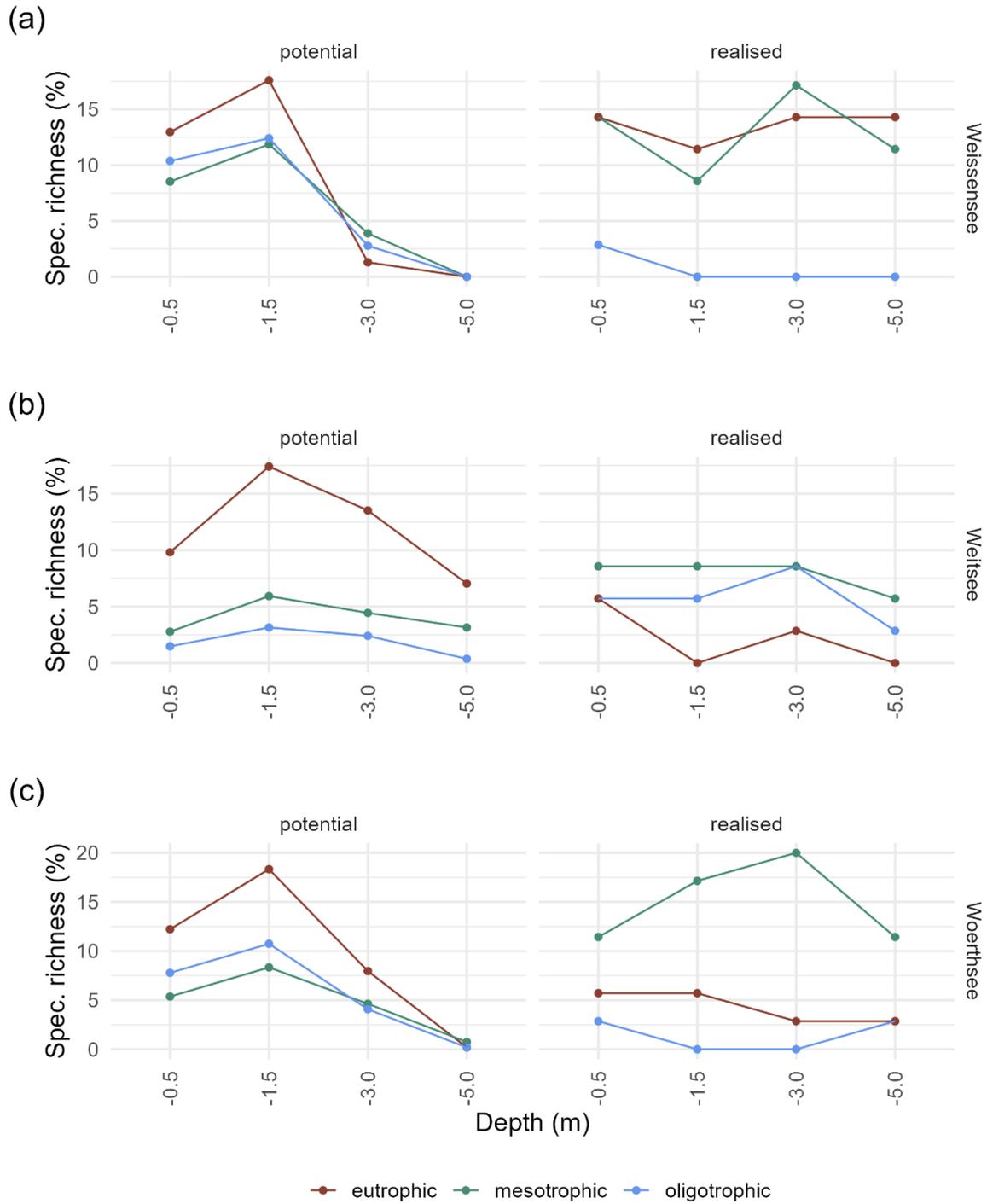


Figure C.10: Comparison of potential and realised species richness for Weissensee (a), Weitsee (b), and Woerthsee (c).

Future scenarios

To determine the traits that significantly influence if a species is a winner or a loser within a specific scenario, we applied a generalized linear model (GLM – see Methods section within the publication). To explore further scenarios, the results for a scenario of temperature increase (+3 °C) (Figure C.) are shown.

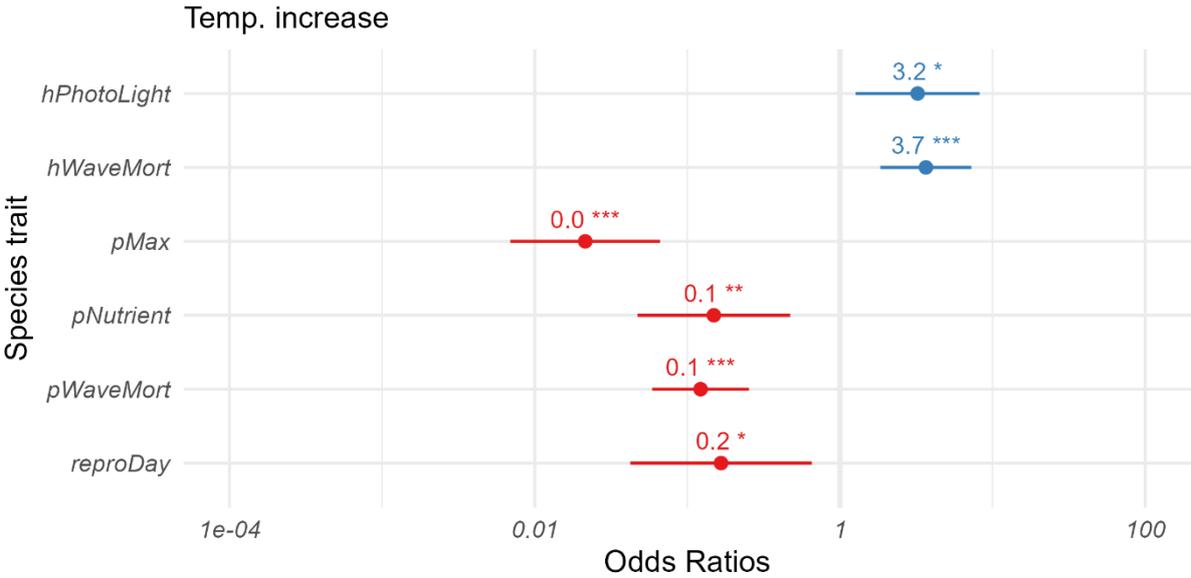


Figure C.11: Winner (blue) and loser traits (red) under increased temperature +3 °C.

Appendix D – ODD

Macrophyte Growth Model – ODD document

The Macrophyte Growth Model (MGM) is a process-based, eco-physiological model that can simulate the growth of submerged macrophytes under different environmental conditions.

MGM is a simplified re-implementation of the model Charisma 2.0 (van Nes et al., 2003) in the programming language Julia (Bezanson et al., 2017). Charisma 2.0 based on the previous model MEGAPLANT (Scheffer et al., 1993) (Figure D.1a). An explicit manual of Charisma 2.0 can be found on the project website (www.projectenaew.wur.nl/charisma/).

In the following sections a model description of the MGM is presented. The model description based on the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010) since the original model already has a documentation. Furthermore, the differences between MGM and Charisma 2.0 are explained in an additional section.

1. Purpose

MGM is designed to simulate the growth of submerged macrophytes under different environmental conditions in multiple depth. The model considers eco-physiological processes of macrophytes which depend on the availability of the resources light, nutrients, and water temperature (Figure D.1b).

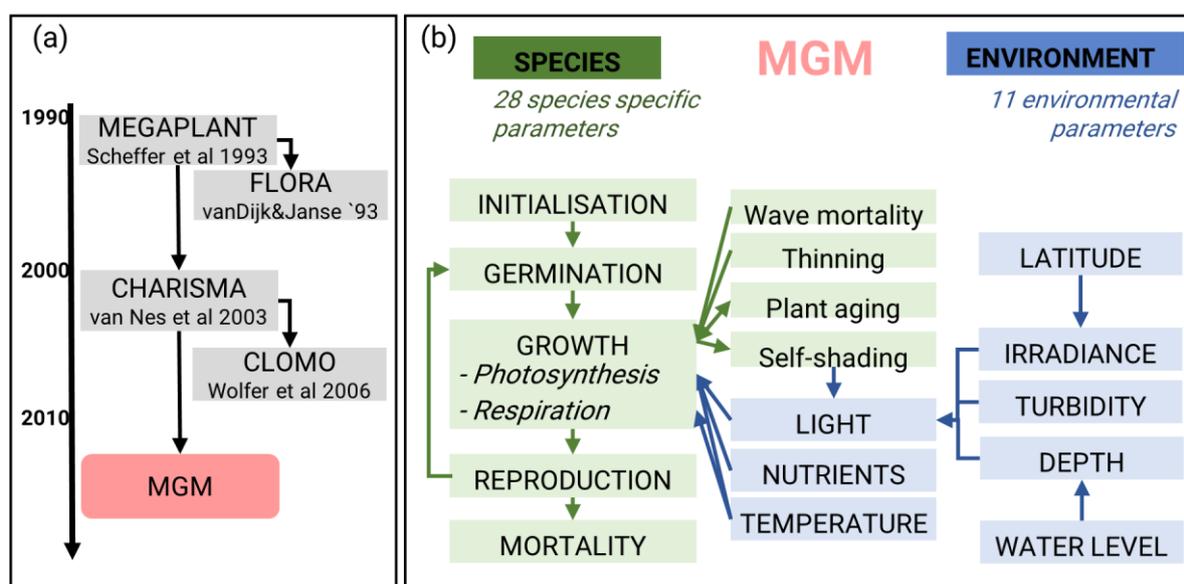


Figure D.1: Model phylogeny of MGM (a) and simplified model scheme (b).

2. Entities, state variables, and scales

Agents

The model simulates the annual life cycle of submerged macrophytes in a lake. One time step represents one day. The model uses the super-individual concept (see section 4: Design concepts). Every super-individual is defined by its biomass, number of represented individuals, its individual weight, height, and the allocated biomass for seed or tuber production.

Two different reproductive strategies are implemented: Reproduction via seeds or / and via tubers. Dependent on the selected reproductive strategy, there can be up to two super-individuals, one from reproduction via seeds and one from reproduction via tubers. Both are competing for light.

Each species is defined by a set of species-specific parameters listed in the section 6. Input data.

Multiple species are not competing for resources, they are simulated simultaneously.

Spatial units

The model is not spatially explicit. Different depths are modelled simultaneously without interaction.

Environment

Lakes are defined by lake specific parameters listed in section 6. Input data. Those define the annual course of water temperature, water level, water turbidity, nutrient content, and irradiance at the water surface. Further lake specific parameters are used to calculate the hourly photosynthetic active light reaching the species dependent on water depth.

3. Process overview and scheduling

Per daily time step each super-individual undergoes the following processes (see Figure D.2). They depend on the day and on the age of the species.

Germination starts at *germinationDay*. On that day, the seed biomass or tuber biomass is transferred in macrophyte biomass dependent on a species-specific ratio (*cTuber*). From this day, daily **growth** dependent on photosynthesis rate and respiration rate starts. The species can grow until its maximal age (*maxAge*) is reached. Then, a complete die-off event occurs. Other processes of **mortality** during the lifespan of the species can be thinning, negative growth (respiration rate > photosynthesis rate), wave mortality and background mortality. **Reproduction** takes place in a defined timespan (between *seedsStartAge* and *seedsEndAge*). In that timespan, a part of the macrophyte biomass is daily allocated until a predefined fraction is reached (*seedFraction* / *tuberFraction*). The allocated biomass is not photosynthetically active.

The seeds / tubers are released on a predefined day (*reproDay*): the allocated biomass for seed / tuber production is transferred into seed biomass / tuber biomass. The species life cycle within the following year starts with the produced seedBiomass / tuberBiomass of the previous year.

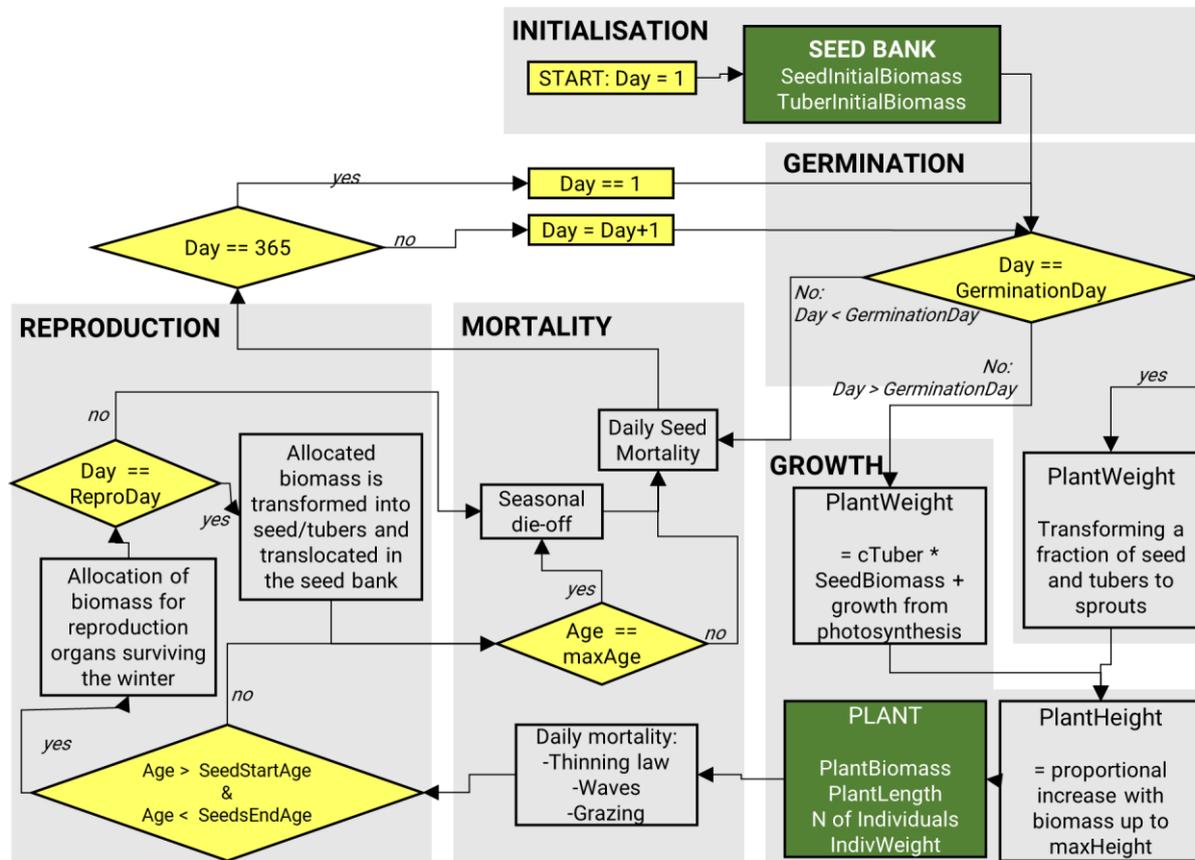


Figure D.2: MGM scheduling and daily processes within the annual cycle.

4. Design concepts

The model is designed as **deterministic** model, no probabilities and stochastic processes are included. Therefore, all results are completely reproducible.

The model uses the **super-individual approach** (Scheffer et al., 1995). Each super-individual represents a distinct number of individuals which all have the same growth rate, individual weight, and height. The advantage is that computational time is reduced. As MGM is not spatially explicit, one super-individual is simulated per run representing the growth at 1m². Since the environmental conditions within on depths in the whole lake are identical, this patch represents the corresponding depth in the whole lake. If multiple depths are simulated, one super-individual represents each depth. If growth from seeds and tubers is used, the model uses two super-individuals, one from growth of seeds, and another one from tubers.

5. Initialization

Each species is initialized with a distinct seed and / or tuber biomass (*seedInitialBiomass* / *tuberInitialBiomass*).

Each lake is initialized with a deterministic annual course of water temperature, water level, water turbidity, nutrient content, and irradiance at the water surface.

6. Input data

To specify the input, input files defining the general settings, lake parameters, and species parameters are necessary. Their parameters are explained in the following three subsections. They must be placed in the folder “input.” If not given, the default settings from *defaults.jl* are used.

General settings

General settings can be defined in a file named *general.config.txt*. The options are explained in Table D.1.

Table D.1: General settings of MGM.

| Parameter | Unit | Description |
|-------------|------|--|
| years | n | Number of years to simulate |
| depths | m | Depths below mean water level to simulate. Multiple depth can be given here |
| yearsoutput | n | Number of last simulated years that get saved in the output files |
| species | - | Relative paths to the species configuration files |
| lakes | - | Relative paths to the lakes configuration files |
| modelrun | - | Folder name of the model run in the output folder (is created automatically) |

Species settings

Species specific settings can be set in the files in the *species* folder. For each species one file is necessary. The parameters are listed in Table D.2.

Table D.2: Species-specific settings within MGM.

| Parameter | Unit | Description |
|----------------------------|----------------------------------|---|
| <i>seedsStartAge</i> | days | Age of the plants where seed formation starts |
| <i>seedsEndAge</i> | days | Age of the plants where seedFraction is reached |
| <i>tuberStartAge</i> | days | Age of the plants where tuber formation starts |
| <i>tuberEndAge</i> | days | Age of the plants where tuberFraction is reached |
| <i>cTuber</i> | fraction | Fraction of tuber weight lost daily when sprouts start growing |
| <i>pMax</i> | h^{-1} | Maximal gross photosynthesis |
| <i>q10</i> | – | Q10 for maintenance respiration |
| <i>resp20</i> | d^{-1} | Respiration at 20 °C |
| <i>heightMax</i> | m | Maximal height |
| <i>maxWeightLenRatio</i> | g | Weight of 1 m young sprout |
| <i>rootShootRatio</i> | fraction | Proportion of plant allocated to the roots |
| <i>fracPeriphyton</i> | fraction | Fraction of light reduced by periphyton |
| <i>bPhotoDist</i> | m | Distance from plant top at which the photosynthesis is reduced factor 2 |
| <i>bPhotoLight</i> | $\mu\text{Em}^{-2}\text{s}^{-1}$ | Half-saturation light intensity (PAR) for photosynthesis |
| <i>bPhotoTemp</i> | °C | Half-saturation temperature for photosynthesis |
| <i>plantK</i> | $\text{m}^{-2} * \text{g}^{-1}$ | Extinction coefficient of plant issue |
| <i>pPhotoTemp</i> | – | Exponent in temp. effect (Hill function) for photosynthesis |
| <i>sPhotoTemp</i> | – | Scaling of temperature effect for photosynthesis |
| <i>BackgroundMort</i> | d^{-1} | Background mortality |
| <i>cThinning</i> | – | c factor of thinning function |
| <i>bWaveMort</i> | m | Half-saturation depth for mortality |
| <i>germinationDay</i> | d | Day of germination of seeds |
| <i>reproDay</i> | d | Day of dispersal of seeds |
| <i>maxAge</i> | d | Maximal plant age |
| <i>maxWaveMort</i> | d^{-1} | Maximum loss of weight in shallow areas |
| <i>pWaveMort</i> | – | Power of Hill function for wave mortality |
| <i>thinning</i> | – | If thinning is applied (TRUE / FALSE) |
| <i>bNutrient</i> | mg l^{-1} | Half-saturation nutrient concentration for photosynthesis |
| <i>pNutrient</i> | – | Power of Hill function for nutrient |
| <i>seedBiomass</i> | g | Individual weight of seeds |
| <i>seedFraction</i> | year^{-1} | Fraction of plant weight allocated to seeds |
| <i>seedGermination</i> | year^{-1} | Fraction of seeds that germinate |
| <i>seedInitialBiomass</i> | g | Initial biomass of seeds |
| <i>seedMortality</i> | d^{-1} | Daily mortality of seeds |
| <i>tuberBiomass</i> | g | Individual weight of tubers |
| <i>tuberFraction</i> | year^{-1} | Fraction of plant weight allocated to tubers |
| <i>tuberGermination</i> | year^{-1} | Fraction of tubers that germinate |
| <i>tuberGerminationDay</i> | dayno | The day that tubers germinate |
| <i>tuberInitialBiomass</i> | gm^{-2} | Initial biomass of tubers |
| <i>tuberMortality</i> | d^{-1} | Mortality of tubers |

Lake settings

Lake specific settings can be defined in the files in the *lakes* folder. One file per lake is necessary. The following parameters (Table D.3) can be set:

Table D.3: Lake-specific settings within MGM.

| Parameter | Unit | Description |
|------------------------|----------------------------------|--|
| <i>fracReflected</i> | – | Light reflection at the water surface |
| <i>iDelay</i> | d | Days after 1st of January where I is minimal |
| <i>iDev</i> | – | Deviation factor to change total irradiation |
| <i>latitude</i> | ° | Latitude of corresponding lake |
| <i>maxI</i> | $\mu\text{Em}^{-2}\text{s}^{-1}$ | Maximal Irradiance |
| <i>minI</i> | $\mu\text{Em}^{-2}\text{s}^{-1}$ | Minimal Irradiance |
| <i>parFactor</i> | – | Fraction of total irradiation that is PAR |
| <i>maxNutrient</i> | mg l^{-1} | Concentration of limiting nutrient in water |
| <i>maxTemp</i> | °C | Maximal mean daily temperature of a year |
| <i>minTemp</i> | °C | Minimal mean daily temperature of a year |
| <i>tempDelay</i> | d | Days after 1st of January where Temp is minimal |
| <i>tempDev</i> | – | Share of temp |
| <i>backgrKd</i> | m^{-1} | Background light attenuation of water (Vertical light attenuation, turbidity) |
| <i>kdDelay</i> | d | Delay, the day number with the minimal light attenuation coefficient |
| <i>kdDev</i> | – | Deviation factor, a factor between 0 and 1 to change the whole light attenuation range |
| <i>maxKd</i> | m^{-1} | Maximum light attenuation coefficient |
| <i>minKd</i> | m^{-1} | Minimum light attenuation coefficient |
| <i>levelCorrection</i> | m | Correction for reference level (MWL) |
| <i>maxW</i> | m | Maximal water level above MWL |
| <i>minW</i> | m | Minimal water level below MWL |
| <i>wDelay</i> | m | Delay of cosine of water level |

7. Submodels

See detailed description of all functions in the manual of Charisma 2.0. All differences and simplifications are described in section 9. Differences to Charisma.

8. Output

The main simulation output consists of different files per species, lake, and depths. The main output types are described in the following table (Table D.4). Each line in every output file represents one day, except of the settings file. The columns are described in the table.

Table D.4: Output files from MGM.

| File name | Description | Columns within files | Units |
|---------------|--|---|---|
| growthSeeds | Daily Growth rates for superindivuum from seeds for selected output years | Photosynthesis rate, Respiration rate, Growth rate | $g * (g * d)^{-1}, g * (g * d)^{-1}, g$ |
| growthTubers | Daily Growth rates for superindivuum from tubers for selected output years | Photosynthesis rate, Respiration rate, Growth rate | $g * (g * d)^{-1}, g * (g * d)^{-1}, g$ |
| seeds | Seedbank daily | SeedBiomass, SeedNumber, GerminatingBiomass | g, g, g |
| tubers | Tuberbank daily | TuberBiomass, TuberNumber, GerminatingBiomass | g, g, g |
| superInd | Sum of superIndSeed and superIndTuber, daily values | Biomass, Number, individual Weight, Height, allocatedSeedBiomass, allocatedTurionsBiomass | g, N, g, m, g, g |
| superIndSeed | Superindivuum from Seeds | Biomass, Number, individual Weight, Height, allocatedSeedBiomass, allocatedTurionsBiomass | g, N, g, m, g, g |
| superIndTuber | Superindivuum from Tubers | Biomass, Number, individual Weight, Height, allocatedSeedBiomass, allocatedTurionsBiomass | g, N, g, m, g, g |
| Temp | Daily value of water temperature | Water temperature | °C |
| Waterlevel | Daily value of water level | Waterlevel | masl |
| Irradiance | Daily value of irradiance at water surface | Irradiance | $\mu E * m^{-2} * s^{-1}$ |
| Light | Daily value of light | Light | $\mu E * m^{-2} * s^{-1}$ |
| Attenuation | Daily value of light attenuation | Attenuation | m^{-1} |
| Settings | Storage of all used input parameters | Settings | - |

9. Differences to Charisma 2.0

This part follows the sections within the manual of Charisma 2.0 and highlights the changes we implemented in MGM. All changes were made to simplify the model and to reduce the number of species-specific parameters.

This version of the model cannot be executed for multiple species. It calculates growth of biomass, number of subindividuals, individual weight and height for two super-individuals from the same species, one originated from seeds, one from tubers.

The grid

MGM is not spatially explicit. But is it depth explicit (calculation of single patches for multiple depths at once). Therefore, no seed dispersal, and no mixing effect for light attenuation or nutrients are included.

Vegetation

Overwintering structures

No changes are made, but seed dispersal is not included as MGM is not spatially explicit.

Growth form

The spreading of shoots under the water surface is not included.

Respiration

No changes are made.

Primary production

Primary production depends on maximum production rate (P_{max}), in-situ light (I), temperature (T), the distance (D) from the tissue to the top of the plant, and the limiting nutrient concentration (N) (Figure D.3). Bicarbonate concentration as limiting factor is ignored as the studied lakes are all not carbon limited.

$$P = P_{max} * f(I) * f(T) * f(D) * f(N)$$

Mortality factors

The changed mortality factors are:

- Background mortality and wave mortality: loss in number of individuals and biomass.
- Negative growth (Respiration > Photosynthesis) results in a loss of biomass.

Grazing

Grazing is completely excluded.

Seasonal die-off

No changes.

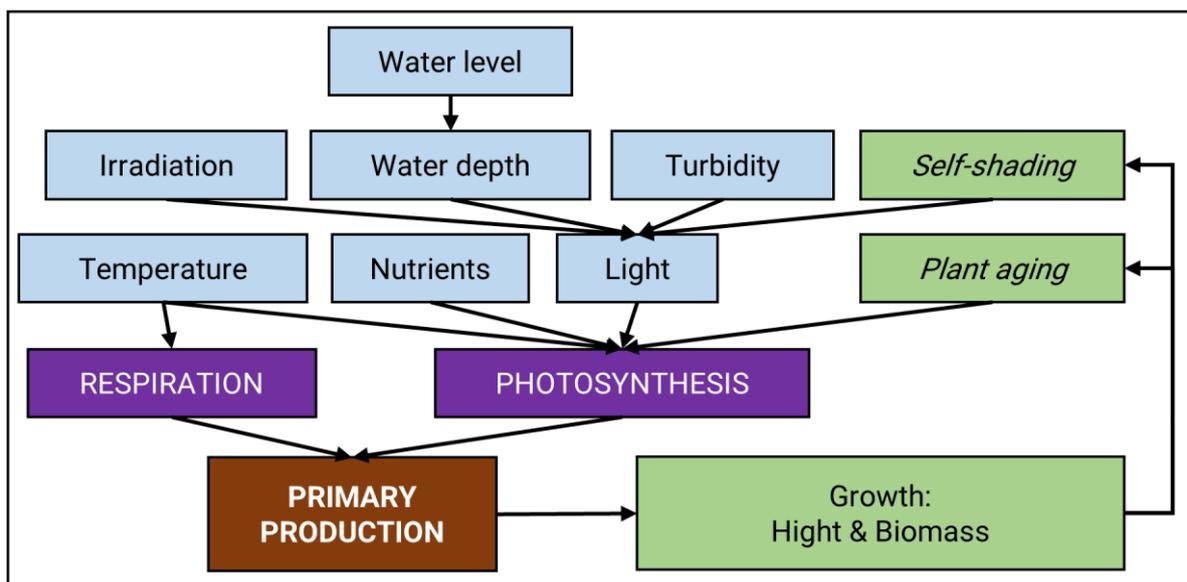


Figure D.3: Primary production within MGM.

Environment

Light

No changes were made: The daily total irradiation follows a sine wave over the year.

Effective irradiation

No changes.

Vertical light attenuation of the water

The extinction is modelled with a cosine function, as suggested in Charisma 2.0. Options and processes from Charisma 2.0 that are excluded:

- Read in daily data.
- Clear water periods.
- The effect of vegetation on the light attenuation.
- Mixing the light attenuation coefficient in grids.

Appendix D – ODD

Temperature

No changes were made. The daily water temperature follows a cosine wave over the year.

Water depth

No changes.

Level of the grid

Excluded, as MGM is not spatially explicit.

Water level

No changes were made. The daily water level values follow a cosine wave over the year. The option to import data is not implemented.

Bicarbonate

Excluded.

Limiting nutrient

No changes.

Publication list

- Lewerentz, A., Hoffmann, M., & Cabral, J. S. (2021). Depth diversity gradients of macrophytes: Shape, drivers, and recent shifts. *Ecology and Evolution*, 11(20), 13830–13845. <https://doi.org/10.1002/ece3.8089>
- Lewerentz, A., Schantz, D., Gröh, J., Knotte, A., Mammen, S. von, & Cabral, J. S. (2021). bioDI-VERSity. Ein Computerspiel gegen das Imageproblem von Wasserpflanzen. *Mitteilungen der Fränkischen Geographischen Gesellschaft*, 67, 29–36. <http://fgg-erlangen.de/fgg/ojs/index.php/mfgg/issue/view/54>
- Lewerentz, A., & Cabral, J. S. (2021). Wasserpflanzen in Bayern. Der Blick auf den See verrät nicht, was unter der Oberfläche passiert. *Mitteilungen der Fränkischen Geographischen Gesellschaft*, 67, 19–28. <http://fgg-erlangen.de/fgg/ojs/index.php/mfgg/issue/view/54>
- Lewerentz, A., Hoffmann, M., Hovestadt, T., Raeder, U., & Cabral, J. S. *in preparation*. Potential change in the future spatial distribution of submerged macrophyte species and species richness: the role of today's lake type and strength of compounded environmental change. *Preprint on Authorea*: DOI: 10.22541/au.165401091.12520929/v1

Affidavit

I hereby confirm that my thesis entitled "Spatiotemporal dynamics of freshwater macrophytes in Bavarian lakes under environmental change" is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

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