

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

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Abstract

Investigating diversity gradients helps to understand biodiversity drivers and threats. However, one diversity gradient is seldomly assessed, namely how plant species distribute along the depth gradient of lakes. Here, we provide the first in-depth characterization of depth diversity gradients (DDG) of submerged macrophytes across different 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 physio-chemical 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 DDG for alpha and gamma richness are predominantly hump-shaped, while beta richness shows a decreasing DDG. Generalized additive mixed-effect models indicate that the maximum alpha richness within the depth transect (R_{max}) is significantly influenced by lake area only, whereas for the corresponding depth (D_{max}) are influenced by light quality, light quantity and layering depth. 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 depended on physio-chemical 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.

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) like (1) latitude (Stehli et al., 1969; Rohde, 1992; Pontarp et al., 2019; Etienne et al. 2019), (2) elevation (Hutchinson 1953, Rahbek 1995, Lomolino 2001, Nogués-Bravo et al. 2008, Colwell and Rangel 2010, Sanders and Rahbek 2012, Graham et al. 2014, Rahbek et al. 2019), (3) tree height in forests (Petter et al. 2016), (4) depth in soils (Rendoš et al. 2016, Jakšová et al. 2019) or (5) depth in water (Rex and Etter 1998, Smith and Brown 2002, Gong et al. 2015). 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. On the one hand, the best studied biodiversity gradients are the large spatiotemporal gradients like the decreasing diversity with latitude (Pontarp et al. 2019) and the decreasing or hump-shaped diversity with elevation (Rahbek 1995). On the other hand, the short spatiotemporal gradients, like depth in freshwaters, are often overlooked.

Freshwater ecosystems have a high biodiversity, but also show a high rate of species loss (Strayer and Dudgeon 2010, Gatti 2016, He et al. 2017), exceeding those of terrestrial systems (Dudgeon et al. 2006). Despite this, studies that focus on the diversity gradient in freshwater are surprisingly scarce, although light gradients in freshwater must represent a very strong driver. The few 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). Thus, it is not clear if the patterns are generalizable for different species groups and even across different lakes.

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) and especially the depth pattern of submerged macrophytes is sparsely studied and remains unclear (Fu et al. 2014a, b, Ye et al. 2018). The few studies that have looked at depth distribution of macrophytes in lakes 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. 2014a, b). Hence, it remains unclear if the described pattern is generalizable and whether it stays robust over time.

The lack of studies is intriguing because the environmental gradients along lake depth represents one of the sharpest found in nature, with strong variation in 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 and 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 and 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 and Puijalon 2011). Moreover, mechanical disturbances, like wind or waves, lose their influence gradually with depth (Van Zuidam and Peeters 2015). Also the probability that water level fluctuations result in drying up the soil (Evtimova and Donohue 2016) is reduced and browsing pressure by water fowl decreases with depth (Bakker et al. 2016). How these different environmental gradients influence the species richness of macrophytes stays 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 and assessing the relative importance of its drivers. Specifically, we ask the following questions:

- 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?
- 3.1. Has the DDG being stable over recent years? 3.2. Are temporal trends general or lake-specific?

To address these questions, we use the macrophytes occurrence data of 274 transects taken along 13 years

across 28 natural deep lakes in Bavaria, that were mapped for the monitoring of the European Water Framework Directive. We expect a hump-shaped DDG (question 1.1) corresponding to previous punctual empirical evidence and following the typical patterns found along elevation. We assume no broad differences between lakes and diversity components as the pattern is supposed to be generalisable (question 1.2). 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 influences resource availability (light, temperature). Finally, we assess for question 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.

Material and Methods

Data and study area

Bavaria has a broad variety of lakes, which vary in size, depth, altitude and physiochemical parameters. Information about surface area and maximal lake depth were provided by Bayerisches Landesamt für Wasserwirtschaft (1987). We obtained data for water level statistics from the hydrological service of Bavaria (<https://www.gkd.bayern.de/>). Physical-chemical data include monthly measurements at the deepest point of the lake. We selected the physical-chemical parameters that were measured for the largest number of lakes. The full list of environmental variables is given in Table 1.

Macrophyte data was 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 and include vegetation surveys for all large lakes of Bavaria ($>0.5 \text{ km}^2$ 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 Fig. 1a). Each transect is subdivided along the depth gradient into four depths (0-1m; 1-2m; 2-4m; $>4\text{m}$). At each depth all species' frequency is sampled in five steps following the scale of Kohler (1978), an estimate of abundance.

Data preparation

Data preparation and analyses were done in R 3.5.3 (R Development Core Team 2019). The code of data analysis is provided as Research Compendium on github. *It will be provided in final version and is not yet added here because of the double-blind review process.*

To have comparable conditions we selected all lakes from the dataset that are deep (maximum depth $>5\text{m}$), not artificial and have a natural water level dynamic (i.e. not influenced by storage power plants) and at least one sampling repetition.

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 1.

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 plants and (III) plants that were not identified down to the species level. 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.

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 of transects (Fig. 1b). The gamma richness for every lake and year was defined as the total number of species per depth range (Fig. 1c). We then calculated an additive beta richness as gamma richness minus alpha richness (Tuomisto 2010) (Fig. 1d).

To further characterize the diversity depth gradient, we identified the peak of the richness depth curve (Fig. 1c). For each transect we filtered the depth with the maximal species number. Thereafter, we averaged this valued across transects per lake and year, from now on termed the depth with maximal alpha richness ($\Delta_{(a,\mu a\xi)}$). The corresponding maximal species number averaged across transects is termed the maximal alpha richness ($P_{(a,\mu a\xi)}$). Similarly, the depth with maximal gamma richness ($\Delta_{(\gamma,\mu a\xi)}$) is the depth of the maximal gamma richness ($P_{(\gamma,\mu a\xi)}$) along depth, as well as maximal beta depth ($\Delta_{(\beta,\mu a\xi)}$) describes maximal beta richness ($P_{(\beta,\mu a\xi)}$) along depth.

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 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 ($D_{max} > -1\text{m}$), shallow hump-shaped (D_{max} between -1 and -2 m), deep hump-shaped (D_{max} between -2 and -4 m) and increasing ($D_{max} < -4\text{m}$) (Fig. 1d). 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). To identify the driving factors on the richness peaks we used Generalized Additive Mixed-Effect Models (GAMMs), computed with the R package ‘gamm4’ (Wood 2011). The $\Delta_{(a,\beta,\gamma,\mu a \xi)}$ and $P_{(a,\beta,\gamma,\mu a \xi)}$ were used as response variables, the lake as random effect. To reduce the high correlations between abiotic factors (Pearson correlation test) we performed a Principle Component Analysis (PCA) analysis 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 the third questions about the temporal change of the depth diversity gradient, we used the *biodiversity time series dataset*. First, we calculate the Invariability Coefficient (IC) as inverse of the Coefficient of Variation (CV):

$$IC = \frac{1}{CV} = \frac{1}{\frac{sd}{mean}} = \frac{mean}{sd}$$

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, $\Delta_{(a,\beta,\gamma,\mu a \xi)}$ and $P_{(a,\beta,\gamma,\mu a \xi)}$, 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).

Results

For the dataset of all macrophytes recordings (*biodiversity dataset*), a total of 75 submerged species is documented in Bavaria. The available taxonomic groups are mainly Spermatophytes (65 species), Charophytes (20 species), Bryophytes (5 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.

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 (Fig. 2a,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 (Fig. 2b). However, all three richness components show high standard deviations in the 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 till 5.6 for gamma richness (see individual DDG curves for all lakes in Supporting information).

Comparing the richness components across depths revealed only significant differences between mid and greater depths, but not for shallower depth (Supporting information).

Plotting the DDG measures for all three richness components (Fig. 2d-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%) (Fig. 2g-i). For beta richness the majority are decreasing curves (40%) while for gamma richness hump-shaped curves with a peak between -1 and -2 m were slightly prevailing (39%)., All depth pattern types are found for all three measures.

The three depth-dependent richness measures are significantly correlated with one another ($p < 0.05$). The strongest correlation shows beta and gamma richness ($\text{cor} = 0.95$), followed by alpha and gamma richness ($\text{cor} = 0.85$) and alpha and beta richness ($\text{cor} = 0.64$). The 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 correlates with each other. Similarly, R_{max} also correlates across the three richness components ($p < 0.05$). For correlation coefficients see Supporting information. However, a Chi-square test shows, that pattern types and richness components are statistically significantly associated ($p = 0.0005$).

Drivers of the depth diversity gradients

The DDG measures correlate with some of the abiotic variables (Supporting information). $P_{(a,\mu a\xi)}$ correlates highly significantly ($p < 0.01$) with *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_4N ($\text{cor} = -0.5, p < 0.01$), SiO_2 ($\text{cor} = 0.62, p < 0.01$) and *spectral absorption coefficient* ($\text{cor} = 0.6, p < 0.01$). $P_{(\beta,\mu a\xi)}$ correlates highly significantly ($p < 0.01$) with *area* ($\text{cor} = 0.55, p < 0.01$). $P_{(\gamma,\mu a\xi)}$ correlates highly significantly ($p < 0.01$) with *area* ($\text{cor} = 0.57, p < 0.01$) and *water level fluctuations* ($\text{cor} = 0.56, p < 0.01$). $\Delta_{(a,\mu a\xi)}$ correlates highly significantly ($p < 0.01$) with O_2 dissolved ($\text{cor} = -0.54, p < 0.01$), *total phosphorus content* ($\text{cor} = 0.6, p < 0.001$), *transparency* ($\text{cor} = -0.67, p < 0.001$) and *temp_{sd}* ($\text{cor} = 0.59, p < 0.01$). $\Delta_{(\beta,\mu a\xi)}$ and $\Delta_{(\gamma,\mu a\xi)}$ 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 (Supporting information). Strongest positive correlations ($\text{cor} > 0.7$ or < -0.7) within abiotic data were found between N_{tot} and NO_3N ($\text{cor} = 0.92, p < 0.01$), *conductivity* and SiO_2 ($\text{cor} = 0.83, p < 0.01$), *chloride* and *conductivity* ($\text{cor} = 0.73, p < 0.01$). Strongest negative correlations showed *transparency* and *total phosphorus content* ($\text{cor} = -0.72, p < 0.01$) and *transparency* and *conductivity* ($\text{cor} = -0.71, p < 0.01$).

Due to the high correlation coefficients between abiotic factors, we performed a PCA (Supporting information). We use the first four axes (81% of total variation – Fig. 3f-i) to address the DDG drivers. The first axis, PC1, can be characterized as the “ SiO_2 & Conductivity axis” (both positive with the axis), explaining 30.1% of the variance. The PC2, the second axis, can be described as the “Temperature & P_{tot} axis” as both abiotic variables have the highest (negative) impact (26.1% of variance). The third axis, PC3, can be named the “Temperature *sd* – Chloride axis” (13.3% of variance) as it ranges from most negative variable *temp_{sd}* to most positive variable *chloride* 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).

The GAMM showed that $\Delta_{(a,\mu a\xi)}$ ($R^2=0.73$) significantly varies with all four PCA axes (Fig. 3a-d). The $\Delta_{(a,\mu a\xi)}$ decreases with PC2 (Temperature & P_{tot} axis) and PC3 (Temp_{sd} – Chloride axis) axes, slightly increases with PC4 axis (O_{2diss} – SAC axis) and increases only for extreme positive values of PC1 axis (SiO_2 & Conductivity axis). The $P_{(a,\mu a\xi)}$ ($R^2=0.44$) is only influenced by the PC1 axis (SiO_2 & Conductivity axis) with a positive linear relationship (Fig. 3e). The GAMM analysis for $\Delta_{(\beta,\mu a\xi)}$, $P_{(\beta,\mu a\xi)}$, $\Delta_{(\gamma,\mu a\xi)}$ and $P_{(\gamma,\mu a\xi)}$ had all $R^2 < 2.1\%$ (see results in Supporting information).

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 $\Delta_{(a,\mu a\xi)}$ (mean=6.62, sd=4.11), of $P_{(a,\mu a\xi)}$ (mean=6.36, sd=2.87), of $P_{(\beta,\mu a\xi)}$ (mean=5.89, sd=2.06) and of $P_{(\gamma,\mu a\xi)}$ (mean=6.52, sd=2.97) were high in comparison to the IV of $\Delta_{(\beta,\mu a\xi)}$ (mean=1.56, sd=0.48) and of $\Delta_{(\gamma,\mu a\xi)}$ (mean=1.78, sd=0.53).

For all lakes depth-independent gamma richness showed a small but significant trend ($p < 0.1$) towards more species (Supporting information). Analysing all lakes together, the DDG measures revealed no significant

common trend ($p > 0.05$) (Supporting information). 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 Supporting information). The $\Delta_{(a, \mu\alpha\xi)}$ 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 Woerthsee). The $\Delta_{(\beta, \mu\alpha\xi)}$ increases significantly at Lake Riegsee, while $\Delta_{(\gamma, \mu\alpha\xi)}$ 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 2).

Discussion

The DDG patterns of macrophytes

We showed, that submerged macrophytes in deep lakes have in general a hump-shaped Depth Diversity Gradients (DDG) for alpha richness, a prevailing decreasing pattern for beta richness and a dominantly hump-shaped pattern for gamma richness (Fig. 2a-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, that show also 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 constrains. 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 make the hypotheses 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 (Fig. 2d-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 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, before limited to one single lake in China (Fu et al. 2014a, b). Although for alpha and gamma richness, hump-shaped curves along depth are predominant (Fig. 2g-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.

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} correlates of the different richness components with a very similar set of abiotic parameters. All R_{max} correlates with area. This reflects species-area relationships (SARs) (Connor and McCoy 1979, Lomolino 2000, Qian et al. 2007, Patiño et al. 2014) for macrophytes, which is also shown by high correlation of area with total gamma richness. Looking at the GAMM results for non-linear responses $P_{(\beta, \mu\alpha\xi)}$ and $P_{(\gamma, \mu\alpha\xi)}$ did not show any significant results, but $P_{(a, \mu\alpha\xi)}$ is exclusively influenced by the “*SiO₂ & Conductivity axis*” (PC1) (Fig. 3). *Area, spectral absorption coefficient* and *water level fluctuations* (WLF) 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), 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. However, it was not shown yet that the size of lakes also influences the shape of DDG.

The $\Delta_{(\beta, \mu a \xi)}$ and $\Delta_{(\gamma, \mu a \xi)}$ could not be explained with abiotic variables, neither by correlations nor by a GAMM. Unlike $\Delta_{(a, \mu a \xi)}$, the gamma, and consequently beta, values along DDG are more variable, indicating spatial heterogeneity and possibly unsaturation (Karger et al. 2014). Still, $\Delta_{(a, \mu a \xi)}$ correlates positively with *phosphorus* and *temperature_sd*, and negatively with *O₂ dissolved* and *transparency*. Furthermore, looking at non-linear influences, the $\Delta_{(a, \mu a \xi)}$ is affected by all four PCA-axes.

The PC2 (*Temperature & P_{tot} axis*) shows the highest influence (Fig. 3). This means that in lakes with high *phosphorus* concentration and/or high *temperature* the DDG peaks in shallower waters. *Phosphorus* is the limiting factor for phytoplankton growth and phytoplankton reduces the light availability for macrophytes. In contrast for macrophytes, it is still debatable whether the *phosphorus* concentration in the water is a limiting growth factor (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 and Freedman 2006). Hence, *phosphorus* might affect macrophytes by promoting phytoplankton growth, which then reduces light availability and shifts DDG to shallower depths. Besides *phosphorus*, *temperature* is a major factor influencing metabolic processes as photosynthesis and respiration. Additionally in lakes, higher *temperature* result in higher nutrient levels due to increased mineralization and internal fertilization processes (Moss 2012). Internal fertilization processes occur when higher water temperatures 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 (*Temperature & 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 $\Delta_{(a, \mu a \xi)}$, which is indicated by the influence of the PC4 (*O₂diss – SAC axis*). With high *O₂diss* 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. Thus, 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 (VanderMeulen et al. 2001, Rajaniemi 2003, Huston 2014).

Besides light, also temperature seems to influence $\Delta_{(a, \mu a \xi)}$, 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 that along PC3 (*Tempsd – Chloride axis*) $\Delta_{(a, \mu a \xi)}$ decreases. A high *temperature_sd* (shallow epilimnion – the upper temperature layer in a stratified lake) promotes a shallow $\Delta_{(a, \mu a \xi)}$, while a low *temperature_sd* (broad epilimnion) allows deeper $\Delta_{(a, \mu a \xi)}$. *Temperature_sd* is positively correlated to *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 (*NH₄N – SiO₂ & Conductivity axis*). Just at very high values of PC1 that $\Delta_{(a, \mu a \xi)}$ becomes shallower. As *conductivity* is negatively correlated with *transparency* (cor=-0.71, $p < 0.001$), we speculate that also here transparency is the actual mechanism that influences $\Delta_{(a, \mu a \xi)}$.

In summary, the main influences on $\Delta_{(a, \mu a \xi)}$ seem to be as expected factors of water quality that influence light quantity (transparency, influenced by phosphorus and temperature), light quality (CDOM) and layering depth (temperature). The main influence on $P_{(a, \mu a \xi)}$ is the lake surface area.

DDG temporal change

We showed that the stability of the pattern depends on the DDG measure (question 3.1). $\Delta_{(\beta, \mu a \xi)}$ and $\Delta_{(\gamma, \mu a \xi)}$

were quite variable measures over years, while $\Delta_{(a,\mu a\xi)}$, $P_{(a,\mu a\xi)}$, $P_{(\beta,\mu a\xi)}$ and $P_{(\gamma,\mu a\xi)}$ are comparatively stable measures. This may be related to the fact that there is neither pair-wise correlation nor explaining model for $\Delta_{(\beta,\mu a\xi)}$ and $\Delta_{(\gamma,\mu a\xi)}$.

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 $\Delta_{(a,\mu a\xi)}$, 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). Thus, the following hypothesis can be set (Fig. 4): (1) As temperatures rise, so do lake surface water temperatures as well (O'Reilly et al. 2015). This seems to result in shallower epilimnion (Kraemer et al. 2015) and generally shallower D_{max} and a lower R_{max} . (2) Furthermore, rising temperature entail higher P content, as they promote internal fertilization. But also extreme weather events combined with enriched fertilization in agriculture can cause fertilization events (Rose et al. 2016), which might result in shallower light depth consequently in shallower DDG. (3) Browning, which is generally increasing due to temperature induced decomposition rates and changes in precipitation events (Sobek et al. 2007, Weyhenmeyer and Karlsson 2009, Guarch-Ribot and Butturini 2016), 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, 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 Fig. 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 Fig. 4).

Implications for diversity gradients in general

Looking at different diversity gradients and generalising the findings might be a chance to get a deeper insight into mechanisms of species richness. The depth diversity gradient (DDG) of macrophytes brings some advantages compared the latitudinal diversity gradient (LDG) or the elevational diversity gradient (EDG). The DDG is formed for shorter scales (few meters) than the EDG, which implies a lower importance of dispersal or connectivity processes. Another big advantage looking at freshwater depth pattern is that it is much easier to use replicates for DDG than for LDG and EDG. For LDG, the options for replicates are restricted as there are mainly two replicates for the two hemispheres, which can be further (pseudo)replicated when studying different taxa or continents (Pontarp et al. 2019). For EDG, comparative studies require a high logistic sampling effort. Thus, studies addressing the overall shape across EDGs and the variables affecting them are not yet clear (Nogués-Bravo et al. 2008, McCain and Grytnes 2010, Kessler et al. 2011, Sanders and Rahbek 2012). Hence, the smaller scales of DDG seem an advantage to do such replicate studies to address the role of energy or productivity in shaping the diversity gradients. Moreover, a comparative study across different gradients (EDG vs. DDG) could yield further insights in understanding diversity drivers.

Besides DDG, there are other small-scale diversity gradients that get studied. One example is the height or vertical diversity gradient (VDG) from forest floor to tree crowns following environmental gradients of light intensity, temperature and humidity. Here, species richness distribution depends on the study species group. Hump-shaped patterns for ferns and lycophytes (Acebey et al. 2017) or vascular epiphytes (Krömer et al. 2007) or decreasing patterns for vascular epiphytes (Wang et al. 2016) were found. The pattern does not seem to be very clear and are strongly influenced by host crown characteristics (Wang et al. 2016). Still, VDG could be the most comparable gradient to DDG for contrasting the role of light and temperature, but paired data with both diversity and environmental data for VDG is even scarcer than for DDG.

The LDG for species generally peak in the tropics (Pontarp et al. 2019). However, looking at freshwater plants, the diversity gradient does not decrease linearly (Alahuhta et al. 2020), but seems to have at sub-tropical to low tropical latitudes (Murphy et al. 2019). Thus, along latitude, the species richness peak is at

a high to intermediate level of solar productivity, which is reflected in our analysis of DDG. This might be explained by the Intermediate Productivity Hypothesis (IPH). The IPH, stating that at low productivity level (deep waters with low light quantity and low temperature) only few species can survive and at high productivity level (shallow waters with high light quantity and high temperature) only few competitive species survive, is highly discussed (Adler et al. 2011, Fraser et al. 2015) and mostly used along LDG. Besides competition, mid-gradient peaks can be explained from an evolutionary perspective as a maximal difference between speciation and extinction rates is expected at intermediate productivity (VanderMeulen et al. 2001). Although quantification of productivity along depth should be attempted, our findings already indicate a key role of light quantity and temperature in shaping DDG.

The hump-shaped curve of the DDG might mirror most elevational diversity gradients (EDG), which often peak at intermediate levels (Kessler et al. 2001, Nogués-Bravo et al. 2008). For both gradients one explanation might be geometry. The mid-domain effect (MDE) explains richness peaks in the middle of gradients by species range overlaps simply via geometric constraints (Colwell et al. 2004). This concept is mainly used to explain the EDG (McCain 2004, Cardelús et al. 2006, Brehm et al. 2007). Also along the depth gradient niches of single species might overlap and create an area of enhanced richness. Nevertheless, to adequately verify the influence of the mid-domain effect, it would be necessary to study single species in relation to environmental variables via mesocosm experiments without competition. Potential niche ranges associated with lake depth (e.g. light or temperature conditions) could then be determined and the overlap of these ranges for all co-occurring species of a particular lake would provide at which depth lies the MDE-predicted maximum number of species. This would make it possible to compare observed vs. MDE-predicted DDGs. Moreover, another important explanatory theory of EDG is the Intermediate Disturbance Hypothesis (IDH). It suggests that species richness is highest at mid-levels of disturbance as species of early and late successional phases can coexist (Connell 1978). Whereas disturbances along EDG are caused by enhanced human activities at lower elevation (Nogués-Bravo et al. 2008), disturbances along DDG are caused by waves, grazing and water level fluctuations at shallower depth. These disturbances act on two different depth patterns: 1) evenly distributed over depth like herbivory by fish or 2) gradually distributed (loosing strength with depth), which can be caused by anthropogenic use, herbivory by birds or mammals, wind, waves (Van Zuidam and Peeters 2015), mechanical disturbance by ice cover, or water level fluctuations (Evtimova and Donohue 2016). The latter was already integrated in our study in a very simple way of taking long term indicators. Further monitoring schemes should target other disturbances, quantifying herbivory, wave height, ice cover or finer resolved water level fluctuations. As herbivores are supposed to eliminate on average 40-48% of plant biomass in freshwaters (Bakker et al. 2016) their influence might be outstanding. The long-term water level fluctuation showed no strong effect on richness measures and it might not be the main explanation of the hump-shaped DDG. Nevertheless, although our findings tend to not support the intermediate productivity/disturbance hypotheses, considering that human (or natural) disturbances in shallow waters should be more prevalent in our data, the intermediate productivity/disturbance hypotheses could still play a role along DDG.

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, Tachingen See 2006, Woerthsee 2008, Eibsee 2016, Schliersee 2008; for gamma richness: Eibsee 2011 & 2016, Grosser Ostersee 2008, Tachingen See 2006 and Woerthsee 2008). For these lakes, which are mostly lakes with a high water transparency, it might be interesting to extend sampling to deeper water 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 hypothesis, 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 productivity, slope, soil properties (components, grain size distribution and nutrient content), ice cover duration 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.

Conclusion

Our study makes a first step towards a 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 (Fig. 4). Well-known hypotheses of biogeography that may 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 ($P_{(a,\mu a\xi)}$) and light quality, light quantity and layering depth influencing the species richness peak depth ($\Delta_{(a,\mu a\xi)}$). Although we found that the DDG in general remained stable over past few years for most lakes, we still found shifting trends for richness metrics for some lakes. However, these trends showed to be diverse across lakes. Whereas climate change might be more ubiquitous, land use change may be lake specific. This suggests that water management strategies should consider besides global warming, also 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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Data & Code

Original raw data were publicly available, provided by Bayerisches Landesamt für Umwelt, www.lfu.bayern.de

Code of data analysis are provided as Research Compendium on github: *link will be provided in final version; it is not added here because of the double-blind review process*

Supporting information

Supporting analysis as a separate (R markdown) file

Study overview table

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Tables

Table 1 Overview of the number of datapoints (N), minimum values (Min), maximum values (Max), mean, standard deviation (SD) and median 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.

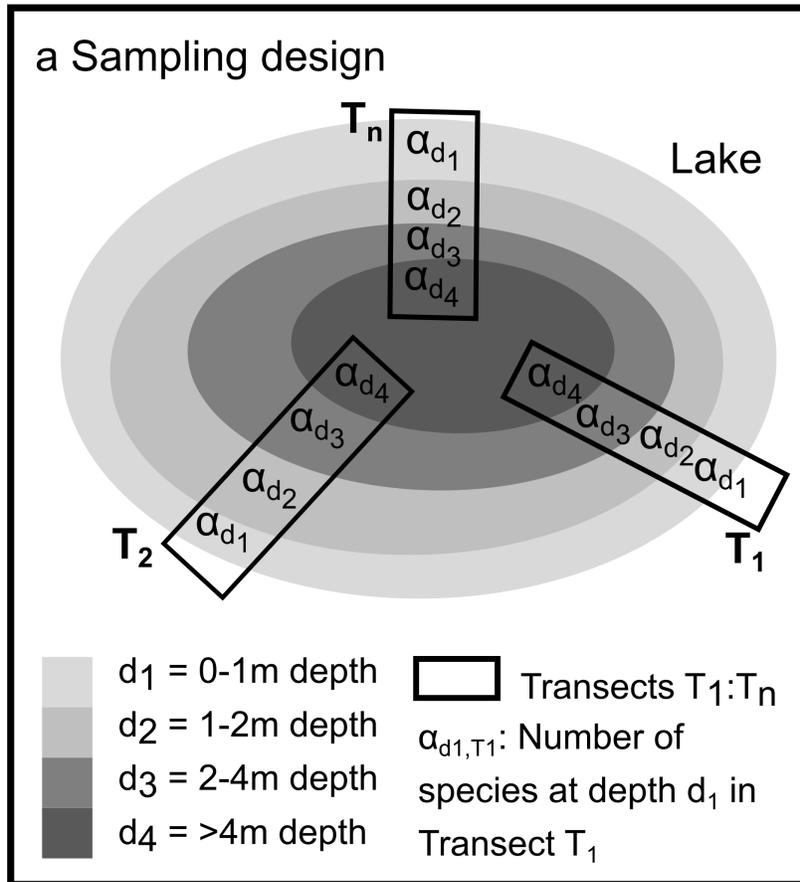
	Variable (unit)	Abbrev.	N	Min (annual mean)	Max (annual mean)	Mean (annual mean)	SD (annual mean)	Median (annual mean)
Geographic variables	Lake area (ha)	<i>Area</i>	12	135	7990.00	1840	2654	624.50
	Water level fluctua- tion (m)	<i>WLF</i>	12	0.2	1.18	0.58	0.28	0.59
Physical- chemical variables	Chloride (mg/l)	<i>Chl</i>	27	0.33	14.98	7.58	3.94	7.61
	Conductivity (μ S/cm)	<i>Cond</i>	27	158.55	372.44	292.57	61.96	309.20
	Total Nitro- gen (mg/l)	<i>N_{tot}</i>	27	0.19	1.22	0.66	0.22	0.65
	Ammonium (mg/l)	<i>NH₄N</i>	27	0.00	0.09	0.02	0.02	0.01
	Nitrogen (mg/l)	<i>NO₃N</i>	27	0.00	1.09	0.37	0.28	0.30
	Dissolved Oxygen (mg/l)	<i>O_{2diss}</i>	27	9.16	11.41	10.23	0.51	10.39
	Total Phos- phorus (mg/l)	<i>P_{tot}</i>	27	0.00	0.02	0.01	0.00	0.01
	pH (-)	<i>pH</i>	27	8.04	8.49	8.32	0.11	8.35
	Silicate (mg/l)	<i>SiO₂</i>	27	0.00	2.86	1.68	0.88	1.64
Water temper- ature (°C)	<i>Temp</i>	27	9.64	19.24	13.38	2.09	13.32	

Variable (unit)	Abbrev.	N	Min (annual mean)	Max (annual mean)	Mean (annual mean)	SD (annual mean)	Median (annual mean)
Transparency (cm^{-1})	<i>Transp</i>	27	242.50	1197.27	451.74	198.39	410.00
Spectral absorp- tion coeffi- cient at 254 nm (1/m)	<i>SAC</i>	27	0.00	24.83	8.85	7.84	5.35
Standard devia- tion of temper- ature mea- sured at 0 m, -2 m, -4 m and -6 m depth (°C)	<i>Tempsd</i>	27	0.23	2.24	0.91	0.58	0.62

Table 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	$\Delta_{(a,\mu a\xi)}$	$P_{(a,\mu a\xi)}$	$\Delta_{(\beta,\mu a\xi)}$	$P_{(\beta,\mu a\xi)}$	$\Delta_{(\gamma,\mu a\xi)}$	$P_{(\gamma,\mu a\xi)}$
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	-	-*	+	+	+	+	+

Lake	Gamma richness	$\Delta_{(a,\mu a\xi)}$	$P_{(a,\mu a\xi)}$	$\Delta_{(\beta,\mu a\xi)}$	$P_{(\beta,\mu a\xi)}$	$\Delta_{(\gamma,\mu a\xi)}$.	$P_{(\gamma,\mu a\xi)}$.
Sign (p<0.1) pos. slope (N lakes)	4	2	2	1	5	3	4
Sign (p<0.1) neg. slope (N lakes)	0	2	0	0	0	0	0



b Richness components

Alpha richness $\bar{\alpha}_{d_j} = \frac{\sum_{i=1}^n \alpha_{d_j, T_i}}{n}$

Gamma richness γ_{d_j} = total number of species across all $\alpha_{d_j, T_1:T_n}$ at depth d_j

Beta richness $\beta_{d_j} = \gamma_{d_j} - \bar{\alpha}_{d_j}$

