Biodiversity effects on the performance of terrestrial plant and phytoplankton communities

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General Introduction

"Biodiversity is the total sum of biotic variation from the level of genes over species and communities to ecosystems (Purvis & Hector 2000)".

Over the last decades a widespread and dramatic decline in biodiversity at both global and local scales has been detected (Loreau et al. 2001, Mouquet et al. 2002, Balvanera et al. 2006). In fact, for some taxonomic groups the estimated species extinction rates are between 10^3 and 10^4 extinctions per 10^6 species-years (Pimm et al. 1995). These high extinction rates are mainly attributed to the increased impact of human activities on natural and managed ecosystems, e.g., by land use changes, climate changes and nitrogen deposition (Sala et al. 2000). The predicted increase of the human population size will furthermore negatively affect biodiversity. For a better understanding of how this biodiversity decline affects ecosystem functions and processes, manipulative experiments relating biodiversity changes to changes in ecosystem processes are required.

The focus of this thesis is related to species diversity (also referred to as community diversity), including species richness (also referred to as species diversity), functional richness (also referred to as functional diversity) and the composition of communities consisting of primary producers. Primary producers are an important link in food chains since they provide the basis for higher trophic levels and contribute most to the total global biomass.

Historically, abiotic and biotic factors or processes that are driving species diversity have been of interest for ecologists. Therefore, diversity has been rather considered as a function of extrinsic factors (Figure 1, arrow 1).

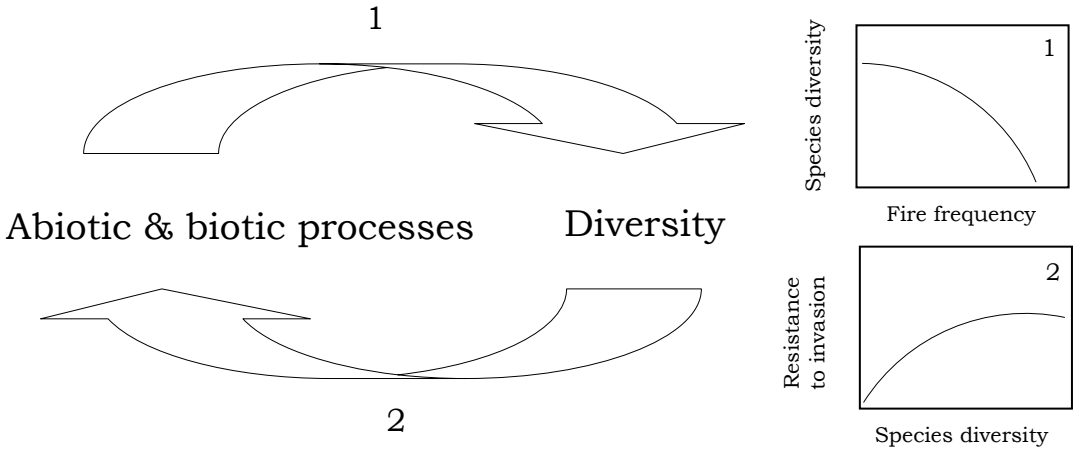

Figure 1: Scheme presenting the two causalities between abiotic and biotic processes and diversity. For example, (1) an increasing fire frequency decreases the diversity of native trees or shrubs and (2) due to the decreasing native diversity the resistance to invasion of grasses also decreases which can promote the fire frequency.

Over the past decades, however, consequences of species loss on abiotic or biotic ecosystem processes have received considerable attention (e.g., Naeem et al. 2002). This topic is embedded in the so-called "biodiversity-ecosystem functioning" context (Figure 1, arrow 2). Here, diversity is the explanatory variable for several community measures of ecosystem functions and processes, such as biomass (also referred to as biomass production), invasibility (e.g., Naeem et al. 2000, Fargione et al. 2003, Sperfeld et al. submitted) or temporal stability (e.g., Pfisterer et al. 2004). So far, these studies were mainly performed in terrestrial ecosystems, especially in grasslands, where positive relationships between diversity and community biomass have already been found (Naeem et al. 1996, Hector et al. 1999, Tilman et al. 2001, Hooper et al. 2005). This indicates that more diverse communities yield a higher total biomass than less diverse communities or monocultures. When a community builds up a higher biomass compared to its component monocultures it is called overyielding (Figure 2); it is an important parameter in the analysis of diversity experiments (Hector 1998, Loreau 1998, Hooper et al. 2005). There are two categories of overyielding: (i) transgressive overyielding, where the community biomass is higher than that of the most productive component monoculture and (ii) non-transgressive overyielding, where the community biomass is between the mean monoculture biomass and that of the most productive monoculture (Figure 2). Underyielding occurs when community biomass is lower than the expected one from its component monocultures (Figure 2).

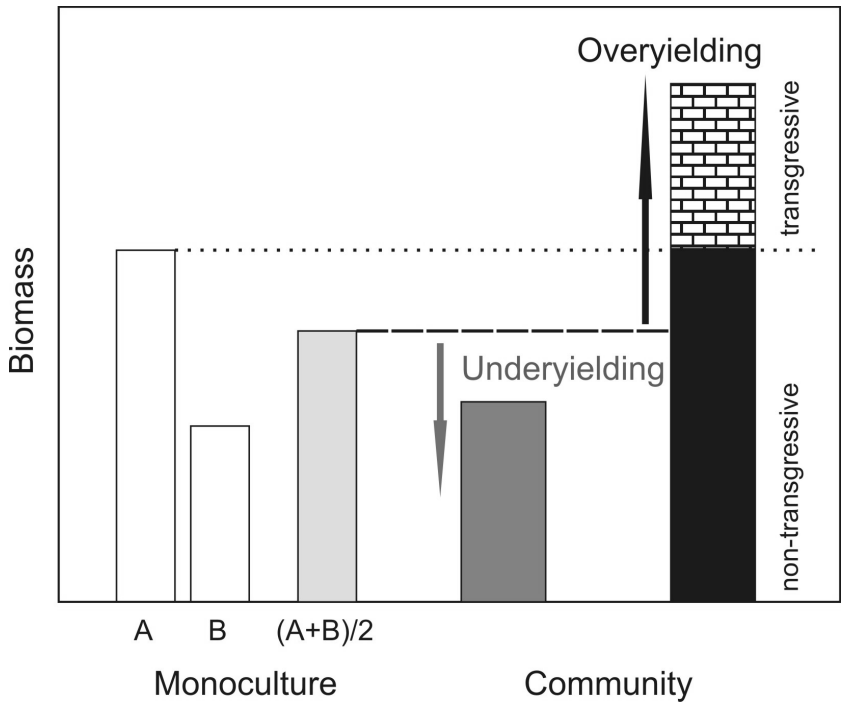

Figure 2: Scheme presenting community underyielding (dark grey) and overyielding, including non-transgressive (black) and transgressive (patterned) overyielding.

The current priority in the biodiversity-ecosystem functioning context is the classification of underlying mechanisms for community overyielding (Loreau et al. 2001). There is an ongoing debate whether the positive effect of species diversity on terrestrial plant biomass may result from a dominance effect or a complementarity effect, or a combination of both (Loreau and Hector 2001). The dominance effect (also referred to as selection or sampling effect) accounts for the higher likelihood of including high-productive species in more diverse communities, thereby leading to a higher community biomass. The complementarity effect indicates resource use partitioning or facilitative interactions among species. A higher resource use complementarity can lead to an enhanced total resource use in more diverse communities, which promotes their higher biomass compared to less diverse communities. Complementarity strongly depends on differences in the functional traits of species (Hooper and Vitousek 1997, Tilman et al. 1997, Hooper 1998, Mikola and Setälä 1998) and less on species diversity *per se* (Díaz and Cabido 2001, Giller et al. 2004); this suggests to consider also functional diversity in biodiversity experiments. Functional diversity comprises not only the number of functional groups but also the presence of particular functional groups that have strong effects on other species of the community (Hooper and Vitousek 1997, Tilman et al. 1997, Symstad et al. 1998, Spehn et al. 2005). Plant community biomasses can be enhanced by the presence of nitrogen-fixing species such as legumes (Spehn et al. 2005, Temperton et al. 2007) and cyanobacteria (Présing et al. 1996, Herrero et al. 2001).

Diversity effects on ecosystem functions such as community plant biomass have mainly been studied at the level of entire communities. However, community responses depend on the performance of the component plant species (Dimitrakopoulos and Schmid 2004, Scherber et al. 2006) since their responses to a changing diversity can be very different (Hector et al. 1999, Troumbis et al. 2000). Analyses of responses comprising all species in a diversity experiment are still missing; this can hamper the understanding of underlying mechanisms at the community-level. In this thesis (Chapter I), the effect of community diversity on individual plant performance of all component species was investigated in the comprehensive biodiversity project "The Jena Experiment" (www.the-jena-experiment.de, plate 1). Plant height, aboveground biomass, and inflorescences production of individuals were measured as performance parameters. The Jena Experiment consisted of 60 plant species common to Central European mesophilic grassland of the *Arrhenateretum* type belonging to four functional groups (grasses, small herbs, tall herbs, and legumes). The experiment involves four blocks with 82 large diversity plots which were established with varying species richness (1, 2, 4, 8, 16, 32, and 60 species), functional richness (1, 2, 3, and 4 functional groups) and community compositions (Roscher et al. 2005).

Plate 1: General experimental design of the Jena Experiment. (A) Aerial view of the total field site, © Forschergruppe Biodiversität, photograph taken by J. Baade, (B) a single 20 x 20m plot including 60 species (Block III, plot 14), © Andrea Schmidtke.

As mentioned above, the effect of diversity on community biomass has been studied mostly using terrestrial plants and only rarely with phytoplankton. This is surprising since aquatic microcosm studies offer a unique insight into the role of diversity that cannot be obtained from terrestrial experiments with their predominantly long-lived organisms (Giller et al. 2004, Gessner et al. 2004). For example, experimental duration times of a couple of weeks often provide population dynamics of phytoplankton equivalent to experiments with terrestrial plant communities running for several years. Indeed, the few studies with phytoplankton revealed positive (e.g., Zhang and Zhang 2006a, b, Weis et al. 2008) and to a lesser extent negative (e.g., Weis et al. 2007) diversity effects on community biomass caused by either the dominance or the complementarity effect, respectively. The underlying mechanisms for these different community responses to a changing diversity, which were also found for terrestrial ecosystems, are still unclear. This gives rise to the question which mechanisms promote the overyielding and underyielding of communities. In this thesis (Chapters II and III), the effect of species diversity and functional diversity on the biomass of phytoplankton communities was investigated using aquatic microcosms to reveal mechanistic basics for underyielding and overyielding. The phytoplankton communities consisted of either eight or twelve algal species belonging to four functional groups (green algae, diatoms, cyanobacteria, and phytoflagellates), and were grown at different levels of functional richness (1, 2, 3, and 4 functional groups) or species richness (1, 2, 4, 8, and 12 species). Underyielding and overyielding at the community and at the species level as well as the temporal dynamics of the individual species were analysed in these two studies.

Community biomass is one key measurement of an ecosystem function. However, invasive species are considered as the most important threat to diversity (Wilcove et al. 1998) and may alter the functioning of ecosystems with potentially large negative impacts (Mack et al. 2000). To date, experimental studies revealed negative (Kennedy et al. 2002, Fargione and Tilman 2005) or positive (Levine 2000, Naeem et al. 2000, Foster et al. 2002) diversity effects on the invasibility which indicates the susceptibility of a community to the invasion by new species. The invasibility of a community seems to be not only affected by diversity but also by a complex interplay of different factors. In this thesis the effect of species diversity (3, 4, and 6 species), productivity (nutrient concentration) and herbivory (presence or absence of a generalist grazer) on the invasibility of phytoplankton communities was studied using microcosms (Chapter IV). Two functionally diverse invaders were chosen: the filamentous and less-edible cynaobacterium *Cylindrospermopsis raciborskii* which is known to be a successful invasive species in temperate regions of Europe and which originates from tropical areas (Padisák 1997), and the unicellular and well-edible phytoflagellate *Cryptomonas* sp.

Outline of the study

This PhD-thesis consists of four chapters which can be read independently.

Chapter I: "Community diversity effect on individual plant performance" by Andrea Schmidtke, Tanja Rottstock, Ursula Gaedke and Markus Fischer; in revision, *Oecologia*.

This manuscript provides an experimental analysis of the joint influence of species diversity, functional diversity and community composition on individual plant height, aboveground biomass and the number of inflorescences per plant, including all 60 component species of the Jena Experiment.

Chapter II: "A mechanistic basis for underyielding in phytoplankton communities" by Andrea Schmidtke, Ursula Gaedke and Guntram Weithoff; accepted (27th April 2009), *Ecology*.

This manuscript presents results which reveal a negative diversity effect on the biomass of phytoplankton communities using microcosms, and examines which underlying mechanisms are responsible for this community underyielding.

Chapter III: "Overyielding and underyielding in phytoplankton communities" by Andrea Schmidtke, Guntram Weithoff, Markus Fischer and Ursula Gaedke; submitted, *OIKOS*.

This manuscript is based on the findings of Chapter II and aims to reveal underlying mechanisms for both, community underyielding and overyielding using microcosms with phytoplankton communities.

Chapter IV: "Productivity, herbivory and species' traits and identity rather than diversity influence the invasibility of phytoplankton communities" by Erik Sperfeld, Andrea Schmidtke, Ursula Gaedke and Guntram Weithoff; submitted, *Oecologia*.

This manuscript provides an experimental analysis of the joint effects of productivity, herbivory and diversity on the susceptibility of phytoplankton communities to invasion using microcosms.

Chapter I

Plant community diversity and composition affect on individual plant performance

by Andrea Schmidtke[1], Tanja Rottstock[2], Ursula Gaedke[1], and Markus Fischer[2,3]

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This chapter is in revision, Oecologia

1.1. Abstract

Effects of plant community diversity on ecosystem processes have recently received major attention. In contrast, effects of species richness and functional richness on individual plant performance, and their magnitude relative to effects of community composition have been largely neglected. Therefore, we examined height, aboveground biomass, and inflorescence production of individual plants of all species present in 82 large plots of the Jena Experiment, a large grassland biodiversity experiment in Germany. These plots differed in species richness (1-60), functional richness (1-4), and community composition. On average, in more species-rich communities plant individuals grew taller, but weighed less, were less likely to flower, and had fewer inflorescences. In plots containing legumes, individual legume and non-legume plants grew taller and weighed more than in plots without legumes. In plots containing grasses, individual grass and non-grass plants grew taller and had more inflorescences than in plots without grasses. Species richness and functional richness effects differed systematically between functional groups. The magnitude of the increase in plant height with increasing species richness was greatest in grasses and was progressively smaller in legumes, small herbs and tall herbs. Individual aboveground biomass responses to increasing species richness also differed among functional groups and were positive for legumes, less pronouncedly positive for grasses, negative for small herbs and more pronouncedly negative for tall herbs. Moreover, these effects of species richness differed strongly between species within these functional groups. We conclude that individual plant performance largely depends on the diversity of the surrounding community, and that the direction and magnitude of the effects of species richness and functional richness differs largely between species. Our study suggests that the so far neglected diversity of the surrounding community needs to be taken into account when interpreting drivers of the performance of individual plants.

1.2. Introduction

Over the last decade consequences of declining plant community diversity for ecosystem processes have received considerable attention. Among others, increasing plant community diversity was found to increase community biomass production (Naeem et al. 1996, Tilman et al. 1996, Hector et al. 1999, Roscher et al. 2005) to a similar extent as composition effects do due to the presence of particular functional groups such as grasses and legumes (Hooper and Vitousek 1997, Tilman et al. 1997, Symstad et al. 1998, Spehn et al. 2005). Community diversity effects on ecosystem processes such as biomass production can be attributed to the

sampling or complementarity effect or to a combination of the two (Loreau and Hector 2001). The sampling effect accounts for a higher likelihood of including highly productive species in more diverse communities and the complementarity effect may include facilitative interactions and resource use complementarity of species leading to an increased total resource use and thus, a higher biomass production in more diverse communities. Generally, complementarity is expected to be higher between species of different functional groups than between species of the same functional group, at least to the degree that functional groups differ in plant traits relevant for plant responses to diversity changes. Furthermore, plant community composition can also play an important role. Plant communities with legumes can benefit from their nitrogen fixation (Roscher et al. 2005, Spehn et al. 2005, Temperton et al. 2007) while grasses can negatively affect other species since they are superior competitors for nutrients due to their efficient resource uptake in upper soil layers (Fargione et al. 2003).

Community diversity effects on ecosystem processes have mainly been studied at the level of entire communities. Ultimately, however, community responses and that of single species depend on the performance of individuals (Dimitrakopoulos and Schmid 2004, Scherber et al. 2006). Even when community biomass production increases with increasing community diversity the responses of the component species may differ greatly (Hector et al. 1999, Troumbis et al. 2000). So far, studies on individual plant performance are restricted to several species in microcosm experiments (Dimitrakopoulos and Schmid 2004) or to single phytometer test species in large field experiments (Scherber et al. 2006, Mwangi et al. 2007, Thein et al. 2008). However, responses of resident species are likely to oppose the ones of additionally planted test species because more vigorous residents will more negatively affect additional plants and different responses of different plant species suggest that the study of only one or few test species may easily result in idiosyncratic conclusions. To date, analyses of individual plant responses comprising all species in a large biodiversity experiment are still missing which can hamper the mechanistic understanding of community diversity effects.

Plant responses at the community-level are composed of responses at the individual-level. The increasing plant community biomass with increasing diversity (Naeem et al. 1996, Tilman et al. 1996, Hector et al. 1999, Roscher et al. 2005) may be caused by a higher plant density or a higher average individual biomass which can be in turn caused by large positive responses of some species and small responses of others or vice versa. Strong competition for light generally leads to the dominance of tall species (Aerts 1999). Therefore, it might be expected that more diverse plant communities showing higher biomasses than less diverse communities consist of taller individual plants (Spehn et al. 2000). Plant reproductive responses to

increased community diversity may include an enhanced inflorescence production as a consequence of increasing individual plant height with increasing diversity. Contrary, inflorescence production can also decrease as a response to the higher competition in more diverse communities since resource allocation to competitive abilities such as vegetative growth can result in lower reproduction (Levins 1968).

Grassland communities are well suited for experimental studies investigating the effects of plant community diversity because they are agriculturally important, their diversity is declining, their small-scale neighbourhood relationships invoke strong species interactions and their diversity can easily be manipulated (Loreau et al. 2002). Our study forms part of a large-scale and long-term grassland diversity experiment, the Jena Experiment (described in detail by Roscher et al. 2004). The experimental communities of different diversities and compositions were established in 2002 and by the time of our investigation in 2005, several diversity effects on community performance had already been observed (Fischer et al. 2008). For example, with increasing species richness the community aboveground biomass increased largely due to complementarity effects (Roscher et al. 2005) and the leaf area index also increased with increasing species richness (Daßler et al. 2008, Alexandra Weigelt, personal communication). To extend the understanding of community diversity effects to the individual-level, we examined individual plant performance by measuring height, aboveground biomass, and flower production of plant individuals of all species present in 82 plots of different species richness, functional richness, and composition. We call this ASAP (all species in all plots) approach. We addressed three main questions: (i) How does individual plant performance change with increasing species richness and functional richness, and with the presence or absence of legumes and grasses? (ii) Do these changes differ between species belonging to different functional groups, and (iii) between different species within functional groups?

1.3. Methods

Experimental design

Our study was integrated into the Jena Experiment (www.the-jena-experiment.de) for which grassland communities were sown in spring 2002 on former arable land in Jena, Germany (Roscher et al. 2004). The species pool consists of 60 plant species common to Central European mesophilic grassland of the *Arrhenateretum* type. According to multivariate analyses of species traits 60 species were classified as 16 grasses, 12 small herbs, 20 tall herbs and 12 legumes (Roscher et al. 2004). All legumes were characterized by nitrogen fixation. To account for a gradient in soil characteristics perpendicular to the course of the adjacent River Saale the

experimental area was grouped into four blocks (Roscher et al. 2004). In these blocks 82 large plots of 20m x 20m area were established with different species richness (1, 2, 4, 8, 16 or 60 species per plot) and functional richness (1, 2, 3 or 4 functional groups per plot). For each plot species were randomly selected from species pool. The target plant community was successfully maintained by weeding twice per year. Plots were mowed twice per year (June and September) as it is typical for this type of managed grassland ecosystems. No fertilizer was applied during the experiment. For more details about the experimental design and community establishment in the Jena Experiment see Roscher et al. (2004, 2005).

Data collection

Between mid-March and mid-June 2005, 2630 individuals of all species were sampled in all 82 plots, i.e. shortly before the sites were completely mowed according to the site management of the Jena Experiment which is mimicking the one of managed grasslands in the region (Roscher et al. 2004). For each species we selected 6 plant individuals in each of the plots of lower species richness (1, 2, 4, 8 and 16 species) and 4 in each of the plots of higher species richness (16 and 60 species) by partitioning the sampling area into smaller quadrates. After the random selection of sampling quadrates, the individuals nearest to the tip of a pen randomly thrown into each sampling quadrate were sampled. Selected individuals were clipped 2 cm above ground to simulate the traditional grassland management. We were able to sample whole genets as individuals since at sampling time genets could still be recognised even when consisting of several ramets. Sampling was done block-wise and took about 1.5 weeks per block. As measures of individual plant performance simple morphological and reproductive parameters of each plant individual were recorded. (i) Its height indicated by the longest straight length of individuals from the cutting point, including stem, leaves and floral structures. (ii) The number of inflorescences per individual and (iii) whether an individual plant was in flower or not. Between the block-wise sampling campaigns these parameters were measured to avoid decay of individuals. Afterwards individuals were oven-dried for 48h at 70°C and weighed to the nearest mg to measure (iv) individual aboveground biomass.

Data analysis

For statistical analyses performance parameters were averaged per species and plot to avoid pseudo-replication of species within plots. Performance parameters were analysed with mixed-model analysis of variance (ANOVA) with sequential sums of squares (SS) Type 1. Type 3 SS were not possible due to the hierarchical design of the Jena Experiment where e.g., first fitting plot identity would make tests of species richness effects impossible. For the proportion of flowering the same model was used as a generalised linear model (GLM) with binomial error distribution. Both statistical

approaches were implemented in R (Version 2.3.1, 2006). Aboveground biomass was log-transformed to achieve normality and homogeneity of variances.

The statistical models contained tests between and within communities, and their interactions. Block, plot identity and species identity were fitted as random effects while functional identity and plot identity treatments were fixed. Each model consisted of the following sequence of factors: block (to account for spatial differences and for block-wise sampling), species richness (logarithm of the sown number of species), functional richness (number of functional groups), presence of legumes, presence of grasses, plot identity (which served as error term for the factors mentioned above), functional identity (FI, error term: FI x plot identity), species identity (SI, error term: SI x plot identity), FI x species richness (error term: SI x species richness), FI x functional richness (error term: SI x functional richness), FI x presence of legumes (error term: SI x presence of legumes), FI x presence of grasses (error term: SI x presence of grasses), SI x species richness, SI x functional richness, SI x presence of legumes, SI x presence of grasses, plot identity x FI, and plot identity x SI (which served as error term for interactions of mentioned factors with SI). Significance levels remained the same when effects of functional identity (FI) were tested with species identity (SI) as error term instead of the FI x plot identity interaction as error term. To address potential effects of using Type 1 SS we fitted species richness before functional richness and *vice versa*. In analogy, the interactions of species richness and functional richness with other factors were also fitted in the two different sequences. We mention the few cases of different outcomes of analyses with reversed order of species richness and functional richness in the text. The full model could not be fitted when analysing the likelihood to produce inflorescences because only 68% of the plants produced inflorescences. Therefore, for this variable we only analysed variation between but not within communities.

Realised species richness in the experiment was very close to sown species richness (linear regression: R^2=0.95) and analyses using realised species richness yielded the same results as the ones based on sown species richness. Therefore, we present only the latter in this article. In all mixtures, species were grown at maximum evenness (Roscher et al. 2005) and thus, uneven species abundances within plots are unlikely to play an important role for plant performance.

The presence or absence of a particular functional group may influence individual performance either because individuals of this functional group perform differently than the ones of others, or because the presence of this group changes the performance of the others. Therefore, in separate analyses we calculated the mean performance of individuals of species other

than legumes and the mean performance of individuals other than grasses in plots with legumes and grasses, respectively. We tested these effects of the presence+ (including performance parameter of legumes and grasses), presence- (excluding performance parameter of legumes and grasses although they occurred in the community) and absence of legumes and grasses on the individual parameters height, aboveground biomass, proportion of flowering and number of inflorescences with parametric t-test (SPSS, version 15).

1.4. Results

Effects of community diversity and composition on average individual plant performance

Plant species richness affected plant height, aboveground biomass and proportion of flowering (Table 1, line 2). In plots with higher species richness individual plants grew taller but weighed less (Fig. 1; Table 1, line 2 and 5; significant independently of the fitting sequence of species richness and functional richness) and in plots with higher functional richness plants grew taller (Fig. 1; Table 1, line 4; significant when fitted before species richness). Moreover, plants were less likely to flower in plots with higher species richness (Fig. 1; Table 1, line 2; significant when fitted before functional richness) and in plots with higher functional richness (Fig. 1; Table 1, line 4, significant when fitted before species richness).

In plots with grasses, individuals of all plant species (including grasses) grew taller (Fig. 2; $P<0.001$), tended to be more in flower (Fig. 2; $P=0.109$) and had more inflorescences (Fig. 2; $P<0.024$) than in plots without grasses. When only the performance of non-grasses was considered, this effect was only significant for the proportion of flowering (Fig. 2; $P=0.009$). Thus, fewer non-grass individuals were in flower in plots with grasses. Plant height (Fig. 2; $P<0.001$), proportion of flowering (Fig. 2; $P<0.001$) and number of inflorescences (Fig. 2; $P<0.001$) differed between grasses and non-grasses in plots with grasses. This reflects that grass individuals grew taller than plants of other functional groups, were more in flower and had more inflorescences (Table 2).

In plots with legumes, individuals of all plant species (including legumes) grew taller (Fig. 2; $P<0.001$) and weighed more (Fig. 2; $P<0.001$) than in plots without legumes. When only the performance of non-legumes was considered, these effects remained although they were less pronounced for aboveground biomass (Fig. 2; $P=0.043$). This indicates that the presence of legumes stimulated individual height and aboveground biomass of non-legumes. In plots containing legumes, individuals of all species (including legumes) weighed more than non-legumes (Fig. 2; $P=0.003$) which reflects

that legume individuals weighed more than plants of other functional groups (Table 2).

Species-specific effects of community diversity and composition on individual plant performance

Individual plant height, aboveground biomass and number of inflorescences per plant differed between functional groups (all P-values < 0.001, Table 1, line 9; Table 2). Moreover, effects of species and functional richness on individual plant performance differed between plants of different functional groups (Table 2).

The magnitude of the positive effect of species richness on individual plant height (Fig. 3) increased from tall herbs (slope of the regression line = 1.24, i.e. plant height increased by 1.24 cm for doubling of species richness) to small herbs (1.49) to legumes (3.23) to grasses (5.78). This functional identity x species richness interaction was highly significant when fitted before the functional identity x functional richness interaction (Table 1, line 11). The pattern of the effect of functional richness on individual height of species belonging to different functional groups (data not shown) was very similar to the one of the effect of species richness. The functional identity x functional richness interaction was significant independent of the sequence in which it was fitted in the statistical model (Table 1, line 12 and 13).

The magnitude of the effect of species richness on individual aboveground biomass (Fig. 3) increased from negative for tall herbs (slope = -0.31, i.e. individual aboveground biomass decreased by 0.31g for doubling of species richness) to slightly negative for small herbs (-0.05) to slightly positive for grasses (0.06) to positive for legumes (0.12). This functional identity x species richness interaction was significant independent of the fitting sequence (Table 1, line 11 and 14). Moreover, effects of functional richness on individual aboveground biomass differed significantly between functional groups when these were fitted before the functional identity x species richness (Table 1, line 13).

Responses to the presence or absence of legumes and grasses did not significantly differ between individuals of different functional groups (Table 1, line 15 and 16).

Individual plant height, aboveground biomass and number of inflorescences also differed between species belonging to the same functional group (all P-values < 0.001; Table 1, line 10; Appendix). Moreover, individual species within functional groups responded differently to increasing species richness (Fig. 4) and to functional richness (data not shown). Except for two interactions, all species identity x species richness (Table 1, line 17 and 20) and species identity x functional richness interactions (Table 1, line 18 and

19) were significant for plant height, aboveground biomass, and number inflorescences independent of the fitting sequence. The two exceptions were the species identity x functional richness interaction for height (significant only when fitted after species identity x functional richness interaction; Table 1, line 20) and species identity x functional richness interaction for aboveground biomass (significant only when fitted after species identity x species richness interaction; Table 1, line 18).

Individuals of species belonging to the same functional group showed a similar response in height and aboveground biomass to diversity, both in terms of species and functional richness, except for one case of grasses. While almost all grasses showed a negative relationship between individual aboveground biomass and species richness (Fig. 4), the opposite pattern was found for the effect of functional richness on aboveground biomass of the grasses (data not shown).

Due to the experimental design of the Jena Experiment not all species occurred at all levels of species richness and functional richness. The following examples illustrate responses of two species which were present at least at four species richness levels. Within grasses, the strongest positive effect of species richness on individual height was observed for individuals of the potentially dominant grass *Arrhenatherum elatius*. While the aboveground biomass of *A. elatius* and that of two other grasses increased with increasing species richness, the one of the other grass individuals decreased. Responses of individual plant aboveground biomass were very variable among legume species and ranged from strong decrease over indifference to a strong increase of the species with the heaviest and tallest individuals, *Onobrychis viciifolia*.

1.5. Discussion

Effects of community diversity and composition on average individual plant performance

Due to potentially higher complementarity among species in more diverse communities, a greater individual aboveground biomass could have been expected when species are growing at higher functional richness (e.g., Fargione et al. 2003). In contrast, our results showed that average individual plant aboveground biomass was not strongly affected by functional richness and even decreased with increasing species richness. This suggests that the higher community biomass at higher species richness in the Jena Experiment (Roscher et al. 2005) was either due to an increase in plant density in more species-rich plots or due to the occurrence of species whose response opposes the average trend of decreasing individual aboveground biomass with increasing species richness in our

study. Lower individual aboveground biomass in plots of higher community diversity had not been found for resident individuals earlier but was reported for experimental invaders and explained by increased competition (Scherber et al. 2006, Mwangi et al. 2007). Our finding of decreased individual aboveground biomass with increasing species richness coincides with decreased soil nitrate concentrations in more species-rich communities of the Jena Experiment (Oelmann et al. 2007) and other biodiversity experiments (Hooper and Vitousek 1998, Symstad et al. 1998, Scherer-Lorenzen et al. 2003). At first glance, this suggests resource depletion of more species-rich communities as explanation for reduced individual aboveground biomass. However, reduced soil nitrate concentrations in more diverse communities rather indicate more efficient resource use of more diverse communities than resource depletion. This corresponds with the finding that the strength of the diversity effect on community biomass does not diminish over time in the Jena Experiment (Roscher et al. 2005) and other biodiversity experiments (Pfisterer et al. 2004) which would be expected when resources would be depleted. Moreover, increased nitrogen pool of plant aboveground biomass in more species-rich communities in the Jena Experiment (Oelmann et al. 2007) does not at all indicate a lack of nitrogen as underlying mechanisms of reduced individual aboveground biomass.

Moreover, we found a positive relationship between individual plant height and species richness. Such greater average plant height in more diverse communities had been reported for the community-level by Spehn et al. (2000). At the time of our sampling, the community leaf area index was positively affected by species richness (when fitted before functional richness, $F=32.40$, $P<0.001$) and functional richness (when fitted before species richness; $F=20.07$, $P<0.001$) in the Jena Experiment (Alexandra Weigelt, University of Jena, personal communication) supporting stronger light competition in more diverse communities. Therefore, the observed greater individual plant height suggests an allometric response of plants to this increased competition for light (Weiner 1990). At the same time, the proportion of flowering decreased with increasing species richness. This may result from a trade-off between resource allocation to vegetative height growth and to reproduction (Levins 1968). Counting seeds and monitoring seedling establishment were beyond the scope of our study but it remains to be seen whether reduced flowering in more species-rich communities is related to reduced seed production and seedling establishment. In the Jena Experiment, rates of flower visitation by insects increased with species richness (Ebeling et al. 2008) which may compensate for the reduced number of inflorescences per plant reported here.

Plant performance can be positively affected by the presence of legumes due to their nitrogen fixation. At the community-level this has been reported for

several biodiversity experiments (Roscher et al. 2005, Spehn et al. 2005, Temperton et al. 2007). On the other hand, the presence of grasses can negatively affect other species because they are superior competitors for nutrients (Fargione et al. 2003). Such effects of the presence and absence of legumes and grasses were also apparent in experimental plant communities with different arrival times of different functional types (Körner et al. 2007), underlining their generality. In plots with legumes, individual non-legumes of our study weighed on average 1.5 times more than in plots without legumes. Thus, the presence of legumes stimulated individual aboveground biomasses of other plant individuals. Similarly, Mwangi et al. (2007) who planted individuals of four species as test invaders into the Jena Experiment, and Scherber et al. (2006) who planted Rumex acetosa, found positive effects of legume presence for all test species. Our study extends these findings to all species resident in the experiment and adds the conclusion that legume presence increases individual aboveground biomass of all species contained in the community first because legumes themselves weigh more than non-legumes and second because non-legumes weigh more when legumes are present in the community.

In plots with grasses which are on average taller than other functional groups all individuals grew on average 1.3 times taller than in plots without grasses. However, this effect disappeared when only the individual height of non-grasses was compared between plots with and without grasses. This indicates that the presence of grasses did not affect the height of other species. In contrast, grass presence reduced the proportion of flowering of non-grasses which may be caused by their efficient resource uptake which depletes resources for the other plant species (Fargione et al. 2003). In the above-mentioned phytometer studies adding test invaders to our communities, resident grasses showed a strong negative effect on aboveground biomass of all test invaders (Scherber et al. 2006, Mwangi et al. 2007). This contrasts with the neutral effect of grasses on aboveground biomass of resident species detected in our study and potentially shows constraints of phytometer approaches for drawing conclusions on resident species. Our findings illustrate that it is important to separate contributions of the sheer presence of legumes or grasses to average performance from contributions of their effects on individuals of other plants.

Differential community diversity responses of individuals belonging to different functional groups

We found differences in plant height, aboveground biomass and number of inflorescences between grasses, legumes, tall and small herbs which supported the a priori classification of species -based on multivariate analyses of their characteristics- into these functional groups in the Jena Experiment (Roscher et al. 2004). Moreover, the species richness and functional richness responses of individual plant height and aboveground

biomass differed significantly between plants of different functional groups. In contrast, responses to the presence or absence of grasses and legumes did not differ between individuals of different functional groups. This indicates that it is easier to predict plant performance responses to changes in plant composition than to changes in species richness and functional richness.

Grasses and legumes, the two functional groups with the tallest plants, showed the strongest increase of average plant height with increasing species richness, whereas individuals of small and tall herbs showed a less pronounced increase of average plant height with increasing species richness. This corresponds well with the idea that plastic responses to shading of smaller plants growing constantly under canopy shade are less pronounced than that of larger plants growing under sunny conditions (McLaren and Smith 1978), and with the idea that larger and smaller plants have different mechanisms to capture or use light (Werger et al. 2002, Anten 2005).

The response of individual aboveground biomass to increasing plant community diversity was so far not addressed for resident species but for phytometer species planted into established communities as test invaders. Plant aboveground biomass of four phytometers declined from monocultures to 16-species mixtures and this effect was stronger for small and tall herbs than for grasses and legumes (Mwangi et al. 2007). In our study, individual aboveground biomass of tall herbs decreased pronouncedly with increasing species richness whereas the weak increase of the aboveground biomass of legumes and grasses opposed this pattern. Thus, aboveground biomass response of tall herbs can be responsible for the average decrease of individual aboveground biomass with increasing species richness across all species whereas grasses and legumes may play a key role for the positive relationship between species richness and community aboveground biomass in the Jena Experiment.

Differential community diversity responses of individuals belonging to different species of the same functional group

In our study, species richness responses of individual plant height, aboveground biomass and number of inflorescences differed significantly between species of the same functional group. Moreover, species of the same functional group also responded differently in plant aboveground biomass and number of inflorescences to functional richness. A priori classifications of species into functional groups are very common and are often correlated to above- and belowground morphological traits, phenological traits, and physiological traits. However, classifications into functional groups can be very coarse (Lavorel et al. 1997) and therefore,

species of the same functional group can still differ markedly in characteristics relevant for resource uptake and plant performance.

In our study, responses to the presence or absence of grasses and legumes did not differ between species of the same functional group. Thus, species richness and functional richness, but not species composition, were the important factors causing species-specific responses within functional groups. Our results on individual plant performance generalise previous findings of species-specific contributions to community biomass in large field experiments (Hector et al. 1999, Lorentzen et al. 2008) and of species-specific responses in pot experiments (Dimitrakopoulos and Schmid 2004) and phytometer studies (Mwangi et al. 2007). We found that the potentially dominant grass *Arrhenaterum elatius* was strongly positively affected by species richness. In the Jena Experiment, *A. elatius* showed the greatest relative increase in aboveground biomass of all species in mixtures (Roscher et al. 2005) and it overtopped neighbours in mixtures (Lorentzen et al. 2008) of the so-called dominance experiment, a smaller experiment within the Jena Experiment involving only nine dominant species in the regional grassland of the *Arrhenateretum* type (Roscher et al. 2004). Thus, A. elatius appears to be competitively superior to other species. The relatively tall legume *Onobrychis viciifolia* was also remarkable in our study. Due to its tallness, its position in the competition for light was expected to be better in more diverse communities with various species of different heights than in less diverse communities with more tall conspecificss. *O. viciifolia* showed a strong positive effect of aboveground biomass to species richness possibly caused by such reduced light competition in more diverse communities in combination with its indifference to lower soil nitrogen levels in more diverse communities. Since *O. viciifolia* was the only species reaching aboveground biomasses above 20g per individual its contribution to community aboveground biomass was very high and its positive response contrasting most other species may have largely contributed to the positive effect of species richness on community biomass in the Jena Experiment (Roscher et al. 2005). These results support earlier community-based conclusions of Troumbis et al. (2000) that relationships between community diversity and biomass production in grasslands are strongly influenced by species-specific performances in mixtures.

Conclusions

So far, the effect of community diversity on individual plant performance has received little attention. However, our experimental study clearly showed strong effects of diversity, both in terms of species richness and functional richness, and of species composition, on individual plant height, aboveground biomass, likelihood to flower and the number of inflorescences. Such effects, and their deviation from community means, contribute to a more mechanistic understanding of how increased

community diversity affects ecosystem processes. Moreover, we found that individuals of species belonging to the same or to different functional groups responded differently to species richness and functional richness. In the context of our biodiversity experiment these differential responses of individual plants suggest that community composition will change over time in favour of taller grasses and taller legumes in combination with some smaller but shade-tolerant herbs. This exemplifies that assessing individual plant performance, including the traits examined in this study as well as further morphological, physiological and fitness traits, is highly important to elucidate mechanisms underlying community dynamics. In more general terms, our study indicates that drivers of the performance of individual plants can be better understood when the diversity of the corresponding community is taken into account.

1.6. Acknowledgement

We thank the management team, the gardeners of the Jena Experiment, Lena Blischke, Konstanze Gebauer and Christoph Scherber for help in the field and with measuring plants and Alexandra Weigelt for providing LAI information. Christiane Roscher and Bernhard Schmid provided very helpful comments on an earlier draft. Andrea Schmidtke conducted this work as part of her PhD thesis in a project funded by the Deutsche Forschungsgemeinschaft DFG (grant FI1246/1-2) as part of the DFG Research Unit 456 Jena Experiment. The experiments conducted comply with current German laws.

1.7. Tables

TABLE 1: Summary of the statistical analyses (sequential ANOVA, Type 1 SS) related to the relationships between individual plant performance parameters (height, aboveground biomass, proportion of flowering and number of inflorescences) and main experimental factors. To assess potential effects of the fitting order, species richness was fitted before functional richness and *vice versa* (see Methods) and results of both fitting sequences were given in the text. Main factors in italics indicate the second fitting sequence. The random factors were block, plot identity and species identity. Columns show degrees of freedom (d.f.) and *F*- and P-values for each performance parameter. Bold P-values indicate significant effects of the factor on the performance parameter.

Source of variation	Height			Log(aboveground biomass)			Proportion of flowering			No. inflorescences		
	d.f.	*F*-value	P-value	d.f.	*F*-value	P-value	d.f.	*F*-value	P-value	d.f.	*F*-value	P-value
(1) Block	3	4.39	**0.007**	3	0.53	0.660	3	3.94	**0.012**	3	1.14	0.340
(2) Species richness (log-linear)	1	14.05	**< 0.001**	1	7.54	**0.008**	1	6.57	**0.012**	1	0.12	0.733
(3) Functional richness (linear)	1	1.24	0.269	1	3.38	0.070	1	0.43	0.515	1	0.03	0.869
**********												
(4) Functional richness (linear)	1	11.15	**0.001**	1	0.25	0.0620	1	4.86	**0.030**	1	0.01	0.919
(5) Species richness (log-linear)	1	4.14	**0.045**	1	10.67	**0.002**	1	2.14	0.148	1	0.14	0.715
**********												
(6) Presence of legumes	1	11.06	**0.001**	1	29.99	**< 0.001**	1	1.71	0.195	1	1.32	0.254
(7) Presence of grasses	1	23.42	**< 0.001**	1	2.38	0.127	1	9.99	**0.002**	1	5.75	**0.019**
(8) Plot identity	75	11.35	**< 0.001**	74	6.25	**< 0.001**	75			70	6.46	**< 0.001**
(9) Functional identity (FI)	3	448.40	**< 0.001**	3	69.08	**< 0.001**				3	95.15	**< 0.001**
(10) Species identity (SI)	55	38.50	**< 0.001**	55	30.64	**< 0.001**				48	30.42	**< 0.001**
(11) FI x species richness (log linear)	3	7.00	**< 0.001**	3	6.09	**0.001**				3	1.39	0.261
(12) FI x functional richness (linear)	3	4.17	**0.010**	3	1.57	0.208				3	0.30	0.827
**********												
(13) FI x functional richness (linear)	3	11.26	**< 0.001**	3	3.88	**0.014**				3	1.08	0.370
(14) FI x species richness (log linear)	3	2.08	0.114	3	3.98	**0.013**				3	0.21	0.891
**********												
(15) FI x presence of legumes	2	0.28	0.756	2	1.01	0.373				2	0.43	0.658
(16) FI x presence of grasses	2	2.75	0.080	2	0.97	0.394				2	2.40	0.125
(17) SI x species richness (log-linear)	53	2.18	**< 0.001**	53	1.98	**0.002**				40	1.63	**0.033**
(18) SI x functional richness (linear)	53	1.22	0.173	51	1.77	**0.009**				39	4.01	**< 0.001**
**********												
(19) SI x functional richness (linear)	54	1.45	**0.040**	54	1.65	0.011				42	2.63	**< 0.001**
(20) SI x species richness (log linear)	52	1.96	**0.001**	50	2.12	**< 0.001**				37	3.00	**< 0.001**
**********												
(21) SI x presence of legumes	39	1.17	0.247	37	1.39	0.090				26	1.06	0.411
(22) SI x presence of grasses	29	1.09	0.350	26	1.53	0.063				15	0.57	0.892
(23) Plot identity x FI	65	1.46	**0.028**	54	1.31	0.110				39	1.10	0.358
(24) Plot identity x SI (Residuals)	170			133						81		

TABLE 2: Mean height, aboveground biomass, proportion of flowering, and number of inflorescences of plants of different functional groups averaged over all plots (± standard error). Responses of individual performance parameter to increased species richness (log_2-scale) and functional richness are indicated as slopes of linear regression.

	Grasses	Small herbs	Tall herbs	Legumes
Height (cm)	63.92 ± 2.23	22.64 ± 0.09	36.01 ± 1.52	47.60 ± 2.10
Species richness	5.78	1.49	1.24	3.23
Functional richness	8.14	1.24	2.85	3.33
Aboveground biomass (g)	3.04 ± 2.31	0.79 ± 0.10	1.16 ± 0.15	6.94 ± 1.30
Species richness	0.06	-0.06	-0.31	0.12
Functional richness	0.84	-0.04	-0.28	0.42
Proportion of flowering	0.89 ± 0.02	0.48 ± 0.03	0.33 ± 0.03	0.45 ± 0.04
Species richness	0.00	-0.03	-0.03	-0.03
Functional richness	0.00	-0.06	-0.02	0.01
Number of inflorescences	8.28 ± 0.42	4.05 ± 0.50	5.46 ± 0.57	3.74 ± 0.38
Species richness	0.07	0.10	-0.32	-0.24
Functional richness	0.13	0.25	-0.45	0.14

1.8. Figures

FIGURE 1: The effect of sown species richness (log_2 scale, left) and functional richness (right) on the average individual plant performances. Solid regression lines represent significant relationships, dotted lines non-significant ones. P-values in the panels are from ANOVA models.

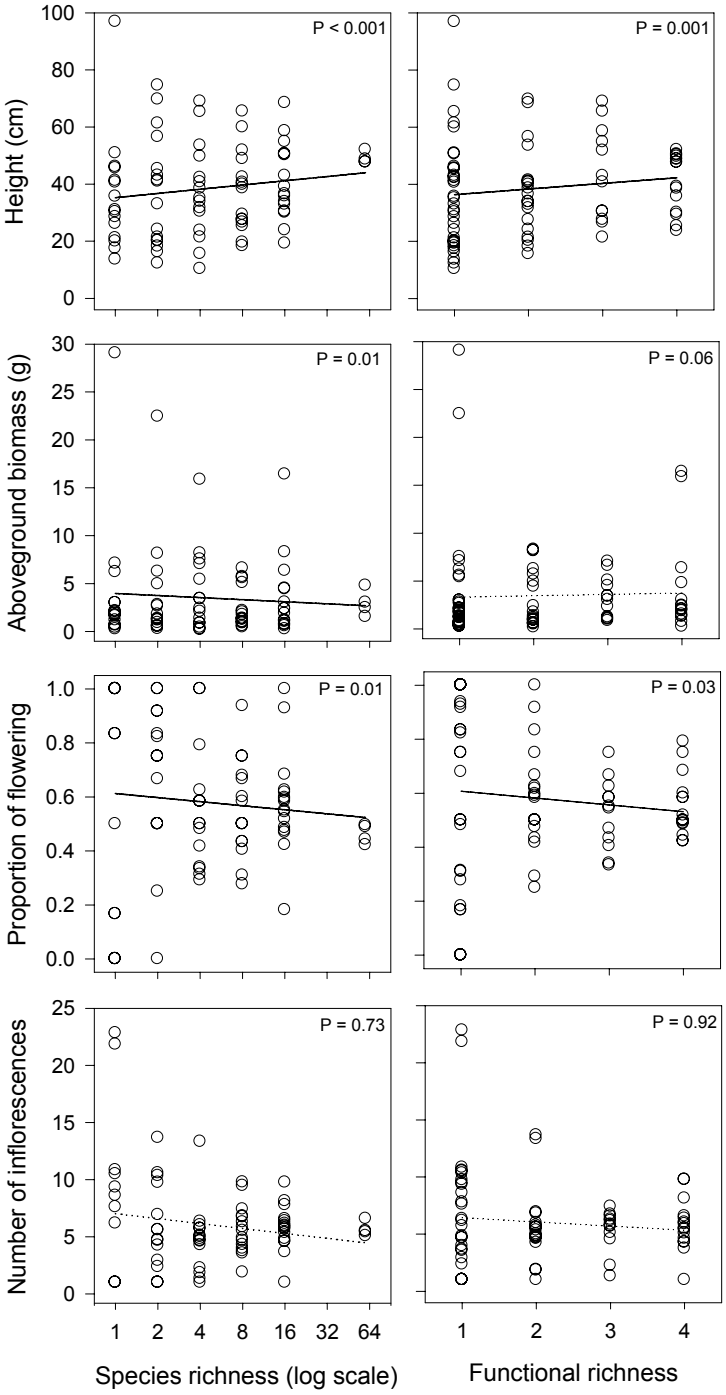


FIGURE 2: Effects of the presence+ (Pre+, including the performance parameter of legumes and grasses), presence- (Pre-, excluding the performance parameter of legumes and grasses although they occurred in the community) and absence (Abs) of grasses (left) and legumes (right) on height, aboveground biomass, proportion of flowering, and number of inflorescences per plant. Columns show mean performance parameters and error bars indicate standard errors (SE). Letters a, b, and c indicate significant differences among treatments ($P < 0.05$).

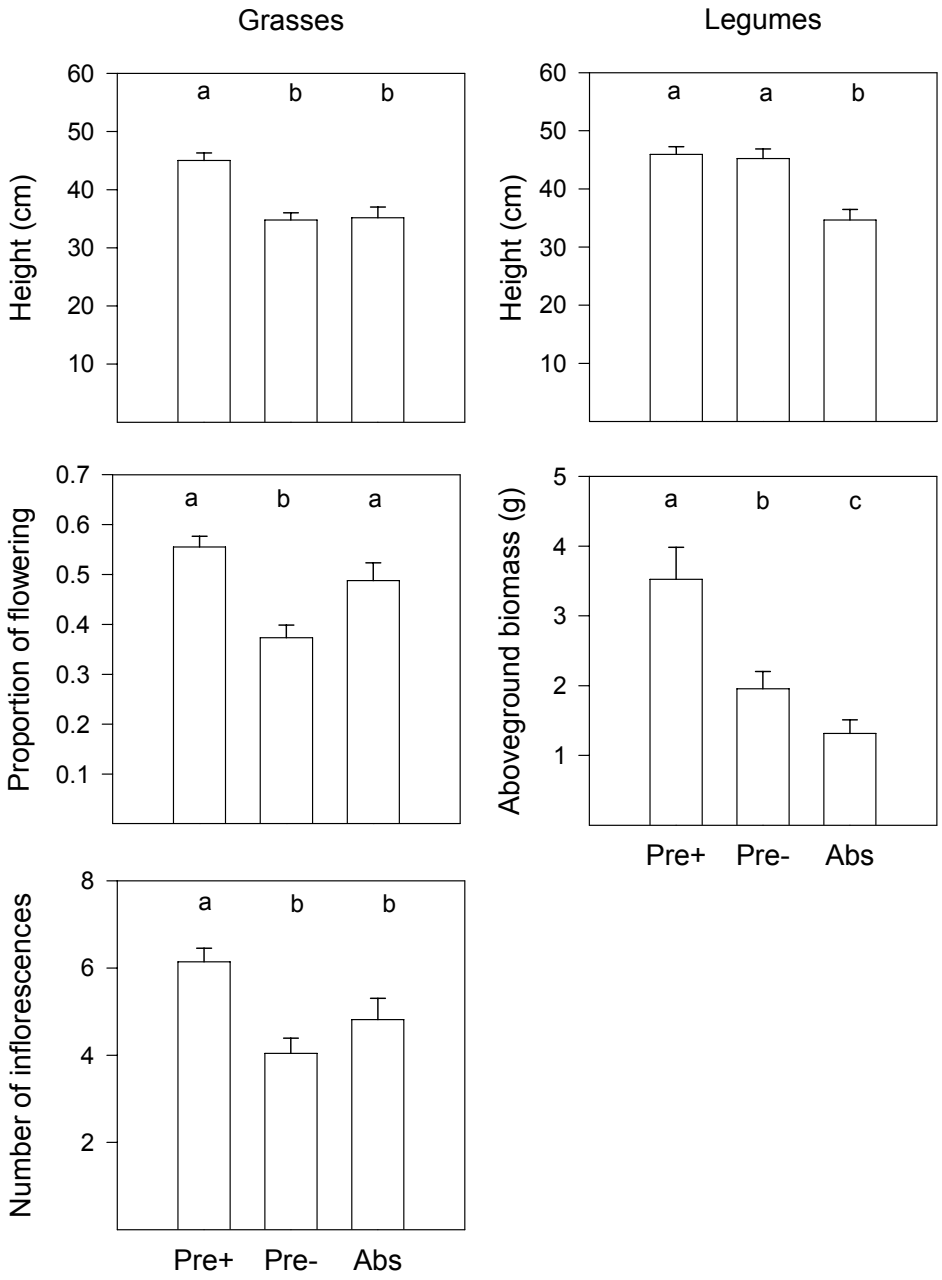


FIGURE 3: The effect of sown species richness (log_2 scale) on height and aboveground biomass for the different functional groups. The single functional groups are represented by different types of fitted regression lines: dotted=grasses, dash=small herbs, dash-dot-dot= tall herbs, solid=legumes.

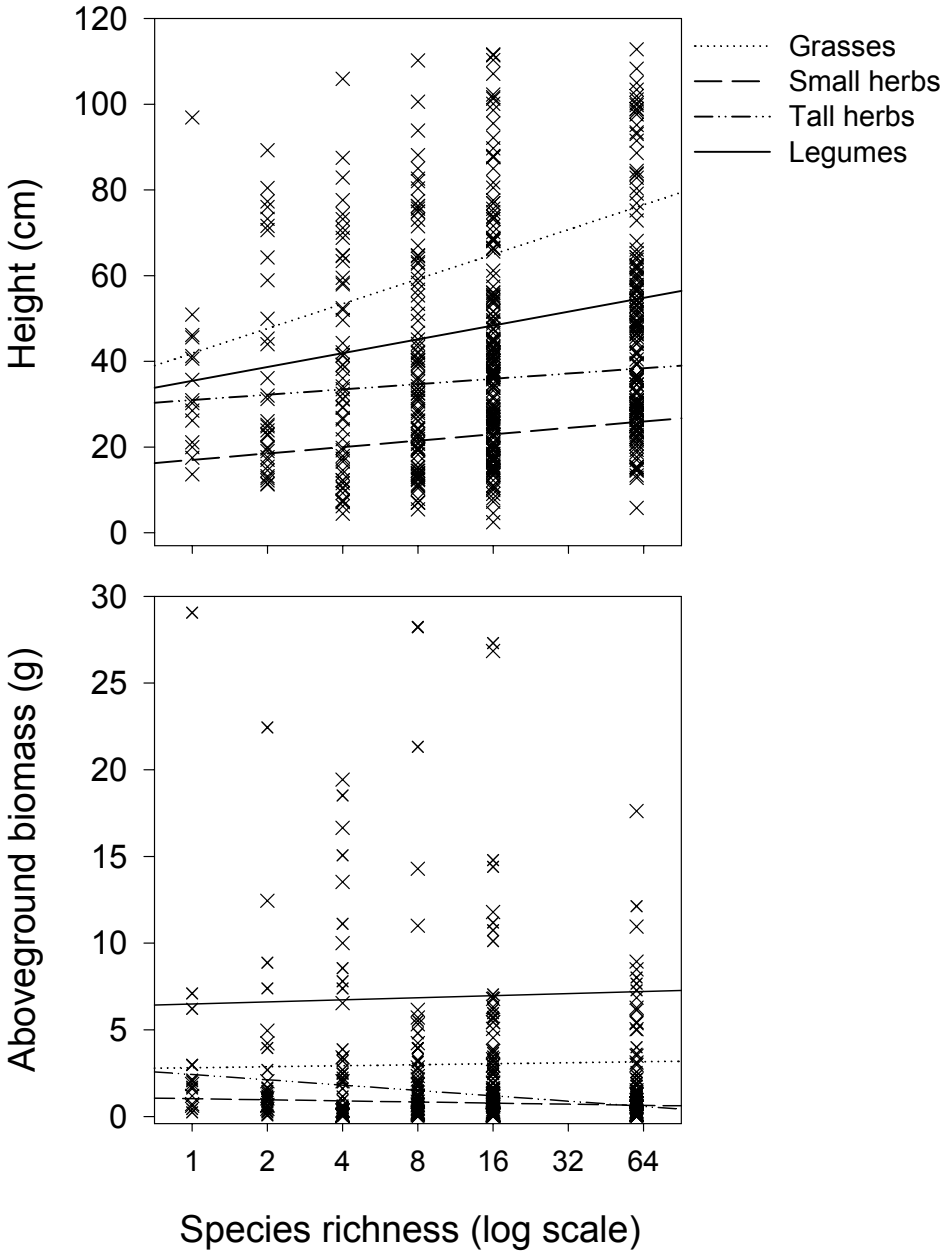
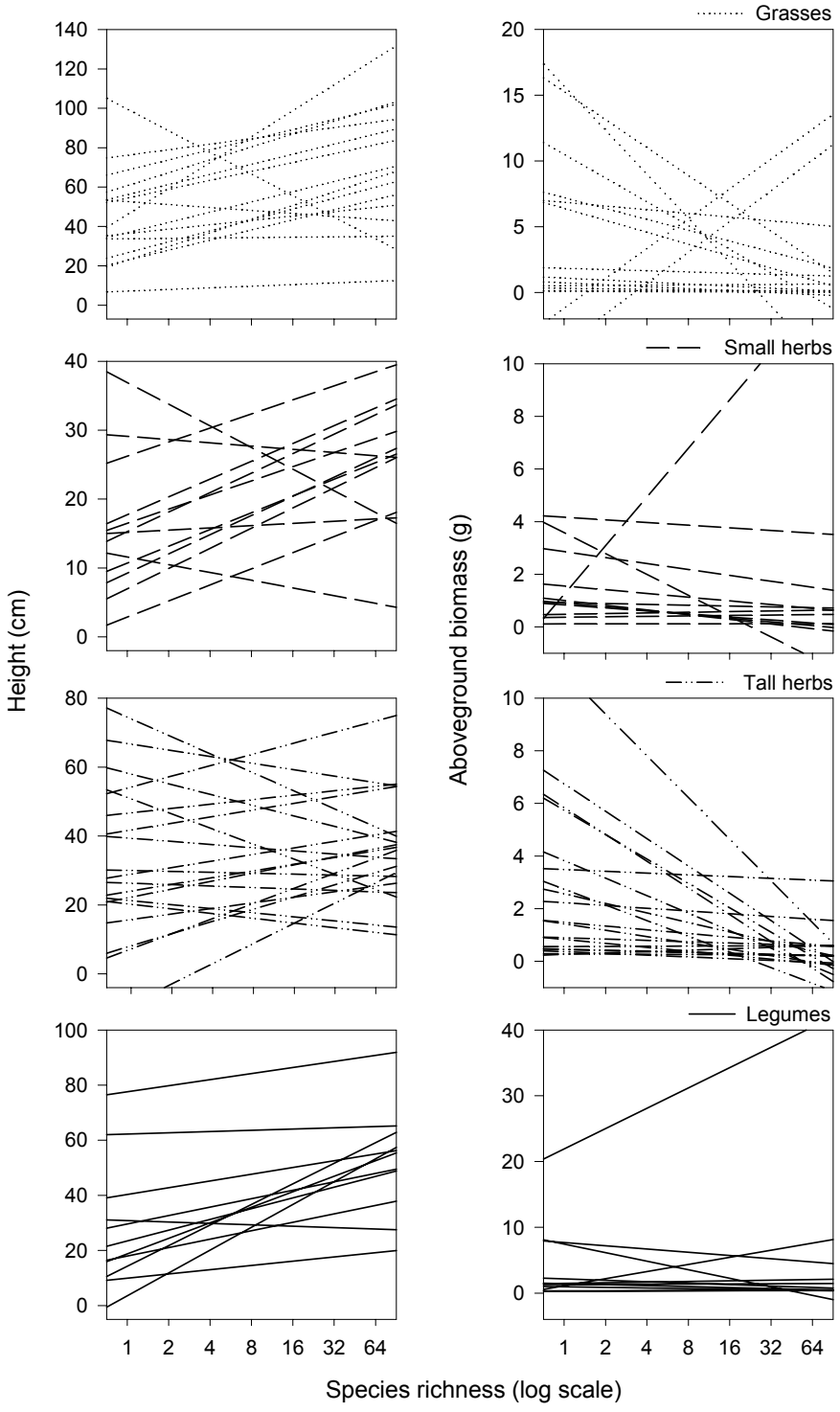


FIGURE 4: The effect of sown species richness (log_2 scale) on height and aboveground biomass for the single species belonging to grasses, small herbs, tall herbs, and legumes. Species are represented by different types of fitted regression lines: dotted=grasses, dash=small herbs, dash-dot-dot= tall herbs, solid=legumes.



1.9. Appendix

TABLE 1: Mean performance parameters of grasses averaged over all plots (± standard error) and effects of species richness (log_2-scale) and functional richness on the performance parameter as indicated by slopes of linear regression.

Species	Height (cm)	Above-ground biomass (g)	Proportion of flowering	No. inflores-cences
Alopecurus pratensis	85.58 ± 2.55	1.42 ± 0.23	0.95 ± 0.03	0.95 ± 0.03
Species richness	6.45	-0.05	0.06	0.06
Functional richness	8.89	0.25	0.02	0.02
Anthoxanthum odoratum	47.57 ± 1.63	0.18 ± 0.02	1.00	8.15 ± 0.27
Species richness	-1.44	-0.04	-6.50×10^{-20}	-0.08
Functional richness	4.23	0.03	-1.44×10^{-19}	-0.25
Arrhenatherum elatius	102.42 ± 3.42	6.12 ± 0.92	1.00	9.90 ± 0.29
Species richness	13.13	2.21	-5.01×10^{-18}	0.57
Functional richness	13.08	2.18	1.14×10^{-19}	0.04
Avenula pubescens	89.51 ± 3.02	2.65 ± 1.06	1.00	11.75 ± 1.61
Species richness	5.37	-0.71	9.21×10^{-18}	-0.38
Functional richness	7.15	0.98	-4.36×10^{-17}	4.40
Bromus erectus	67.14 ± 3.76	5.20 ± 1.40	0.78 ± 0.06	4.20 ± 0.43
Species richness	-9.30	-3.20	-0.27	-1.68
Functional richness	1.84	-3.90	-0.06	-0.70
Bromus hordeaceus	34.24 ± 1.79	0.08 ± 0.02	1.00	3.86 ± 0.26
Species richness	NA	NA	NA	NA
Functional richness	1.70	0.02	-4.38×10^{-17}	0.31
Cynosurus cristatus	44.57 ± 2.37	0.57 ± 0.11	1.00	21.42 ± 1.34
Species richness	5.51	-0.16	-4.49×10^{-17}	-0.38
Functional richness	5.77	0.01	-3.13×10^{-17}	1.81
Dactylis glomerata	78.00 ± 3.22	8.32 ± 1.95	0.94 ± 0.04	8.16 ± 0.46
Species richness	4.64	2.17	-0.03	0.18
Functional richness	8.13	3.11	-0.04	0.10
Festuca pratensis	66.84 ± 2.44	4.16 ± 0.90	0.98 ± 0.02	11.40 ± 0.31
Species richness	4.50	-0.87	0.00	-0.26
Functional richness	4.88	1.88	0.01	0.11
Festuca rubra	43.88 ± 1.86	0.58 ± 0.06	0.73 ± 0.06	6.27 ± 0.55
Species richness	2.08	0.01	-0.04	-0.44
Functional richness	2.78	0.00	-0.09	-0.97

Holcus lanatus	45.07 ± 3.39	3.20 ± 1.17	0.67 ± 0.08	6.67 ± 0.82
Species richness	4.53	-2.02	-0.05	-0.15
Functional richness	11.86	2.21	0.04	0.55
Luzula campestris	9.12 ± 1.34	0.05 ± 0.01	0.27 ± 0.12	0.60 ± 0.27
Species richness	0.82	-0.01	-0.17	-0.38
Functional richness	3.01	-0.03	0.17	0.44
Phleum pratense	56.07 ± 2.19	4.16 ± 0.75	0.69 ± 0.06	0.69 ± 0.06
Species richness	4.13	-1.17	0.18	0.18
Functional richness	10.78	0.89	0.06	0.06
Poa pratensis	35.37 ± 2.26	0.36 ± 0.06	0.89 ± 0.05	6.46 ± 0.48
Species richness	4.13	-1.17	0.18	0.18
Functional richness	10.78	0.89	0.06	0.06
Poa trivialis	49.82 ± 2.91	0.14 ± 0.02	1.00	7.49 ± 0.15
Species richness	6.44	0.00	1.87×10^{-19}	0.02
Functional richness	7.82	0.03	-1.57×10^{-18}	-0.08
Trisetum flavescens	85.34 ± 2.72	5.88 ± 0.85	1.00	10.78 ± 0.21
Species richness	2.25	-0.27	-1.01×10^{-18}	0.06
Functional richness	1.79	0.47	1.34×10^{-18}	-0.17

TABLE 2: Mean performance parameters of small herbs averaged over all plots (± standard error) and effects of species richness (log_2-scale) and functional richness on the performance parameter as indicated by slopes of linear regression.

Species	Height (cm)	Above-ground biomass (g)	Proportion of flowering	No. inflores-cences
Ajuga reptans	11.73 ± 1.02	0.43 ± 0.04	0.92 ± 0.05	6.44 ± 0.63
Species richness	2.71	0.02	-0.02	0.86
Functional richness	2.80	0.03	0.04	1.66
Bellis perennis	20.60 ± 0.95	0.13 ± 0.02	1.00	1.23 ± 0.06
Species richness	2.56	0.00	-9.03×10^{-19}	0.10
Functional richness	2.71	0.00	3.35×10^{-18}	0.02
Glechoma hederacea	16.70 ± 1.12	0.28 ± 0.05	0.55 ± 0.08	2.00 ± 0.36
Species richness	0.22	-0.17	-0.13	0.64
Functional richness	-0.59	-0.16	0.18	-1.00
Leontodon autumnalis	28.59 ± 2.86	0.89 ± 0.25	0.2 ± 0.06	2.63 ± 1.18
Species richness	3.23	0.02	0.01	0.12
Functional richness	3.77	0.02	-0.05	0.42

Leontodon hispidus	26.15 ± 1.99	0.43 ± 0.06	0.55 ± 0.09	0.59 ± 0.11
Species richness	-4.13	-0.13	-0.30	-0.33
Functional richness	6.08	0.22	0.40	0.44
Plantago lanceolata	23.33 ± 1.01	0.54 ± 0.06	0.25 ± 0.04	0.26 ± 0.05
Species richness	2.75	0.02	-0.05	-0.05
Functional richness	4.18	0.05	-0.05	-0.06
Plantago media	26.97 ± 1.78	1.99 ± 0.21	0.43 ± 0.06	0.43 ± 0.06
Species richness	-0.36	-0.20	-0.14	-0.14
Functional richness	-2.17	-0.56	-0.20	-0.20
Primula veris	8.14 ± 0.82	0.46 ± 0.10	0.39 ± 0.09	3.75 ± 0.93
Species richness	-0.97	-0.23	-0.23	-2.13
Functional richness	-0.13	0.04	0.03	0.56
Prunella vulgaris	18.20 ± 1.18	1.18 ± 0.28	0.11 ± 0.04	0.11 ± 0.04
Species richness	3.13	-0.15	0.03	0.03
Functional richness	1.06	-0.17	-0.11	-0.11
Ranunculus repens	17.32 ± 1.17	0.43 ± 0.09	0.33 ± 0.07	0.76 ± 0.19
Species richness	2.94	-0.14	-0.09	-0.33
Functional richness	0.56	-0.42	0.33	-0.98
Taraxacum officinale	32.12 ± 1.64	1.72 ± 0.24	0.55 ± 0.06	0.55 ± 0.06
Species richness	2.90	0.27	-0.02	-0.02
Functional richness	2.33	0.19	-0.09	-0.09
Veronica chamaedrys	24.04 ± 0.89	0.23 ± 0.02	0.90 ± 0.04	11.45 ± 0.91
Species richness	1.88	-0.01	0.01	-1.64
Functional richness	3.05	-0.01	0.00	-0.97

TABLE 3: Mean performance parameters of tall herbs averaged over all plots (± standard error) and effects of species richness (log_2-scale) and functional richness on the performance parameter as indicated by slopes of linear regression. In spring 2005, *Cardamine pratensis* was not found in plots.

Species	Height (cm)	Above-ground biomass (g)	Proportion of flowering	No. inflores-cences
A*chillea millefolium*	23.21 ± 1.50	0.24 ± 0.03	0.02 ± 0.02	0.02 ± 0.02
Species richness	3.71	-0.01	-0.03	-0.03
Functional richness	4.40	-0.00	-0.02	-0.02
Anthriscus sylvestris	16.46 ± 1.75	0.12 ± 0.03	0.00	0.00
Species richness	-1.94	-0.08	NA	NA
Functional richness	1.91	0.02	NA	NA

Campanula patula	36.35 ± 1.92	0.37 ± 0.06	0.83 ± 0.07	5.93 ± 0.73
Species richness	-1.65	-0.16	-0.26	-1.26
Functional richness	-2.27	-0.12	-0.16	-1.95
Carum carvi	22.27 ± 1.87	0.30 ± 0.09	0.09 ± 0.05	0.58 ± 0.33
Species richness	1.87	-0.03	-0.03	-0.19
Functional richness	5.47	0.01	-0.07	-0.43
Centaurea jacea	56.35 ± 2.88	3.02 ± 0.95	0.92 ± 0.05	2.92 ± 0.52
Species richness	-0.83	-1.36	-0.01	-0.66
Functional richness	-1.71	-1.88	0.01	-0.86
Cirsium oleraceum	31.19 ± 2.75	1.74 ± 0.26	0.03 ± 0.03	0.03 ± 0.03
Species richness	2.15	-0.09	-0.03	-0.03
Functional richness	3.58	-0.07	-0.03	-0.03
Crepis biennis	34.71 ± 3.18	2.16 ± 0.57	0.32 ± 0.06	5.35 ± 1.54
Species richness	-4.13	-1.03	-0.15	-2.22
Functional richness	-0.84	-1.09	-0.13	-2.03
Daucus carota	22.05 ± 2.36	0.81 ± 0.44	0.02 ± 0.02	0.10 ± 0.10
Species richness	0.69	-0.45	-0.01	-0.5
Functional richness	2.67	-0.38	-0.01	-0.04
Galium mollugo	51.20 ± 2.88	1.11 ± 0.19	0.50 ± 0.07	3.35 ± 0.58
Species richness	1.26	-0.37	-0.07	-0.45
Functional richness	7.79	-0.12	0.06	0.60
Geranium pratense	30.33 ± 1.98	0.93 ± 0.14	0.00	0.00
Species richness	2.24	-0.15	NA	NA
Functional richness	3.92	0.01	NA	NA
Heracleum sphondylium	16.81 ± 1.88	0.79 ± 0.52	0.00	0.00
Species richness	-1.01	-1.09	NA	NA
Functional richness	6.45	0.25	NA	NA
Knautia arvensis	65.79 ± 2.71	3.11 ± 0.55	0.92 ± 0.03	3.42 ± 0.29
Species richness	3.21	-0.01	0.04	-0.17
Functional richness	4.80	0.06	0.07	-0.17
Leucanthemum vulgare	49.48 ± 1.60	0.58 ± 0.04	1.00	1.10 ± 0.05
Species richness	1.91	0.01	-6.89×10^{-22}	-0.02
Functional richness	3.94	0.01	-8.25×10^{-20}	0.01
Pastinaca sativa	24.83 ± 3.17	0.34 ± 0.09	0.00	0.00
Species richness	7.99	0.04	NA	NA
Functional richness	15.24	0.08	NA	NA
Pimpinella major	27.13 ± 1.99	0.50 ± 0.07	0.00	0.00
Species richness	4.98	0.06	NA	NA
Functional richness	8.73	0.10	NA	NA

Ranunculus acris	36.31 ± 2.30	0.71 ± 0.09	0.60 ± 0.06	4.62 ± 0.63
Species richness	1.27	-0.7	-0.03	-0.74
Functional richness	3.21	-0.03	-0.02	-0.60
Rumex acetosa	42.17 ± 3.09	1.64 ± 0.75	0.26 ± 0.07	3.46 ± 1.04
Species richness	-1.38	-0.95	0.04	0.49
Functional richness	0.94	-0.55	-0.01	-0.09
Sanguisorba officinalis	28.22 ± 3.40	0.78 ± 0.24	0.06 ± 0.06	0.06 ± 0.06
Species richness	-0.86	-0.27	0.07	0.07
Functional richness	0.05	-0.47	0.09	0.09
Tragopogon pratensis	56.02 ± 3.60	2.23 ± 0.61	0.65 ± 0.11	1.30 ± 0.31
Species richness	-5.59	-0.93	-0.24	-0.17
Functional richness	-3.91	-0.42	-0.10	-0.65

TABLE 4: Mean performance parameters of legumes averaged over all plots (± standard error) and effects of species richness (log_2-scale) and functional richness on the performance parameter as indicated by slopes of linear regression. In spring 2005, *Trifolium fragiferum* was not found in plots.

Species	Height (cm)	Above-ground biomass (g)	Proportion of flowering	No. inflores-cences
Lathyrus pratensis	49.10 ± 2.06	0.93 ± 0.11	0.23 ± 0.06	0.33 ± 0.09
Species richness	2.37	-0.16	-0.02	-0.02
Functional richness	5.23	-0.11	0.02	0.07
Lotus corniculatus	37.90 ± 1.30	1.37 ± 0.19	0.28 ± 0.05	1.07 ± 0.27
Species richness	3.82	-0.28	-0.07	-0.09
Functional richness	4.40	-0.61	-0.13	-0.29
Medicago lupulina	27.39 ± 3.12	0.87 ± 0.24	0.62 ± 0.08	3.03 ± 0.79
Species richness	7.24	-0.16	0.04	-0.26
Functional richness	8.97	-0.21	0.06	0.45
Medicago x varia	63.20 ± 2.03	6.02 ± 0.76	0.20 ± 0.05	0.87 ± 0.26
Species richness	0.53	-0.47	-0.00	-0.02
Functional richness	2.11	-0.97	0.04	0.16
Onobrychis viciifolia	84.10 ± 2.15	31.08 ± 3.02	0.99 ± 0.01	6.01 ± 0.37
Species richness	2.00	2.99	0.01	-0.20
Functional richness	2.58	2.51	-0.01	-0.13
Trifolium campestre	14.48 ± 1.31	0.36 ± 0.13	0.90 ± 0.06	2.38± 0.45
Species richness	1.50	0.01	0.05	0.64
Functional richness	0.99	0.11	0.05	0.54

Trifolium dubium	25.81 ± 1.67	1.61 ± 0.52	1.00	13.73 ± 2.23
Species richness	3.56	0.30	1.83×10^{-17}	2.34
Functional richness	4.90	0.77	$2{,}36 \times 10^{-17}$	4.50
Trifolium hybridum	41.46 ± 1.75	1.77 ± 0.23	0.41 ± 0.06	0.77 ± 0.14
Species richness	3.61	0.16	0.06	0.12
Functional richness	4.19	0.17	0.13	0.22
Trifolium pratense	40.19 ± 2.84	5.30 ± 0.90	0.34 ± 0.07	0.59 ± 0.16
Species richness	6.09	1.11	-0.00	0.01
Functional richness	3.58	0.81	0.02	0.05
Trifolium repens	29.20 ± 0.95	2.62 ± 0.62	0.59 ± 0.07	0.59 ± 0.07
Species richness	-0.60	-1.38	-0.08	-0.08
Functional richness	-0.94	-2.24	-0.11	-0.11
Vicia cracca	46.67 ± 2.56	0.43 ± 0.07	0.02 ± 0.02	0.06 ± 0.06
Species richness	6.44	0.01	-0.02	-0.06
Functional richness	3.27	-0.12	-0.01	-0.02

Chapter II

A mechanistic basis for underyielding in phytoplankton communities

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2.1. Abstract

Species richness has been shown to increase biomass production of plant communities. Such overyielding occurs when a community performs better than its component monocultures due to the complementarity or dominance effect, and is mostly detected in substrate-bound plant communities (terrestrial plants or submerged macrophytes) where resource use complementarity can be enhanced due to their differences in rooting architecture and depth. Here, we investigated if these findings are generaliseable for free-floating phytoplankton with little potential for spatial differences in resource use. We performed aquatic microcosm experiments with eight phytoplankton species belonging to four functional groups to determine how species and community biovolume varies in relation to the number of functional groups, and hypothesised that an increasing number of functional groups within a community promotes overyielding. Unexpectedly, we did not detect overyielding in any algal community. Instead, total community biovolume tended to decrease with an increasing number of functional groups. This underyielding was mainly caused by the negative dominance effect which originated from a trade-off between growth rate and final biovolume. In monoculture, slow-growing species built up higher biovolumes than fast growing ones, whereas in mixture a fast-growing but low-productive species monopolised most of the nutrients and prevented competing species from developing high biovolumes expected from monocultures. Our results indicated that the magnitude of the community biovolume was largely determined by the identity of one species. Functional diversity and resource use complementarity were of minor importance among free-floating phytoplankton possibly reflecting the lack of spatially heterogeneous resource distribution. As a consequence, biodiversity-ecosystem functioning relationships may not be easily generaliseable from substrate-bound plant to phytoplankton communities and *vice versa*.

2.2. Introduction

The potential consequences of species loss for ecosystem functioning have received considerable attention during the last decade (e.g., Naeem et al. 2002). Several studies have focused on the effect of species richness on grassland biomass production as a key measure of ecosystem functioning. In these terrestrial experiments, species richness increase plant biomass production of communities, i.e., more diverse communities realise a higher total biomass than less diverse communities or monocultures (Naeem et al. 1996, Tilman et al. 1996, Hector et al. 1999, Mulder et al. 2001). When a community builds up a higher biomass compared to its component

monocultures it is called overyielding. In general, two categories of overyielding have been distinguished; (i) transgressive overyielding, describing an outcome where the community biomass production is higher than that of the most productive component monoculture, and (ii) non-transgressive overyielding, occurring when the community biomass production lies between the mean monoculture biomass production and that of the most productive monoculture. Communities are considered to be underyielding when community biomass is lower than the expected one from its component monocultures.

The positive effect of species richness on plant biomass production may result from either a dominance effect or complementarity effect (Loreau and Hector 2001). The dominance effect (also referred to as selection or sampling effect) accounts for the higher likelihood of including highly productive species in more diverse communities, thereby leading to a higher community biomass production. The complementarity effect relies on reduced competition among species in more diverse communities due to differences in species traits (Fridley 2001). In this scenario, interspecific competition in a community might be lower than intraspecific competition in monocultures (Stoll and Prati 2001) and higher biomass production in more diverse communities may be achieved because complementarity of species traits can lead to an increased total resource use. This resource use complementarity is thought to reflect species-specific differences in the spatio-temporal use of resources, the requirements of resources, or the ratios of resource demands. Moreover, the complementarity effect may also arise from facilitation among species within a community. In terrestrial long-term biodiversity experiments, the positive relationship between species richness and plant biomass production was explained mainly by complementarity among species, particularly in later years of the experiments (e.g., Fargione et al. 2007, Cardinale et al. 2007).

Fox (2005) distinguishes between trait-dependent complementarity which is restricted to species with certain traits (e.g., high growth rate or high biomass production), and trait-independent complementarity which occurs when all species perform better in mixture than in monoculture. In both cases, species are thought to be function better in mixtures than expected from monoculture but not at the expense of other species. The complementarity effect is strongly based on differences in functional traits of the species (e.g., resource use and biomass production) (Hooper and Vitousek 1997, Tilman et al. 1997, Hooper 1998, Mikola and Setälä 1998) and less on species richness *per se* (Díaz and Cabido 2001, Giller et al. 2004). Thus, functional traits have to be considered in biodiversity experiments (Hooper et al. 2002) and the division of species into functional groups (Walker et al. 1999) can lead to a better understanding of

mechanisms, in particular for complementarity, that are responsible for the species richness effect on plant biomass production.

To date, the effect of species and functional diversity on biomass production has been studied mostly using substrate-bound terrestrial or submerged plants and only rarely with phytoplankton. The meta-analysis of Balvanera et al. (2006) shows that the effect of biodiversity on ecosystem processes varied between different types of ecosystems (forest, grassland, marine, freshwater, bacterial microcosms, soil communities and marshes). In particular, the way that individuals interact may differ greatly between substrate-bound and free-floating species. For example, terrestrial and submerged plants that grow on a substrate exhibiting environmental heterogeneity in resource supply may differ sufficiently in rooting architecture and depth to permit spatial complementarity in resource use among species. In contrast, phytoplankton are free-floating species without roots and often lack spatially structured resource use in such a relatively homogenous environment at a small scale. Such differences between taxa suggest both that the potential for complementarity is higher for substrate-bound plants than for phytoplankton species and that resource use complementarity may be limited in pelagic algal communities. Consequently, we hypothesised that overyielding is less important in phytoplankton communities than in substrate-bound plant communities.

We performed experiments in a two-stage design using aquatic microcosms. In a first step, the phytoplankton community consisted only of species which belonged to one functional group with similar competitive abilities. In a second step, we added other functional groups to the first one to assemble communities that comprised one to four functional groups. These species exhibited different competitive abilities but had the same potential for spatial resource use in pelagic environments. Using this arrangement, we sought to determine whether a phytoplankton community consisting of one functional group exhibits underyielding and whether an increasing number of functional groups promotes overyielding in phytoplankton communities. To date, biodiversity experiments in terrestrial systems have quantified overyielding mainly at the level of entire communities. Instead, we calculated overyielding both at the community and at the species level and analysed the temporal dynamics of the individual species to elucidate mechanisms underlying the effect of functional diversity on the biomass production of phytoplankton communities.

2.3. Methods

Experimental design and performance

The experiments were performed with eight algal species belonging to four functional groups (Table 1) that lacked know differences in spatial resource use. Classification of the phytoplankton species into functional groups was based on their morphology (e.g., cell size, cell shape) and on functional traits (e.g., motility, demand for silica) of the species (Weithoff 2003, Table 1). The functional traits were more similar within one functional group than between functional groups. The functional group of green algae consisted of five species, whereas the other functional groups were represented by one species each. The algal species were obtained from the Experimental Phycology and Culture Collection of Algae (SAG, Göttingen, Germany) and were cultured in sterile WC medium (Nichols 1973). The eight algal species are typical and widespread in freshwater lakes and can co-occur in lakes (e.g., mesotrophic Lake Constance).

The culture medium contained 2.5 µM phosphate, 50 µM nitrogen and 5 µM silicate. Our medium was designed explicitly to promote potential co-limitation by several nutrients and thus, to maintain the target species richness for the duration of the experiment. Because diatoms such as *Asterionella formosa* are known to be good competitors for phosphorous (Tilman 1982, Interlandi et al. 1999) a silicate concentration was chose which was slightly above the half saturation concentration for growth derived from a field study (3.35 µM, Michel et al. 2006) but potentially limits the growth of the diatom. The experiments included monocultures of all eight species, and four levels of functional group richness (functional diversity) consisting of the five green algal species and either none, one, two or three of the other functional groups (Table 2). Each treatment was grown in duplicate. This simplified design was selected to balance experimental tractability and realism. All eight monoculture treatments were inoculated with ca. 0.3 mm^3/L. The initial total biovolume of the green algal community was ca. 1.5 mm^3/L for all mixtures, thus 0.3 mm^3/L for each species. The other functional groups had also an initial total biovolume of ca. 1.5 mm^3/L in mixtures which was divided by their number of the functional groups present (1, 2 or 3) and these biovolumes were combined with the green algal biovolume. The initial inocula resulted in approximately four generations of the single species growing in monocultures and mixtures during the experiment.

The microcosms (Erlenmeyer flasks, 300 mL) contained 100 mL algal suspension of which 15 mL were replaced with fresh medium every other day resulting in a daily dilution rate of 0.075. This low dilution rate ensured both the potential for new algal production during the experiment without

imposing a substantial mortality rate and established strong competition for nutrients and facilitates comparison with terrestrial studies lacking herbivory or other factors which reduce plant biomass. The experiments were performed in a climate-controlled chamber at 20 ± 1°C under a 16:8 h light:dark cycle at a light intensity of 73 µmol photons m^{-2} s^{-1}, measured in air. This light intensity is below photoinhibition and high enough to support exponential phytoplankton growth in monocultures and mixtures. The Erlenmeyer flasks were manually shaken twice a day to avoid algal growth on the wall and the position of the flasks was altered randomly every other day. Sub-samples for algal biovolume determination (15 mL) were taken after 0, 2, 6, 12, 21 days and fixed with Lugol´s iodine solution. At least 600 cells per species and sample were counted under an inverted microscope (Thalheim, Germany) and the size of ca. 30 randomly chosen algal cells was measured for each species in each sample using a video-aided image analyser (Thalheim, Germany) of the microscope.

Numeric analysis

For each species, cell volumes (µm³) were calculated according to the method of Hillebrand et al. (1999) while biovolumes (mm³/L) were estimated as the product of cell density and volume. In this study, the term biovolume is used as a synonym for the term biomass production. Biovolumes were not converted into biomasses (e.g., Menden-Deuer and Lessard 2000) to avoid uncertainties arising from substantial species-specific variability in cell carbon content, particularly in strongly limited conditions (unpublished data). Preliminary mass-balance calculations suggested that the important nutrients (phosphate, nitrogen, silicate) were incorporated completely into algal biomasses at the end of the experiment. The cell volume (µm³) of each species remained constant during the experiment and thus, daily growth rates of each algal species were derived from the slope of linear regressions of the logarithm of the cell density vs. time until a plateau was reached.

At the community level, potential overyielding was assessed based on the phytoplankton community biovolume after 21 days by calculating the relative yield total (*RYT*) of Fridley (2001 and references therein) and the index $D_{\max}$ of Hooper and Dukes (2004) as measures of non-transgressive and transgressive overyielding, respectively. The *RYT* was calculated as $RYT = \sum_{i=1}^{S} RY_i$, S is the total number of species in the mixture and RY_i the relative yield of species i with $RY_i = \frac{O_i}{M_i}$, O_i is the biovolume of species i observed in the mixture, and M_i its biovolume in monoculture (Hector 1998). A value of $RYT > 1$ implies non-transgressive overyielding in mixtures and $RYT < 1$ demonstrates the occurrence of interference among species,

leading to underyielding in mixtures. The index $D_{\max}$ was calculated as $D_{\max} = \frac{O_T - \max(M_i)}{\max(M_i)}$, $O_T = \sum_{i=1}^{S} O_i$ is the observed final biovolume in mixture and max(M_i) is the maximum monoculture biovolume of the component species. A value of $D_{\max} > 0$ indicates transgressive overyielding (Loreau 1998).

To identify potential mechanisms causing over- and underyielding at the community level, over- and underyielding was also calculated at the species level. In this approach, the yield exponent y_i estimates whether a species over- or underyields in its mixture. According to the model of Lambers et al. (2004), y_i was calculated as $y_i = \log_S\left(\frac{O_i}{M_i}\right)$. Yield exponents greater than -1 indicate that the species *i* overyields, while values less than -1 imply that species *i* is an underyielding species that performs less well in the mixture than expected from its monoculture. If y_i equals -1, the species *i* produces the same biovolume in mixture as expected from its monoculture.

In the tripartite partition method (Fox 2005), which is a modification of the additive partition technique of Loreau and Hector (2001), the net biodiversity effect (ΔY) was measured as the difference between the observed final biovolume (O_T) of a mixture and its expected biovolume based on the monoculture biovolume of its component species. Fox´s equations partition the net biodiversity effect into three effects; trait-independent complementarity (first part), dominance (second part), and trait-dependent complementarity (third part) which were calculated as following:

$$\Delta Y = S * \overline{M} * \overline{RY} + S * Cov(M_i, \frac{RY_i}{RYT} - RY_{E,i}) + S * Cov(M_i, RY_i - \frac{RY_i}{RYT})$$

$\overline{M}$ is the averaged monoculture biovolume, $\overline{RY} = \frac{1}{S} * \sum_{i=1}^{S} RY_i$ is the averaged relative yield of the species in mixture, and $RY_{E,i} = \frac{1}{S}$ is the expected relative yield of species *i* in mixture ($\sum_{i=1}^{S} RY_{E,i} = 1$, for a substitutive experimental design). Both trait-independent ($S * \overline{M} * \overline{RY}$) and trait-dependent

complementarity ($S*Cov(M_i, RY_i - \frac{RY_i}{RYT})$) are positive when species perform better in mixture than expected based on monoculture biovolumes but not at the expense of other species. The dominance effect ($S*Cov(M_i, \frac{RY_i}{RYT} - RY_{E,i})$) quantifies the extent to which a species performs better in mixture than expected based on monoculture biovolume at the expense of other species and takes a positive value when species with high monoculture biomasses are also the dominant species in mixture. In case of underyielding at the community-level (RYT < 1), the term $RY_i - \frac{RY_i}{RYT}$ (in trait-dependent complementarity calculations) is always negative. The absolute value of this term generally increases with increasing values of RY_i which implies for underyielding communities that the term becomes more negative for higher values of RY_i. As a consequence, the covariance between M_i and $RY_i - \frac{RY_i}{RYT}$ is positive when species with *low* monoculture biovolumes obtain high relative yields in mixture. This interpretation contrasts that of previously studies of overyielding communities (Fox 2005) in which a positive covariance was used to indicate that species with *high* monoculture biovolumes attain high relative yields in mixture. Hence, when analysing the trait-dependent complementarity with the tripartite partition method, a clear distinction between over- and underyielding communities is required.

The statistical analyses were performed using SPSS software (version 12). Differences between biovolumes, growth rates, overyielding indices (RYT, $D_{\max}$) and yield exponents among treatments were tested using the non-parametric Kruskalis-Wallis test. Linear regressions were used to test for the effect of growth rates on final biovolumes in monoculture and mixtures.

2.4. Results

Overyielding at the community level

Community biovolumes

Neither the green algal community nor the communities consisting of several functional groups exhibited any evidence of overyielding by the end of the experiment (Fig. 1). The mean (±SD) biovolume of the most productive monoculture (*Oocystis marsonii*, 52.4 ± 0.66 mm^3/L) was much higher than that of all communities and no community biovolume was higher than the mean monoculture biovolume (30.1 ± 18.41 mm^3/L). The community biovolume was not affected by the number of functional groups (x^2=6.5,

P=0.09) but decreased by around 14% from the lowest (one) to the highest (four) functional group diversity level (Fig. 1). The community biovolumes of the two and three functional group diversity level did not differ significantly between the various species compositions (both x^2=3.4, P=0.180).

Indices and tripartite partition method

The values of the relative yield total (RYT) were mostly lower than one with a mean (±SD) of 0.74 ± 0.17 indicating that non-transgressive overyielding did not occur on average (Fig. 2). In contrast, the RYT was around or slightly higher than one for three communities (Fig. 2), mainly because of *Monoraphidium minutum* which reached high relative yields of 0.67 in these communities compared to 0.43 in communities where RYT was lower than one. Functional diversity did not significantly affect the RYT values of the communities (x^2=1.96, P=0.58).

Algal communities built up only 20-27% of the biovolume of the most productive species in monoculture (Fig. 1, *O. marsonii*). D_{max} values were negative (-0.9 to -0.7) at all functional diversity levels (data not shown) and did not differ significantly from each other (x^2=6.92, P=0.08). Thus, transgressive overyielding ($D_{max} > 0$) did not occur in any community.

Community biovolumes of the mixtures were 14 to 23 mm^3/L lower than those expected from monocultures leading to a mean (± SD) net biodiversity effect (ΔY) of -18.7 ± 3.0. The partitioning analyses revealed that the absolute magnitude of the dominance, trait-independent, and trait-dependent effects differed significantly (x^2=33.55, P < 0.001). The dominance effect (-13.6 ± 2.) was the largest effect in the experiment and mostly negative, indicating that a species with a low monoculture biovolume attained a high observed relative yield in the communities at the expense of other species. The effect size of the trait-independent complementarity was also mostly negative (-8.4 ± 5.7) indicating interspecific competition or some other processes with the same effect within the phytoplankton communities. The trait-dependent complementarity had the smallest effect and was mostly positive (3.3 ± 2.3). Due to the underyielding in the communities, these positive values imply that species with low monoculture biovolumes attained high observed relative yields in mixture not at the expense of other species. None of the effect sizes depended on the number of functional groups (x^2=1.74, P=0.63; x^2=4.94, P=0.18; x^2=3.34, P=0.34, respectively).

Overyielding at the species level

In spite of the prevalence of underyielding in the communities, the yield exponent (y_i) of *M. minutum* was consistently higher than -1 (Fig. 3) indicating that this species overyielded in all mixtures independent of

functional diversity. All other green algal species underyielded as indicated by their negative mean (± SD) yield exponents of -1.7 ± 0.5, -1.6 ± 0.1 and -1.7 ± 0.2 for *C. vulgaris*, *A. gracilis* and *S. obliquus*, respectively (Fig. 3). *O. marsonii* went extinct in all diversity treatments and was always an underyielding species. Of the other functional groups, *A. formosa* was exhibited variable yield exponents which tended to decrease with increasing functional diversity (x^2=5.19, P = 0.08, Fig. 3). In contrast, C*ryptomonas* sp. and *P. agardhii* were consistently underyielding species as indicated by their high mean (±SD) negative yield exponents of -1.8 ± 0.2 and -2.2 ± 0.1, respectively (Fig. 3). Overall, only *M. minutum* consistently overyielded in the algal mixtures.

Temporal dynamics of species biovolumes

In monoculture, the biovolumes of the individual species usually increased after a short lag-phase of three days until a plateau was reached after six to twelve days (data not shown). In mixture, a similar temporal pattern was found with biovolume plateaus mainly reached after six to twelve days (Fig. 4). In contrast, *O. marsonii* went extinct at all functional diversity levels after 6 to 21 days, whereas the biovolume of *A. formosa* increased until day 2 and declined steadily thereafter. The species-specific temporal patterns of the biovolumes were recurrent in all treatments (data not shown).

At the end of all experiments, *M. minutum* reached the highest mean (±SD) relative biovolume (0.48 ± 0.07) in all communities while *Chlorella vulgaris* (0.09 ± 0.07), *Ankistrodesmus gracilis* (0.19 ± 0.04) and *Scenedesmus obliquus* (0.15 ± 0.03) all reached similar relative biovolumes in each treatment. Hence, the relative biovolume of these species were statistically independent of the number (P = 0.12 to 0.49) and type (P = 0.09 to 0.77) of the other functional groups present. The mean (±SD) relative biovolume of the other functional groups (diatoms, cyanobacteria, and flagellates) decreased from 0.19 ± 0.24 to 0.05 ± 0.03 during the course of the experiment.

Species final biovolumes vs. species growth rates

Monoculture

In monoculture, final biovolumes (x^2=14.52, P=0.04) and growth rates (x^2=14.65, P=0.04) differed significantly among all species (n=8). Moreover, the biovolume of all individual species decreased with increasing growth rate (F = 4.59, P = 0.05, Fig. 5a). When considering only green algal species (n=5) this negative relationship was highly significant (F=20.47, P=0.002) whereas it was not significant for the three species of the other functional groups (F=4.96, P=0.09). Because of this and due to the fact that the relative fraction of the other functional groups was very low at the end of

the experiment (0.05 ± 0.03) the subsequent analysis of the relationship between biovolume and growth rate refers mainly to the green algal species.

Among green algal species, *O. marsonii*, *S. obliquus* and *A. gracilis* reached high mean (±SD) biovolumes (52 ± 0.7 mm^3/L, 48 ± 3.8 mm^3/L, 47 ± 4.5 mm^3/L, respectively) with low mean (±SD) growth rates (0.59 ± 0.02 d^{-1}, 0.68 ± 0.00 d^{-1}, 0.59 ± 0.00 d^{-1}, respectively). In comparison, *M. minutum* and *C. vulgaris* established low biovolumes (15 ± 1.8 mm^3/L and 20 ± 4.2 mm^3/L) with high growth rates (0.77 ± 0.02 d^{-1} and 0.85 ± 0.05 d^{-1}). The inverse relationship between biovolume and growth rate was observed also for the diatom *A. formosa* which reached the lowest mean (±SD) biovolume in monoculture (8 ± 0.1 mm^3/L) of all species with the highest growth rate (0.90 ± 0.01 d^{-1}). *Planktothrix agardhii* and *Cryptomonas* sp. had low growth rates and built up lower biovolumes than expected from the relationship among the green algae.

Mixture

In mixture, significant differences between final biovolumes (x^2=89.01, P < 0.001) and growth rates (x^2=73.34, P< 0.001) were found among all species (n=8). However, contrary to results from monocultures trials, the biovolume increased strongly with increasing growth rates (F = 25.16, P < 0.001, Fig. 5b) in mixtures. In particular, *M. minutum* was characterized by low biovolumes in monoculture and built up the highest mean (±SD) biovolumes (7 ± 1.8 mm^3/L) in mixtures due to its high mean (±SD) growth rate (0.67 ± 0.06 d^{-1}). The opposite pattern was found for *O. marsonii* which went extinct in all mixtures before the end of the experiment, even though it was the most productive species in monoculture. The growth rates and biovolumes of the other species (*C. vulgaris*, *A. gracilis*, *S. obliquus*, *Cryptomonas* sp., *A. formosa* and *P. agardhii*) fell between the extremes of *M. minutum* and *O. marsonii*. Consequently, communities were strongly dominated by the fast-growing species with the lowest monoculture biovolume (*M. minutum*).

2.5. Discussion

Underyielding in phytoplankton communities

To date, positive relationships between diversity and primary production have been found predominately in terrestrial systems (Naeem et al. 1996, Hector et al. 1999, Tilman et al. 2001, Hooper et al. 2005) and a few in aquatic ecosystems (Engelhardt and Ritchie 2001, Downing and Leibold 2002, Bruno et al. 2005, 2006, Zhang and Zhang 2006, Weis et al. 2008). In aquatic experiments submerged plants or corals were mostly investigated where spatial resource use complementary may occur in a similar manner as in substrate-bound terrestrial plants. In contrast, our experiments with free-floating phytoplankton demonstrated that an algal community

consisting of one functional group underyielded and unexpectedly, communities consisting of several functional groups did not exhibit overyielding. Instead, the biovolume of the algal mixtures tended to decrease with increasing functional diversity and demonstrated that underyielding occurred at the community and mostly at the species level.

In our study, the RYT values were mostly below one indicating that 13 of 16 algal communities underyielded. Overyielding (RYT near 1) occurred only in three communities in which *Monoraphidium minutum* and *Asterionella formosa* had much higher than expected biovolumes and high relative yields. In monoculture, these two species were less productive than the other species which built up 2 to 9 times higher monoculture biovolumes. Thus, the observed community biovolume was lower than the expected one indicating underyielding despite a RYT value near one. These patterns may reflect a well-known limitation of the RYT method (Loreau 1998, Fridley 2001). For example, Loreau (1998) calculated RYT values of 1.25 although the observed biomass of a two species community was lower than the expected one. This result was arose because more productive species in monoculture had a lower than expected yield in mixture whereas the other less productive species maintained a yield similar to that in monoculture. Consequently, the calculation of the RYT based on the relative yields of the species appears inappropriate to detect non-transgressive overyielding in communities with strong differences in the species-specific monoculture biomasses. Instead, we conclude that all communities underyielded in our experiment.

The underyielding of the algal communities was mostly contributed to the negative dominance effect which was also found for other phytoplankton communities (e.g., Weis et al. 2007). In our study, *M. minutum* reached the highest observed relative yield at the expense of other species in all mixtures, but built up only low biovolumes in monoculture and mixture which promoted community underyielding. The trait-independent complementarity also contributed to the underyielding, as the mostly negative values indicated strong interspecific competition within the communities. This result is consistent with the competitive suppression of highly productive species in mixtures that has been shown to result in an only weakly positive or even negative net biodiversity effect (Loreau and Hector 2001, Hooper and Dukes 2004). This pattern was found for the high-productive species *Oocystis marsonii* in the present study. The trait-dependent complementarity played a minor role for the net biodiversity effect. Given underyielding of the algal communities, the positive values of the trait-dependent complementarity support that few low-productive species became dominant in mixture but not at the expense of other species. To conclude, the presence of a low-productive species such as *M. minutum* was the important mechanism leading to community

underyielding. Specifically, this species appeared to enhance interspecific competition or other similar negative effects and to decrease the biovolume of all component species, including the one with the highest monoculture biovolume. Thus, species identity had a greater effect on community biovolume than functional diversity.

In principle, the magnitude of the effect sizes can vary with diversity (Fox 2005). However, in our study, none of the effect sizes was significantly related to functional diversity indicating that an increasing functional diversity did not enhance resource use complementarity among the functional groups. The classification of phytoplankton species into functional groups aims to give information about their potential for resource use complementarity (e.g., Díaz & Cabido 2001, Bengtsson et al. 2002). For our species, resource partitioning may have only occurred in time or as a function of resource type in these well-mixed microcosms. In this case, all species appear to belong to one meta functional group with respect to spatial use of resources despite their strong differences in other functional traits. In terrestrial ecosystems, such spatial resource use arises e.g., due to differences in rooting architecture. Presumably, these differences are lacking both in our microcosms and natural phytoplankton communities. Such an absence of spatial partitioning of resources could also contribute to the consistent underyielding of our algal communities when compared to overyielding observed in grassland biodiversity experiments.

Many previous biodiversity experiments have been of short duration, even though positive effects of diversity on ecosystem processes such as niche partitioning and positive interactions may increase with time (e.g., Cardinale et al. 2007, Gamfeldt and Hillebrand 2008). However, in the paleolimnological study of Rusak et al. (2004), diatom species richness was negatively correlated with diatom production during the 2000 years and species identity appeared to play a large role in determining this inverse relationship. This result corresponds well with our negative effect of functional diversity on algal biovolume which was mainly caused by a negative dominance effect although our experiment was only run for 21days. However, this length of time was sufficient to allow approximately four generations of the algal species and this length of time is equivalent to that of terrestrial experiments run for years. As a result, our experiment appears to be of sufficient duration to allow for both intra- and interspecific competition, leading to improved estimation of overyielding indices. This interpretation is also supported by the fact that the experiments ran under equilibrium conditions; the biovolume plateau of the monocultures and mixtures was mostly reached after six to twelve days and remained nearly constant until the end of our experiment.

Overyielding species had high growth rates but low biovolumes

Previous research demonstrates that the most productive species in monoculture is not necessarily the predominant taxon in mixture (Hector et al. 2002). This observation may be explained by a trade-off between growth rate and final biovolume, at least for our system. For example, species with high growth rates built up low biovolumes in monoculture (low-productive species), whereas species with low growth rates built up high biovolumes (high-productive species). In addition, unproductive species with high growth rates in mixtures reached relatively high biovolumes by quickly monopolising the nutrients before they could be attained by high-productive species due to their low growth rates. This trade-off may arise from a positive correlation between growth rate and nutrient demand per unit carbon implying that in monoculture, specifically the fast-growing *M. minutum* converted the available nutrients into a lower final biovolume in units of carbon than slow-growing species. In mixture, the fast-growing *M. minutum* quickly incorporated most of the nutrients before slow-growing species could acquire the resources. Such trade-offs between competitive ability or other life history traits and growth rates are ubiquitous (Grime 1997, 2001, Tessier et al. 2000). For example, if the competitive ability is correlated negatively with biomass production then a negative correlation between diversity and primary productivity will be found (Loreau 2000).

We suggest that underyielding in diverse phytoplankton communities occurs when fast-growing but low-productive species reach high relative yields in mixture. In analogy, overyielding would be expected when fast-growing but high-productive species are dominant in diverse algal community. Such conditions can occur if fast-growing species build up high and slow-growing species low biovolumes in monoculture. Hence, we infer that the occurrence of community under- or overyielding is strongly influenced by the relationship between final biovolume and growth rate independent of the system under consideration. So far, studies about temporal dynamics of species enabling estimates of growth rates are rare in terrestrial and aquatic biodiversity experiments but are required for a better understanding of the underlying mechanism of the biodiversity-ecosystem functioning relationship.

The generality of our findings may be restricted by the limited number of species (n=8) and functional groups (n=4) and the simultaneous change in species and functional diversity. Consequently, further research is needed with additional taxa and functional groups to generalize our understanding of the relationship between community diversity and biomass. The applied nutrient concentrations (phosphorous, nitrogen) were in a range typical for moderately eutrophic lakes (Wetzel 2001) and our light intensity enabled exponential growth of the species in monoculture and mixtures, further studies which expand the range of these variables would be useful. In fact,

a higher (or lower) resource level can lead to a higher (or lower) community biomass and probably to changes in the relative species composition. Fortunately, the resource level *per se* is not a causal factor for underyielding since the net biodiversity effect is independent of the absolute amount of the community biomasses.

Conclusions

Our results provide evidence for underyielding in phytoplankton communities which can mainly be explained by the occurrence of a negative dominance effect caused by a trade-off between growth rate and final biovolume. Resource use complementarity among phytoplankton species was independent of functional diversity and of minor importance in contrast to substrate-bound plants which may originated from a lacking possibility of spatial resource partitioning between free-floating algal species. Hence, the relationships between functional diversity and biomass production and its underlying mechanism may not be easily generaliseable from substrate-bound plant to phytoplankton communities and vice versa. Further comparable research among different types of ecosystems is needed for the identification of patterns and causal mechanisms.

2.6. Acknowledgements

We wish to thank Melanie Hartwich for counting phytoplankton samples, and Helmut Hillebrand who offered valuable comments on an earlier version of the manuscript. We also thank the editor and two anonymous reviewers for constructive reviews that highly improved this manuscript. Andrea Schmidtke conducted this work as part of her PhD funded by the German Research Foundation (DFG contract GA 401/10-1).

2.7. Tables

TABLE 1: Phytoplankton species and their classification into four functional groups based on mean cell size (*growing in WC-limited medium, 14 days), motility and demand for silica (Weithoff 2003).

Species	Functional group	Cell size* (μm^3)	Motility	Demand for silica
Monoraphidium minutum	Green algae	13	–	–
Chlorella vulgaris	Green algae	13	–	–
Ankistrodesmus gracilis	Green algae	30	–	–
Scenedesmus obliquus	Green algae	54	–	–
Oocystis marsonii	Green algae	75	–	–
Asterionella formosa	Diatom	386	–	+
Planktothrix agardhii	Cyanobacteria	5607	+ (gas vacuoles)	–
Cryptomonas sp. (SAG 26.80)	Phytoflagellate	324	+ (flagella)	–

TABLE 2: Species combinations of the different functional diversity levels. FG = functional group(s).

	1 FG	2 FG	2 FG	2 FG	3 FG	3 FG	3 FG	4 FG
Green algae (5 species)	x	x	x	x	x	x	x	x
Diatom		x			x	x		x
Cyanobacteria			x		x		x	x
Phytoflagellate				x		x	x	x

2.8. Figures

FIGURE 1: Biovolumes (mm3/L) of the individual monocultures and of the phytoplankton communities at different functional diversity levels. The horizontal line represents the mean biovolume of the monocultures.

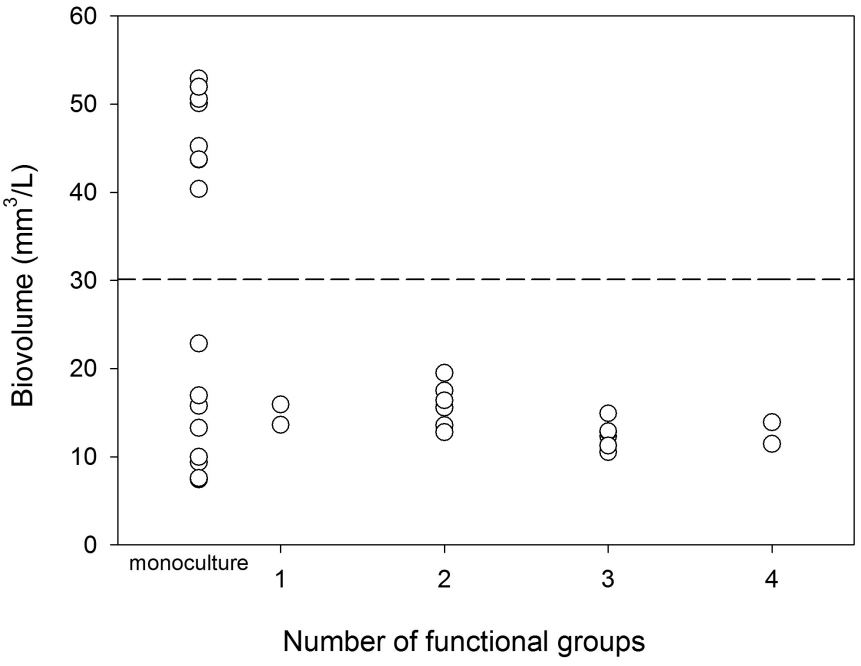


FIGURE 2: Relative yield total (RYT) of all phytoplankton communities at different functional diversity levels. The horizontal line represents the RYT value below which underyielding occurs.

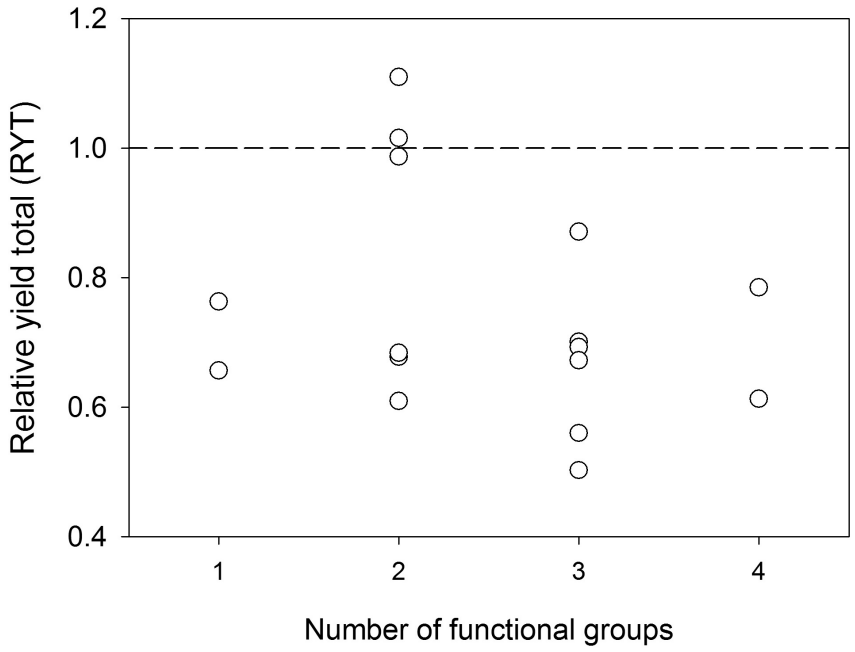


FIGURE 3: Yield exponents (y_i) of the green algal species at different functional diversity levels. Not shown for *Oocystis marsonii* because it went extinct in all diversity treatments

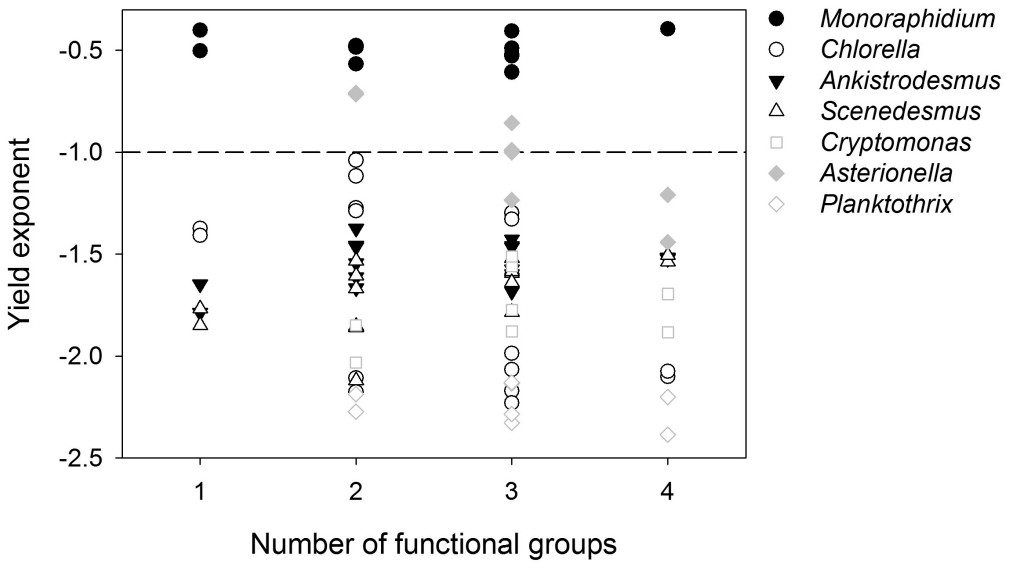


FIGURE 4: Temporal dynamics of the biovolumes (mm^3/L) of all green algal species (a) alone, (b) together with the other functional groups (averaged over all diversity levels) and (c) temporal dynamics of the other functional groups (averaged over all diversity levels).

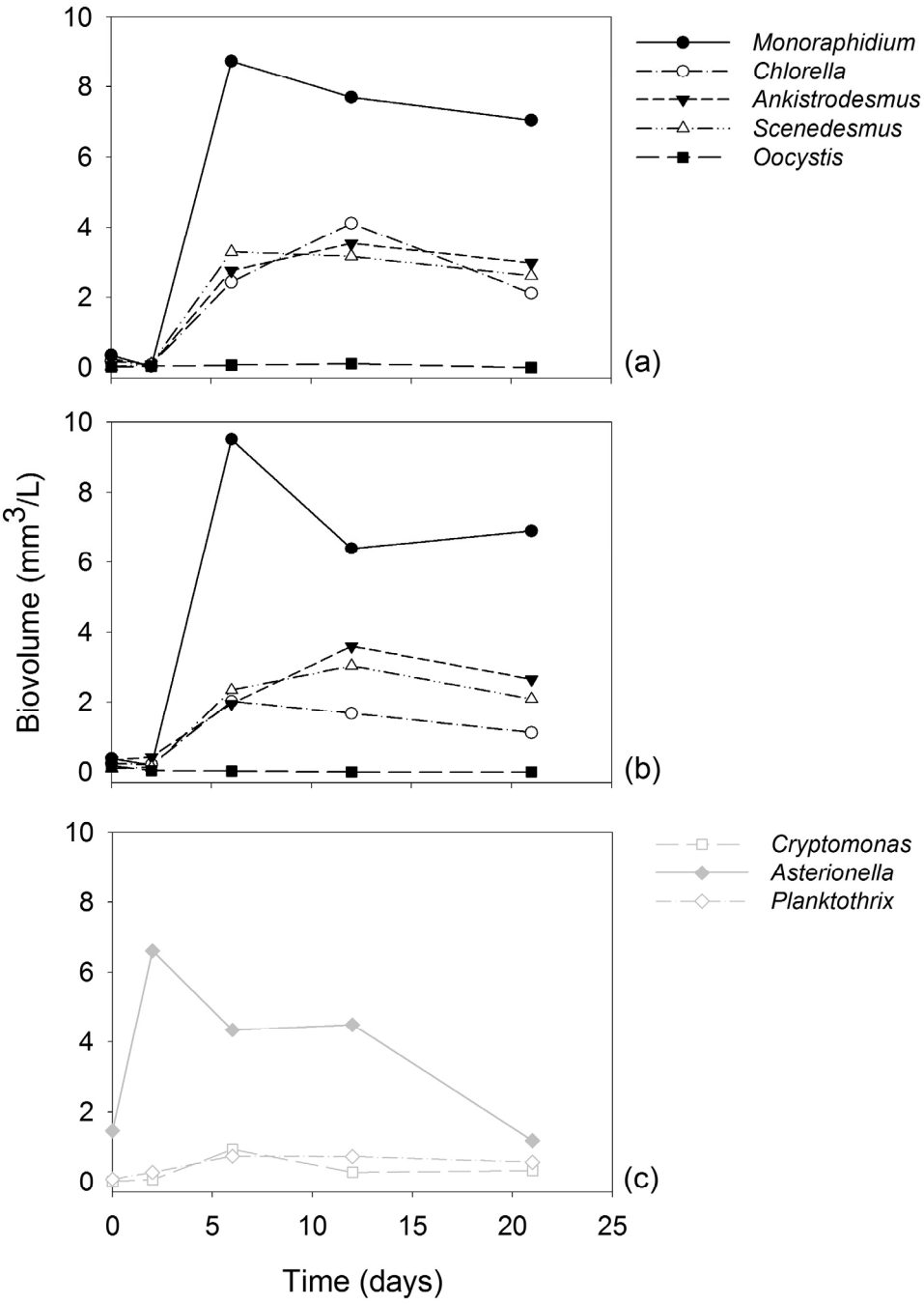
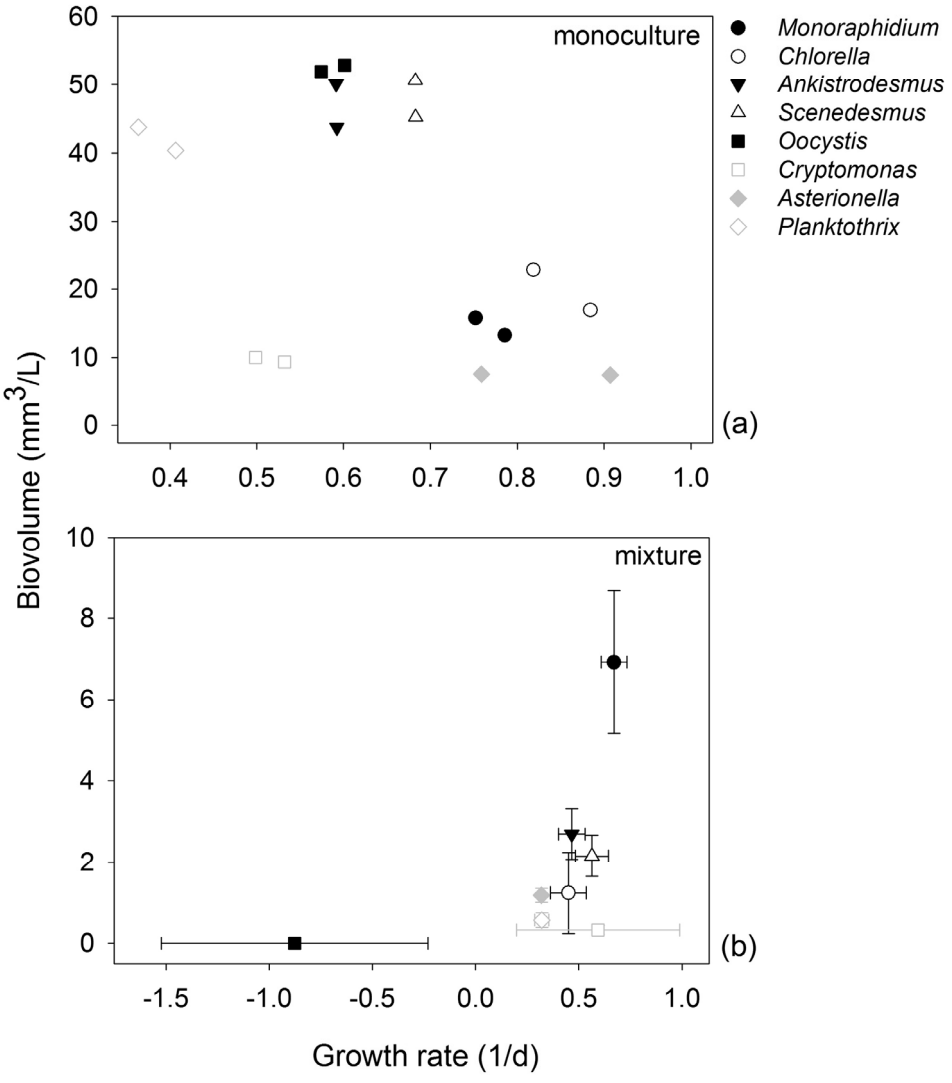


FIGURE 5: Growth rates (1/d) and final biovolumes (mm^3/L) of all individual green algal species in monoculture (a) and averaged for all functional diversity treatments (b). Error bars show standard deviations. Please note the different scales of the x- and y-axes in the graphs.



Chapter III

Overyielding and underyielding in phytoplankton communities

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3.1. Abstract

The effect of diversity on ecosystem functions such as e.g., community biomass has received much attention over the past decade. It has been shown for numerous grassland and some freshwater communities that diversity tends to enhance community biomass. However, some studies also provide evidence for community underyielding which gives rise to the question which mechanisms promote community overyielding and underyielding. A previous study revealed that community underyielding resulted from a negative relationship between the biomass of the component species and their growth rates in monoculture. In this case, communities were dominated by one fast-growing and low-productive species which prevented slow-growing and high-productive species from developing their high expected biomasses in mixtures. These findings suggest that community overyielding occurs when the biomass of the component species is positively correlated with their growth rates in monoculture.

We performed an extensive microcosm experiment with phytoplankton communities differing in species diversity (1, 2, 4, 8 and 12 species), functional diversity (1, 2, 3, and 4 functional groups), and composition to test the effect of diversity on community biomass. We found positive relationships between species/functional diversity and community biomasses but functional diversity played an inferior role. Community overyielding was mainly caused by a positive trait-independent complementarity effect. This effect can be attributed to resource use complementarity and/or facilitative interaction among the species although their underlying mechanisms are less clear for free-floating algal communities. Overyielding of more diverse communities occurred when the biomass of the component species was positively correlated with their growth rates in monoculture. In other words, more diverse phytoplankton communities were dominated by fast-growing and high-productive species leading to their observed overyielding.

The emergent pattern for community overyielding and underyielding from the relationship between biomass and growth rate of the component species in monoculture may be generaliseable to communities of other ecosystems.

3.2. Introduction

Over the past two decades, consequences of species loss for ecosystem functioning have received considerable attention (e.g., Chapin et al. 2000, Naeem et al. 2002). Many field and laboratory studies revealed a positive diversity effect on the conversion of resources into community biomass (reviewed by Balvanera et al. 2006, Cardinale et al. 2006, 2007). When a community builds up a higher biomass than its component monocultures it

is called overyielding. In general, two categories of overyielding have been distinguished; (i) transgressive overyielding, describing an outcome where the community biomass is higher than that of the most productive component monoculture, and (ii) non-transgressive overyielding, occurring when the community biomass lies between the mean monoculture biomass and that of the most productive monoculture. Community overyielding may result from a dominance and/or complementarity effect (Loreau and Hector 2001). The dominance effect (also referred as to selection and sampling effect) accounts for a higher likelihood of including a high-productive species in a more diverse community. The complementarity effect may arise from resource use partitioning (or niche differentiation) among species leading to an enhanced resource use in more diverse communities. More precisely, Fox (2005) distinguishes between trait-dependent complementarity which is restricted to species with certain traits (e.g., high growth rate or high biomass), and trait-independent complementarity which occurs when most of the species perform better in mixture than in monoculture. Moreover, the complementarity effect also indicates facilitative interactions among species within a community. Complementarity is based on differences in the functional traits of species (Hooper and Vitousek 1997, Tilman et al. 1997, Hooper 1998, Mikola and Setälä 1998) and less on species richness *per se* (Díaz and Cabido 2001, Giller et al. 2004). This suggests to consider functional diversity in biodiversity experiments. Functional diversity accounts for the number of functional groups within a community and also for the presence of particular functional groups which can positively or negatively affect the biomass of other component species (Hooper and Vitousek 1997, Tilman et al. 1997, Symstad et al. 1998, Spehn et al. 2005). For example, plant community biomasses can be enhanced by the presence of nitrogen-fixing species such as legumes (Spehn et al. 2005, Temperton et al. 2007) and cyanobacteria (Présing et al. 1996, Herrero et al. 2001).

Negative relationships between diversity and community biomass have also been reported (Hooper and Vitousek 1997, Weis et al. 2007, Schmidtke et al. 2009) although positive diversity effects were found more often. Community underyielding occurs when the community biomass is lower than expected from its component monocultures. In a theoretical study, it was speculated that community underyielding is expected when the competitive abilities of species are negatively correlated with their biomass (Loreau 2000). This indicates that community underyielding is common when one or more low-productive species become dominant in mixtures. This has been already shown for phytoplankton communities where underyielding was caused by the dominance of a low-productive species in the mixtures (Schmidtke et al. 2009). Furthermore, interspecific competition or some other processes with the same effect within communities can also lead to community underyielding.

Diversity effects on ecosystem functions including e.g., community biomasses have been studied for different types of ecosystems, but more frequently for grassland communities than for freshwater ones (Balvanera et al. 2006). As a consequence, such analyses of diversity effects are still underrepresented for aquatic communities as e.g., phytoplankton assemblages. This is surprising since aquatic microcosm studies offer a unique insight into the role of diversity and its underlying mechanism that cannot be obtained from terrestrial experiments with their predominantly long-lived organisms (Giller et al. 2004, Gessner et al. 2004).

As mentioned above, pattern of different relationships between species diversity and community biomass have been detected but to date, their underlying mechanisms are less clear. Community underyielding can arise from a negative relationship between the biomass of individual species and their growth rate in monoculture (Schmidtke et al. 2009). In this case, a high growth rate is achieved at the cost of low biomass and it leads to the dominance in mixture by quickly monopolising most of the nutrients which prevents slow-growing and high-productive species from developing high biomasses as expected from their monoculture. On the base of these former findings, community overyielding can be expected when the biomass of component species are positively correlated with their growth rates in monoculture. In this case, diverse communities are dominated by one or more fast-growing and high-productive species leading to community overyielding.

We performed aquatic microcosm experiments with an extensive design to get a broad range of community responses. The phytoplankton communities differed in species diversity (1, 2, 4, 8, and 12 species), functional diversity (1, 2, 3, and 4 functional groups) and community compositions to explore the effect of species diversity and functional diversity on their community biomasses. The trait-independent/trait-dependent complementarity effect and the dominance effect were partitioned qualitatively to elucidate the underlying mechanisms for the diversity effect on community biomass. The aim of our experimental study was to test whether community overyielding and underyielding emerge from the relationship between the biomass of the individual species and their biomass in monoculture. Therefore, this relationship was calculated separately for each community to generate a potential framework for the occurrence of community overyielding and underyielding.

3.3. Methods

Species pool and experimental design

The species pool consisted of twelve species (Table 1) which were obtained from the Experimental Phycology and Culture Collection of Algae (SAG, Göttingen, Germany). The twelve species are abundant and widespread in lakes where they can co-occur (e.g., mesotrophic Lake Constance, Stüber 1998). Based on their morphological and functional traits, i.e., cell size, motility and demand for silicate (Table 1, Weithoff 2003) they were divided into four functional groups (green algae, phytoflagellates, diatoms, and cyanobacteria). The experimental design included all 12 species in monocultures in duplicate (n=24) and mixtures of two (n=17), four (n=14), eight (n=14) and twelve (n=3) species resulting in a total of 72 microcosms. The species compositions of the 2, 4 and 8 species mixtures were obtained by random selection from the species pool (see Appendix, Table 1). To investigate the effect of functional diversity the number of functional groups was also varied in these mixtures as independently as possible comprising one (n=12), two (n=11), three (n=12) or four (n=13) functional diversity levels.

The culture medium (Nichols 1973) contained 2.5 µM phosphate, 50 µM nitrogen and 5 µM silicate. Our medium was explicitly designed to promote co-limitation by several nutrients and thus, to maintain the target species richness for the duration of the experiment. In the experimental substitutive design, the average total initial biovolume (as a surrogate for biomass, see below) of algal communities was 2 mm^3 L^{-1} for the monocultures and mixtures. Microcosms (Erlenmeyer flasks, 300 mL) contained 150 mL algal suspension and medium was not replenished during the experiment (batch cultivation) to establish strong competition among species. The experiments were performed in a climate chamber at 20 ± 1°C under a 16:8 h light:dark cycle at a light intensity of 73 µM photons cm^{-2} s^{-1}, measured in air. This intensity was below light-saturated conditions but high enough to support exponential phytoplankton growth in monocultures and mixtures. Erlenmeyer flasks were manually shaken twice a day to suspend algae and to avoid algal growth on wall. The position of flasks was randomly altered every other day. Sub-samples for algal biovolume determination (10 mL) were taken on day 0, 4, 8, 12, 16 and 20 and fixed with Lugol´s iodine. At least 600 cells per species and sample were counted (Utermöhl, 1931) under an inverted microscope (Thalheim, Germany) and the size of 30 randomly chosen cells of each species (excluding cyanobacteria) was measured (Hillebrand et al. 1999) at each diversity level and sampling date using the microscope video aided image analyser (Thalheim, Germany).

Calculations and statistical analysis

As a surrogate for biomass the biovolume ($mm^3\ L^{-1}$) of each species in each treatment was estimated by multiplying the number of algal cells by their species-specific cell volumes which was calculated according to the method of Hillebrand et al. (1999). The species-specific growth rates per day were derived by fitting linear regression lines to the logarithm of the biovolume vs. time until a plateau was reached.

The relative fractions of the individual species were calculated as quotient of the biovolume of species *i* observed in mixture (O*i*) and the total biovolume of the corresponding mixture. This observed relative fraction was divided by the expected relative fraction of species *i* in the mixture (1/number of species) to get standardized fractions.

Overyielding at the community level was calculated at the end of the experiment (20 days) by using the relative yield total (*RYT*, see Fridley 2001 and references therein) and the index $D_{\max}$ (Hooper and Dukes 2004). A value of $RYT > 1$ implies non-transgressive overyielding and a value of $D_{\max} > 0$ indicates transgressive overyielding (Loreau 1998). Overyielding at the species level was also calculated at the end of the experiment by using the yield exponent y_i (according to the model of Lambers et al. 2004) which estimates whether a species is an overyielding or underyielding species in its mixture. Values greater than -1 indicate that the species *i* overyields and yield exponents less than -1 imply that species *i* is an underyielding species.

The net biodiversity effect (ΔY) was estimated by the difference between the observed end biovolume of a community and the expected biovolume based on the monoculture biovolume of its component species. The tripartite partition method of Fox (2005) was used to partition the net biodiversity effect into three effects (Equation 1): trait-independent complementarity (first part), dominance (second part) and trait-dependent complementarity (third part):

$$\begin{aligned}\Delta Y &= S * \overline{M} * \overline{RY} \\ &+ S * Cov(M_i, \frac{RY_i}{RYT} - RY_{E,i}) \\ &+ S * Cov(M_i, RY_i - \frac{RY_i}{RYT})\end{aligned} \qquad \text{(Equation 1)}$$

where S is the number of species in the mixture, $\overline{M}$ is the averaged monoculture biovolume, $\overline{RY} = \frac{1}{S} * \sum_{i=1}^{S} RY_i$ is the average relative yield of the

species in mixture with $RY_i = \frac{O_i}{M_i}$ being the relative yield of species i (O_i is the biovolume of species i observed in the mixture, M_i its biovolume in monoculture), $RY_{E,i} = \frac{1}{S}$ is the expected relative yield of species i in mixture ($\sum_{i=1}^{S} RY_{E,i} = 1$ for a substitutive experimental design as used here) and $RYT = \sum_{i=1}^{S} RY_i$.

The effect size of trait-independent and trait-dependent complementarity is positive when species perform better in mixture than expected based on monoculture biovolumes but not at the expense of other species. The dominance effect quantifies the extent to which a species performs better in mixture than expected based on monoculture biovolume at the expense of other species.

So far, the tripartite partition method (Fox 2005) was used for overyielding communities. In case of underyielding at the community level (i.e., RYT < 1) the term of the trait-dependent complementarity $RY_i - \frac{RY_i}{RYT}$ is negative. This was found for 10 communities in the present study. In general, the absolute value of this term increases with increasing values of RY_i which implies for underyielding that the term becomes more negative for higher values of RY_i. As a consequence, the covariance between M_i and $RY_i - \frac{RY_i}{RYT}$ is positive when species with *low* monoculture biovolumes obtain high relative yields in mixture. This stands in contrast to the previously established interpretation appropriate for overyielding communities (Fox 2005) where a positive covariance indicates that species with *high* monoculture biovolumes attain high relative yields in mixture. Hence, for communities with *RYT* < 1 (n=10 in this study) the values of the trait-dependent complementarity were multiplying by -1 enabling an interpretation of the TDC independent of the underyielding or overyielding status of the communities.

The statistical analyses were performed using SPSS (version 14). To test the effect of species diversity and functional diversity (1) on community end biovolumes, (2) on the relative yield total, (3) on $D_{\max}$, (4) on the net biodiversity effect, (5) on the three parts of the net biodiversity effect , (6) on the yield exponent, and (7) to test the effect of the species-specific growth rates on the end biovolumes of the individual species in monoculture and mixture non-parametric Spearman's rank correlation coefficients (r_S) were

calculated. Differences between community biovolumes, *RYT*, D_{max}, ΔY, and the three parts of the net biodiversity effect were tested using the non-parametric Kruskalis-Wallis test (x^2) or the Mann-Whitney U (U) test.

3.4. Results

Temporal dynamics of monocultures and mixtures

The total biovolume of monocultures and mixtures increased exponentially until almost constant biovolumes were reached after 8 to 12 days (Fig 1). During this period of exponential growth, the algal growth rates had a mean (±SD) of 0.37 ± 0.28 d^{-1} (averaged over all treatments and species) allowing on average for 5.3 ± 3.04 generations in monoculture and mixture. After reaching the plateau, algal growth rates were close to zero (0.002 ± 0.07 d^{-1}, averaged over all treatments and species from day 8-20) indicating intra- and interspecific competition within the communities until the end of the experiment. Thus, an experimental duration time of 20 days was sufficient to analyse potential aspects of overyielding at the community and species level.

Overyielding at the community level

Total community biovolume was positively correlated with species diversity (Fig 2a, r_S=0.36, P=0.01) and functional diversity (Fig 2b, r_S =0.32, P=0.03). The presence of the high-productive cyanobacterium *Cylindrospermopsis raciborskii* (Cyl) affected the total community biovolumes: they were higher when Cyl was including in mixtures (Fig 2, U=72, P<0.001).

The values of the relative yield total (RYT) were mostly greater than 1 with a mean (± SD) of 1.97 ±1.39 indicating non-transgressive overyielding. The RYT values were positively affected by species diversity (Fig 3a, r_S=0.54, P<0.001) and functional diversity (Fig 3a, r_S=0.57, P<0.001). It was significantly lower at the lowest species diversity level than at the three higher levels (U=94, P<0.001). The values of D_{max} were positive for 31% of the communities indicating transgressive overyielding for these communities without a distinct relationship with species diversity (Fig 3b, r_S=-0.19, P=0.20) and functional diversity (Fig 3b, r_S=-0.06, P=0.70). Positive values of D_{max} occurred more frequently at the 4 species diversity level than at other diversity levels (U=143, P=0.03).

The observed end biovolumes in mixtures were on average 46 mm^3 L^{-1} higher than the ones expected from monocultures and thus, positive values of the net biodiversity effect (ΔY) were mostly found. The values of ΔY were positively correlated with species diversity (Fig 4a, r_S=0.37, P=0.01) and functional diversity (data not shown, r_S=0.36, P=0.01). They were

significantly lower at the lowest species diversity level (U=136, P=0.01) than that at the three higher levels (4, 8 and 12 species).

The three components of ΔY differed significantly (x^2=26, P<0.001) in respect to their average absolute values (Fig 4b). The trait-independent complementarity (mean ± SD, 55.21 ± 88.36) was mostly higher (U=1139, P<0.001) than the trait-dependent complementarity (-10.44 ± 41.08, note the modulation in case of underyielding in the methods) and the dominance effect (-1.53 ± 18.94) whereas the trait-dependent complementarity and the dominance effect did not differ significantly (U=973, P=0.19). The mostly positive values of trait-independent complementarity indicating processes which promote most of the species within the community, were positively correlated with species diversity (Fig 5b, r_S=0.55, P<0.001). The absolute values of the trait-dependent complementarity decreased with increasing species diversity (Fig 5b, r_S= -0.40, P=0.005) and its mostly negative values indicated that species with low monoculture biovolumes became often dominant in mixtures but not at the expense of other species (see modulation in the methods when communities underyielded). The dominance effect was negatively correlated to species diversity (Fig 4b, r_S= -0.43, P=0.002). Its mostly positive values at lower diversity levels indicate that a species with a high monoculture biovolume reached high relative yields in these mixtures and its predominantly negative values at higher diversity levels imply that a species with a low monoculture biovolume attained a high relative yield in the communities at the expense of other species. When removing the lowest species diversity level from the analysis, the trait-independent complementarity was unrelated to species diversity (r_S=0.19, P=0.31) while the trait-dependent complementarity (r_S= -0.37, P=0.04) and the dominance effect (r_S= -0.39, P=0.03) still decreased (Fig 4b).

The effect sizes of the individual mechanisms tended to depend on the yielding status of a community, i.e., whether the phytoplankton community exhibited underyielding (n=9, RYT<1), non-transgressive overyielding (n=24, RYT> 1, D_{max}< 0) or transgressive overyielding (n=15, RYT> 1, D_{max}> 0), respectively (Fig 4c, trait-independent complementarity: x^2=22, P<0.001; trait-dependent complementarity: x^2=9, P=0.03, dominance effect: x^2=5, P=0.09). Underyielding mostly resulted from a negative trait-independent and trait-dependent complementarity (Fig 4c) while both non-transgressive and transgressive overyielding were mainly caused by a positive trait-independent complementarity (Fig 4c) which did not differ between the two kinds of overyielding (U=138, P=0.47). The effect sizes of the trait-dependent complementarity and the dominance effect were positive for transgressive and negative for non-transgressive overyielding (Fig 4c).

Overyielding at the species level

The different species exhibited a continuum from overyielding to underyielding (Fig 5a). While the green algae only consisted of overyielding species the other three functional groups included both over- and underyielding species. The mean (± SD) yield exponent of *Asterionella formosa* (As, 0.07± 0.62), *Chlamydomonas reinhardtii* (Chl, -0.20 ± 0.48), *Monoraphidium minutum* (M, -0.30 ± 0.34), *Cylindrospermopsis raciborskii* (Cyl, -0.66 ± 0.35), *Scenedesmus obliquus* (S, -0.77 ± 0.39), *Haematococcus pluvalis* (H, -0.78 ± 0.55), and *Ankistrodesmus gracilis* (A, -0.94 ± 0.40) were higher than -1 indicating that these species were overyielding species. Underyielding species with values below -1 were *Planktothrix agardhii* (P, -1.36 ± 0.56), *Cyclotella meneghiniana* (Cyc, -1.37 ± 0.51), *Anabaena flos-aquae* (An, -2.11 ± 0.52), *Cryptomonas* sp. (Cry, -2.72 ± 0.95) and *Stephanodiscus minutulus* (St, -3.79 ± 0.95). St was the only species which went extinct in seven out of fourteen 8 species mixtures and in all three 12 species mixtures and thus, its yield exponent could not be calculated at the highest species diversity level.

The yield exponents of some species were either positively or negatively affected by species diversity (Fig 5b). The yield exponent of the overyielding species Chl (r_S= -0.47, P=0.03) and Cyl (r_S= -0.51, P=0.03) decreased with increasing species diversity whereas those of the underyielding species P (r_S=0.59, P=0.01), Cry (r_S=0.85, P<0.001) and St (r_S=0.75, P=0.02) were positively correlated with species diversity. When considering all twelve species together, the Spearman`s rank correlation coefficients between species diversity and yield exponent tended to increase with decreasing mean yield exponent (Fig 5b). That is, the higher the underyielding status of a species is, the more positive is the diversity effect on the yield exponent and *vice versa.*

End biovolumes vs. growth rates

In monoculture and mixtures, the end biovolumes of all species were positively correlated with their growth rates (r_S=0.51, P=0.01 and r_S=0.65, P<0.001, respectively). This indicates that fast-growing species built up high biovolumes and slow-growing species reached low biovolumes in monoculture and mixtures.

In mixture, the standardized fractions of the individual species were positively correlated with their growth rates (Fig. 6, r_S=0.59, P<0.001) and thus, fast-growing species achieved higher biovolumes in mixtures than expected from monocultures. C*ylindrospermopsis raciborskii* reached higher standardized fractions in mixtures than expected from the relationship among the other algal species (Fig 6).

The net biodiversity effect of the phytoplankton communities tended to be positively correlated with the Spearman`s rank correlation coefficient (r_S) between the biovolume of the individual species and their growth rate in

monoculture (Fig 7a, including data from Schmidtke et al. 2009). Pronounced positive net biodiversity effects only occurred when the rank correlation coefficient (r_S) between the biovolume of the component species and their growth rate in monoculture was higher than 0 (Fig 7a). This pattern became more obvious when the 2 species mixtures were excluded from the analyses.

3.5. Discussion

Overyielding and underyielding in phytoplankton communities

The diversity effect on community biomass has emerged as a major field within the biodiversity-ecosystem functioning debate. To date, rather positive (reviewed by Balvanera et al. 2006, Cardinale et al. 2006, 2007, Zhang & Zhang 2006a, b, Weis et al. 2008) than negative (Hooper and Vitousek 1997, Weis et al. 2007, Schmidtke et al. 2009) relationships were found in terrestrial and aquatic ecosystems. In the present study, 77% of the phytoplankton communities exhibited overyielding (net biodiversity effect >0) and 23% of these communities showed underyielding. We suggest that this pattern of different diversity-community biomass relationships can be derived from different relationships between the biomass of the individual species and their growth rate in monoculture, at least for more diverse phytoplankton communities (Fig 7b). Community overyielding was frequently found when biovolumes and growth rates of the component species in monoculture were positively correlated (Fig 7b) promoting high abundances of fast-growing and high-productive species in mixtures. A negative relationship can lead to community underyielding and in this case, one or more fast-growing and low-productive species will become abundant in mixtures (Schmidtke et al. 2009). We conclude that overyielding and underyielding of more diverse phytoplankton communities emerged from the relationship between biomass and growth rate of the component species in monoculture.

At a temporal scale, our findings are supported by a study of Weis et al. (2007). Using three phytoplankton species in batch, community overyielding was detected after an experimental duration time of 9 days. This overyielding was caused by the dominance of a fast-growing and high-productive green algal species. After 23 days, however, the communities underyielded because a slow-growing and low-productive species became competitively superior to the two fast-growing ones and thus, dominated the community at the end of the experiment. In our study, such strong changes in species composition did not occur since the slow-growing species did not outcompete fast-growing ones until the end of the experiment. Rather, most species maintained an almost constant biomass plateau throughout the experiment (21 days) which prevented a potential transition from

community overyielding to underyielding. Presumably, fast-growing species quickly incorporated most of the nutrients which were consequently not available for slow-growing ones since no rapid nutrient-turnover occurred in our batch microcosms. In more complex communities with multiple trophic levels, especially small and fast-growing species may experience high losses, e.g., by grazing. This will ensure a continuous nutrient availability for all species promoting shifts in the community composition which in turn, may influence the degree of overyielding in a long run. Hence, our findings are generaliseable to other communities and systems as long as the initial community structure prevails.

Community overyielding was mainly caused by the complementarity effect

In the present study, the trait-independent complementarity (TIC) contributed most to the observed community overyielding, indicating that many species performed better in mixture than in monoculture but not at the expense of other species. This can be the result of resource use complementarity and/or facilitative interactions among component species. Complementarity generally arises from species-specific differences in the spatial-temporal use of resources, in the requirements of resources, or in the ratios of resource demands. Zhang and Zhang (2006b) argued that resource use complementarity is more important in grassland communities while facilitation is stronger in algal communities. Facilitative interactions can also be enhanced in high-stress and nutrient-poor environments (Callaway and Walker 1997, Mulder et al. 2001, Callaway et al. 2002) and thus, facilitation might play an important role in our nutrient-limited phytoplankton communities. However, we assumed that both facilitation and resource use complementarity attributed to the large amount of the TIC in our study although their underlying mechanisms are less clear for free-floating phytoplankton communities than for substrate-bound plants.

The trait-dependent complementarity (TDC) and the dominance effect (D) contributed less to community overyielding but they explained why 31% of the algal communities exhibited transgressive overyielding (RYT>1 and $D_{\max}$>0) in our experiment. Before plant mixtures begin to yield more biomass than the most productive monoculture, a high degree of complementarity is needed (Cardinale et al. 2008). This is in concordance with the present study where total complementarity (TIC+TDC) among species was higher for transgressive overyielding (78 ± 80, mean ± SD) than for non-transgressive overyielding (44 ± 52, mean ± SD) communities. In addition, non-transgressive overyielding communities were characterized by the dominance of a low-productive species at the expense of other ones whereas in transgressive-overyielding communities a high-productive species became dominant at the expense of other species. This mainly caused the weaker positive net biodiversity effect in the phytoplankton

communities with non-transgressive overyielding (42± 45) compared to transgressive overyielding communities (88 ±81).
Some phytoplankton communities exhibited underyielding in the present study which was mainly caused by a negative trait-independent complementarity (TIC). Thus, interspecific competition or some other processes with the same effect within these phytoplankton communities lead to their underyielding.

The magnitude of the three above-mentioned mechanisms can vary with diversity (Fox 2005). The species diversity effect on the net biodiversity effect exhibited a positive relationship until the 4 species diversity level and tended to decrease subsequently in our study. This decrease at higher diversity levels (4-12 species) was caused by the increasing occurrence of one or more low-productive species (D, TDC) with increasing species diversity while the trait-independent complementarity (TIC) remained almost constant.
We found that species diversity can positively or negatively affect the species-specific yield exponent. Underyielding species (often slow-growing and low-productive) underyielded less and most of the overyielding species (often fast-growing and high-productive) overyielded less in more diverse communities. This indicates that underyielding species benefitted from higher and overyielding species from lower interspecific competition. The importance of a reduced intraspecific competition in more diverse communities which could increase the potential for resource use complementarity was probably enhanced for the underyielding species whereas it remained low for the overyielding species. Complementarity is strongly based on differences in functional traits of the species (Hooper and Vitousek 1997, Tilman et al. 1997, Hooper 1998, Mikola and Setälä 1998). While most of the overyielding species belonged to the same functional group (green algae), underyielding species belonged to different functional groups. This supports that the increasing species diversity did not enhance the likelihood for resource use complementarity among overyielding species due to their functional similarity. Contrary, it seemed to be higher for underyielding species in more diverse communities supporting an increasing abundance of low-productive species with increasing species diversity.

Functional diversity is of minor importance for overyielding
The consequences of N-fixation by legumes or cyanobacteria received great attention in the context of facilitative interactions in biodiversity studies (Huston 1997, Huston et al. 2000, Fridley 2001). In the present study, both community biomasses and the relative yield total (RYT) were enhanced at higher functional diversity levels and communities with the cyanobacterium Cy*lindrospermopsis raciborskii* (Cyl, n=30) had higher biomasses than communities without Cyl (n=18). Cyl can potentially act as a facilitator in

our communities due to N-fixation (Présing et al. 1996) but the other species reached the same biomasses in communities with and without it. Thus, the presence of *Cylindrospermopsis raciborskii* did not stimulate the biomasses of other species indicating no facilitation by this species. Rather, the presence of Cyl which was the most productive species in monoculture, increased the community biomass directly by its much higher biomasses than of the other species of these mixtures. The probability of including the high-productive species *Cylindrospermopsis raciborskii* in the community increased stronger for increasing functional diversity than for species diversity which may have caused the linear positive relationship between functional diversity and community biomass. However, at a given species level, functional diversity did not affect community biovolume and RYT (data not shown). The effect of functional diversity can be outweighed by large differences in species-specific rates of productivity (Bruno et al. 2005, 2006, Griffin et al. 2009) and species used in this study differed greatly in their carrying capacities and growth rates. These differences tended to be higher within than among functional groups explaining the lack of a functional diversity effect at fixed species diversities.

Our findings derived from microcosms fitted well with those from field studies of *Cylindrospermopsis raciborskii* (Cyl). Cyl is known to be a successful invasive species in temperate regions of Europe originating from tropical areas (Padisák 1997) and to be competitively superior to many other species due to its strong competitive abilities for phosphorous and nitrogen (Istvánovics et al. 2000, Burford et al. 2006). In our study, *Cylindrospermopsis raciborskii* became more dominant than expected in more diverse communities. It reached high biomasses in all mixtures with moderate growth rates (0.35 ± 0.05 SD) which were slightly higher than those in the field (0.15-0.28 d^{-1}, Wiedner et al. 2007) supporting its high potential to invade species-rich phytoplankton communities.

Conclusion

This experimental study revealed a positive effect of species/functional diversity on the biomass of phytoplankton communities. Most of the communities showed overyielding and only some communities underyielded. The overyielding of the phytoplankton communities was mainly caused by a positive trait-independent complementarity effect which can be attributed to resource use complementarity and/or facilitative interactions among the component species. Community overyielding of more diverse communities was frequently found when the biomass of the component species and their growth rates were positively correlated in monoculture. In this case, fast-growing and high-productive species become dominant whereas slow-growing and low-productive species are less abundant in mixtures. Including data from a previous study in the analyses, community underyielding was mostly observed when the biovolumes of the component species were negatively affected by their

growth rates in monoculture. This emergent pattern from monocultures might be generaliseable to communities of other ecosystems but further comparable research is needed to support our conceptual framework for the occurrence of community overyielding and underyielding.

3.6. Acknowledgement

We wish to thank Melanie Hartwich, Ina Wiegand and Maike Piepho for counting phytoplankton samples. Andrea Schmidtke conducted this work as part of her PhD funded by the German Research Foundation (DFG contract GA 401/10-1).

3.7. Tables

TABLE 1: Species pool and the assignment of species to the four functional groups based on mean cell size (*growing in WC-limited medium, 14 days), motility and demand for silica (Weihoff 2003).

Species	Abbr.	Functional group	Cell size* (μm^3)	Motility	Demand for silica
Monoraphidium minutum	M	Green algae	8	_	_
Ankistrodesmus gracilis	A	Green algae	17	_	_
Scenedesmus obliquus	S	Green algae	49	_	_
Cryptomonas sp. (SAG 26.80)	Cry	Phytoflagellates	326	+ (flagella)	_
Chlamydomonas reinhardtii	Chl	Phytoflagellates	251	+ (flagella)	_
Haematococcus pluvalis	H	Phytoflagellates	1977	+ (flagella)	_
Cyclotella meneghiniana	Cyc	Diatoms	349	_	+
Stephanodiscus minutulus	St	Diatoms	100	_	+
Asterionella formosa	As	Diatoms	252	_	+
Planktothrix agardhii (non N-fixer)	P	Cyanobacteria	4941	+ (gas vacuoles)	_
Anabaena flos-aquae (N-fixer)	An	Cyanobacteria	327	+ (gas vacuoles)	_
Cylindrospermopsis raciborskii (N-fixer)	Cyl	Cyanobacteria	306	+ (gas vacuoles)	_

3.8. Figures

FIGURE 1: The mean biovolume of monocultures and mixtures over experimental time.

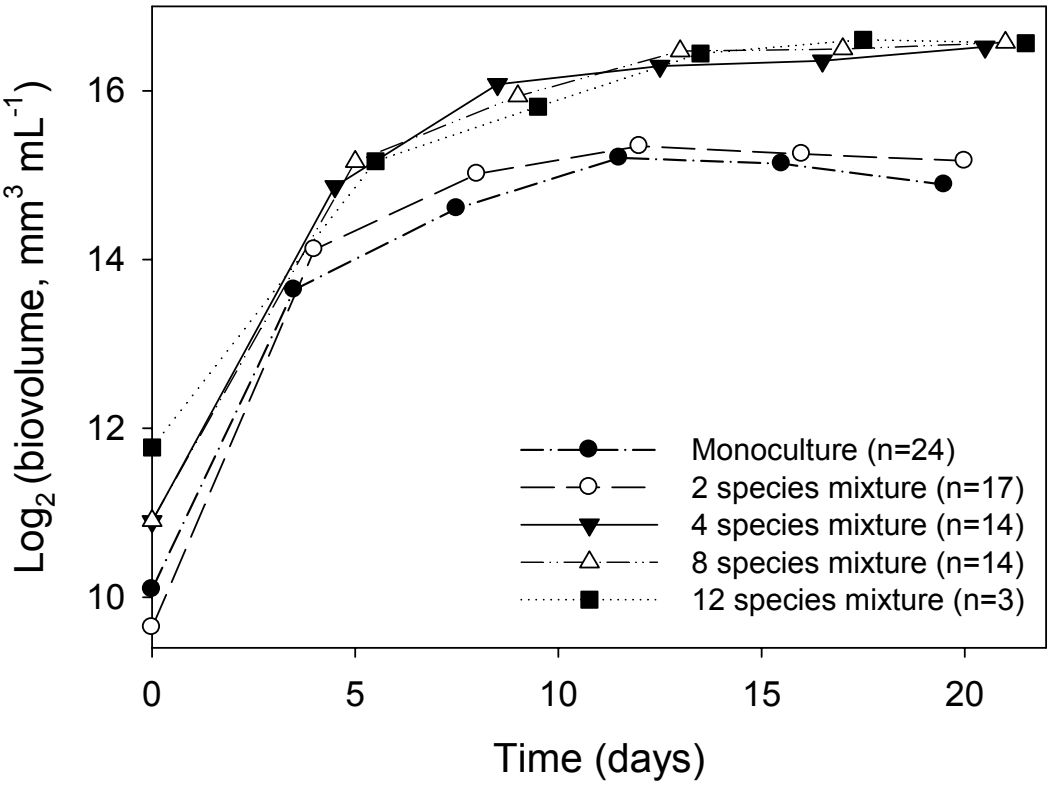


FIGURE 2: End biovolumes of the monocultures (M) and mixtures depending on (a) species diversity and (b) functional diversity. Open circles indicate community biovolumes without the cyanobacterium *Cylindrospermopsis raciborskii* (Cyl).

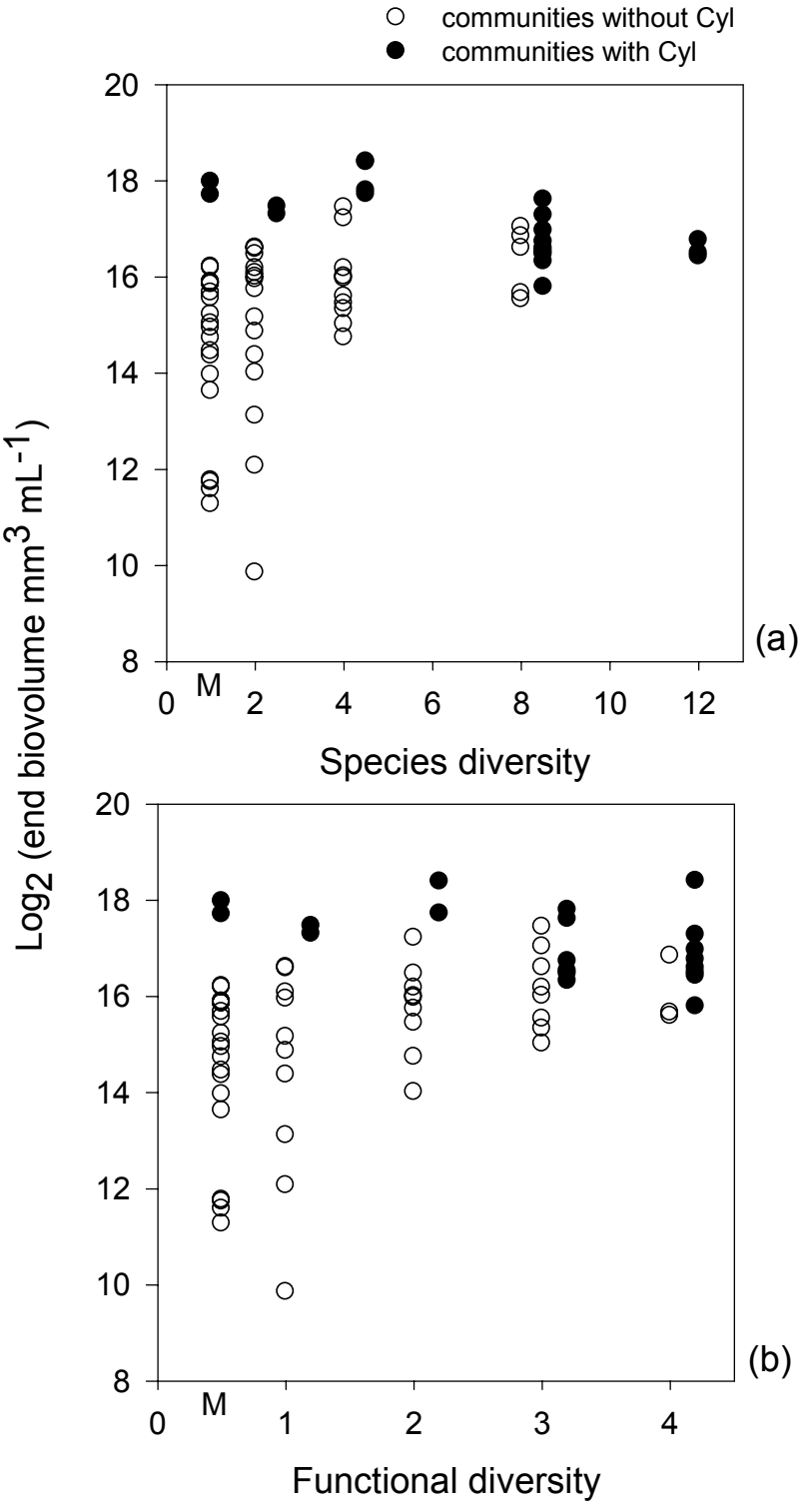


FIGURE 3: Effect of species diversity (left) and functional diversity (right) on (a) relative yield total (RYT) and (b) D_{max} of the mixtures. The solid lines represent (a) the RYT value above which non-transgressive overyielding occurs and (b) the D_{max} value above which transgressive overyielding occurs. Error bars indicate standard deviations.

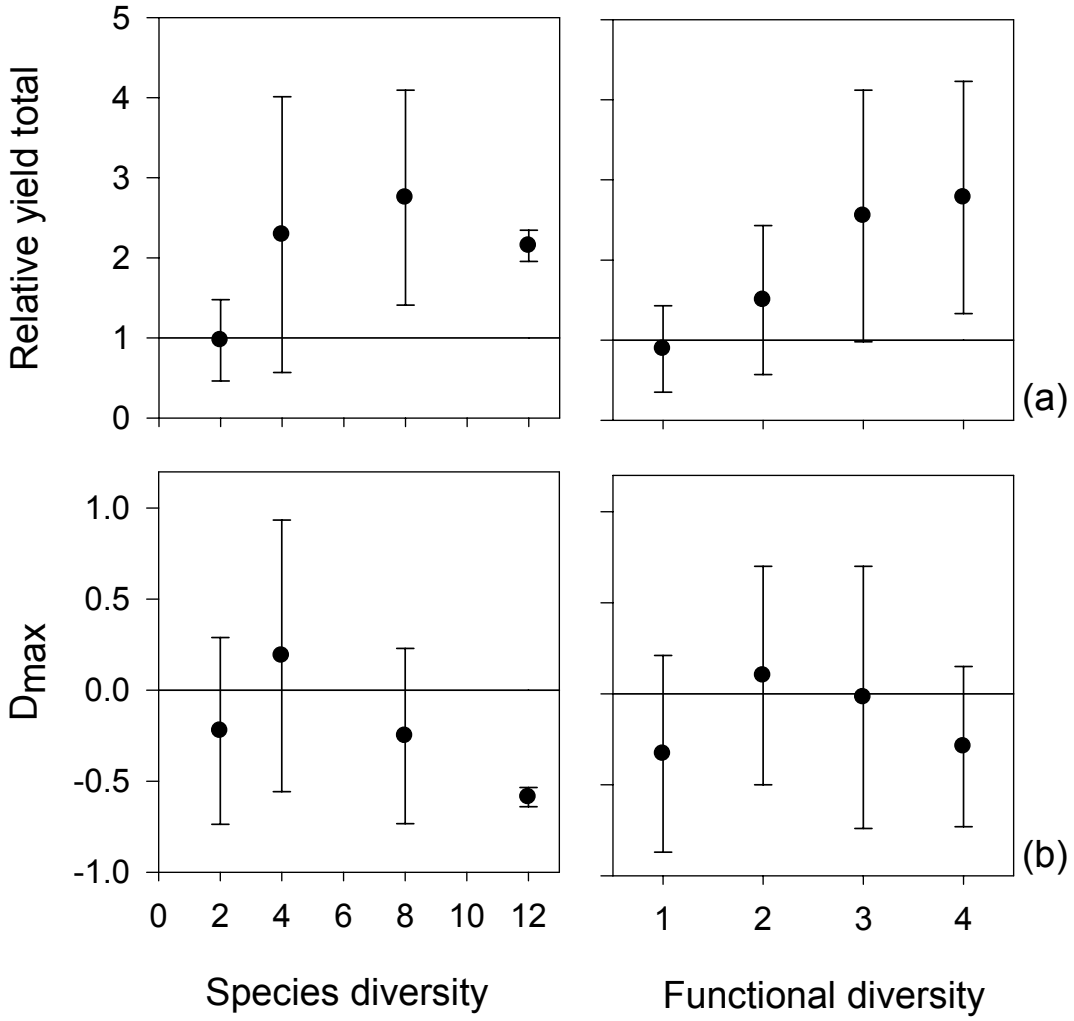


FIGURE 4: (a) Net biodiversity effect and (b) effect sizes of the trait-independent (TIC) and trait-dependent (TDC) complementarity, and of the dominance effect (D) depending on species diversity. (c) Effect sizes of TIC, TDC, and D of communities showing underyielding (UY, RYT<1), non-transgressive overyielding (NTOY, RYT>1), and transgressive overyielding (TOY, RYT>1, D_{max}>0).

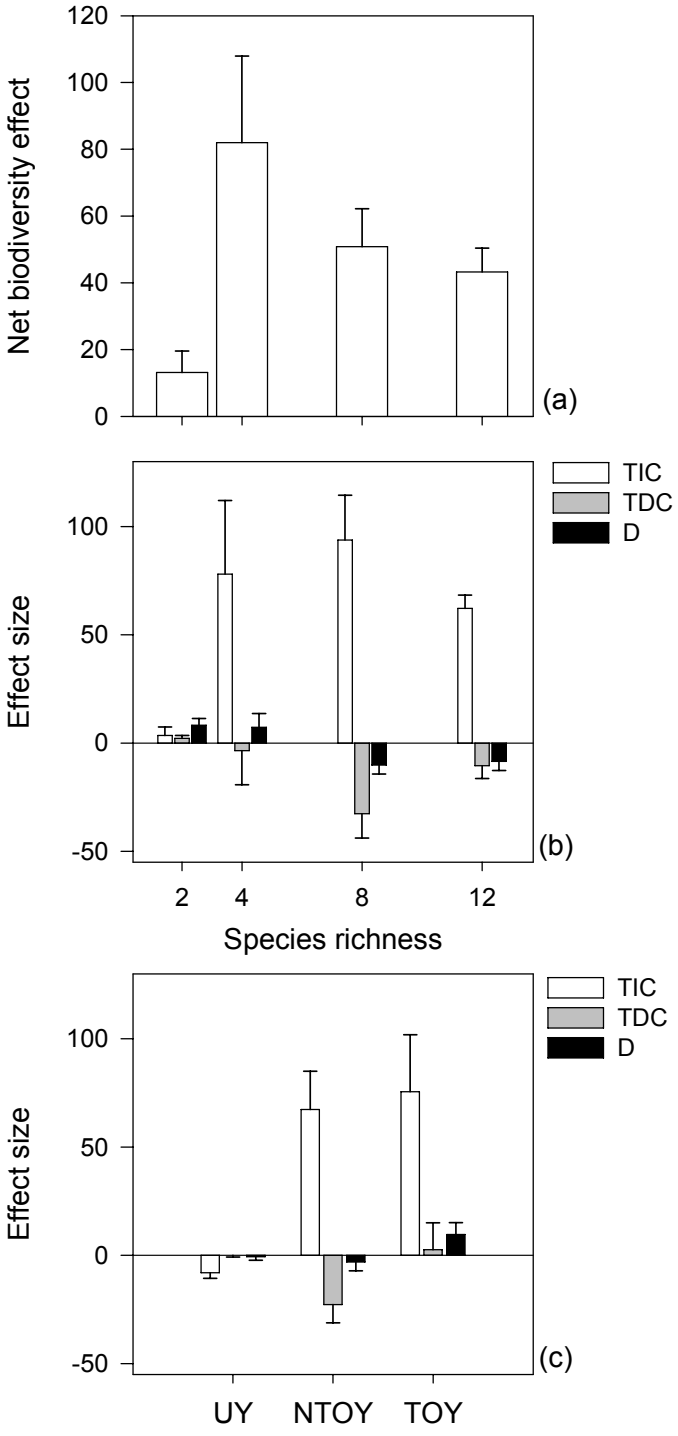


FIGURE 5: (a) Mean yield exponents of the individual species for the 2, 4, 8 and 12 species diversity levels and (b) Spearman´s rank correlation coefficients (r_S) of the regression of the species-specific yield exponents against species diversity for the individual species. Squares for diatoms, diamonds for phytoflagellates, circles for green algae, and triangles for cyanobacteria. Species were ordered according to their mean yield exponent (As=*Asterionella formosa*, Chl=*Chlamydomonas reinhardtii,* M=*Monoraphidium minutum,* S=*Scenedesmus obliquus*, H=*Haematococcus pluvalis,* Cyl=*Cylindrospermopsis raciborskii*, A=*Ankistrodesmus gracilis,* P=*Planktothrix agardhii,* Cyc=*Cyclotella meneghiniana,* An=*Anabaena flos-aquae*, Cry=*Cryptomonas* sp., and St=*Stephanodiscus minutulus* which went extinct at the highest diversity level). Error bars indicate standard deviations and the dashed line represents the yield exponent value above which species overyielded. Negative signs indicate r_S <-0.1, ± stands for -0.1 < r_S < 0.1, and positive signs for r_S >0.1. Asterisks indicate significant effects of species diversity on yield exponents (* P<0.05, ** P<0.01 and *** P < 0.001).

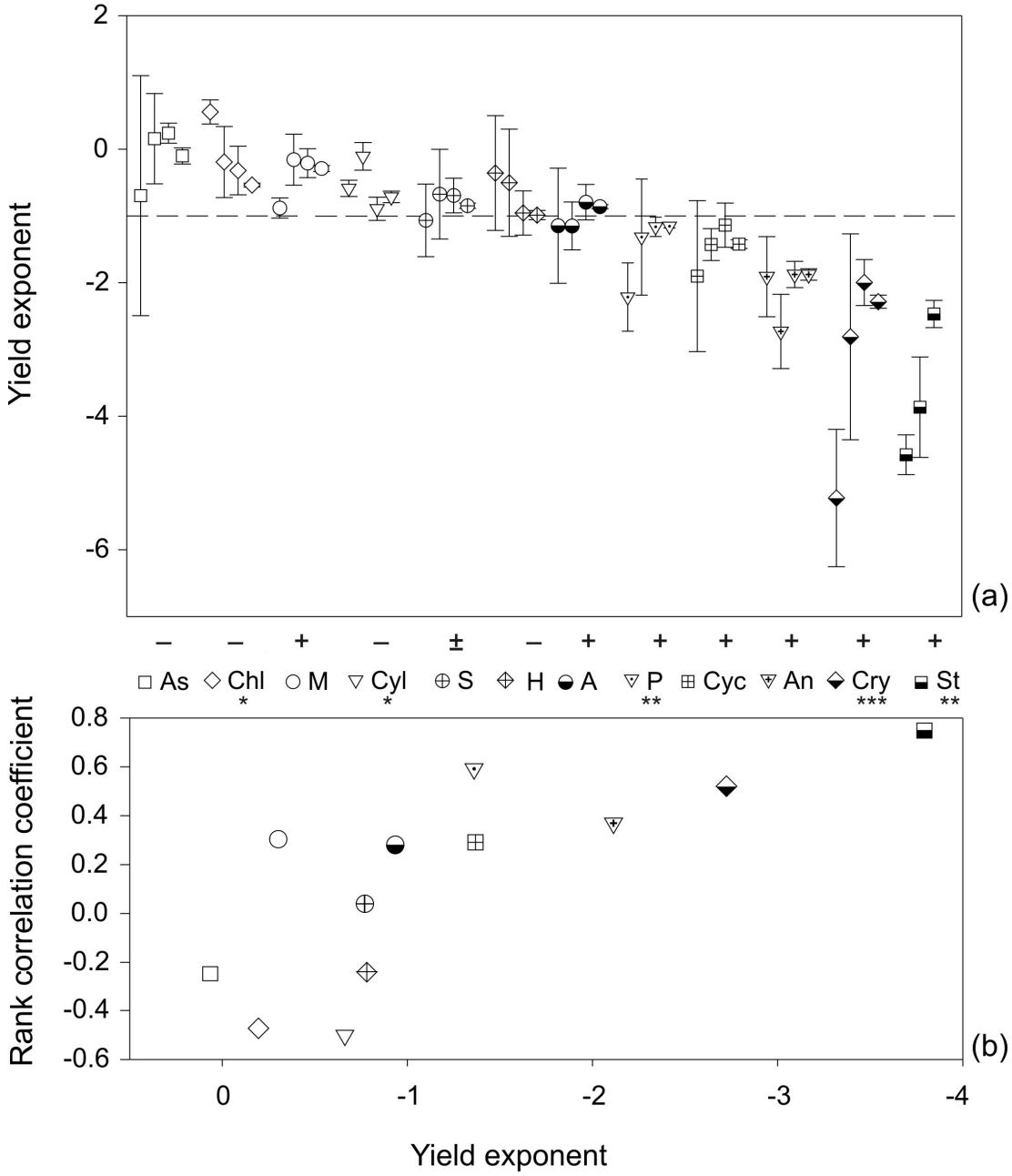

Yield exponent
2
0
-2
-4
-6
(a)
– – + – ± – + + + + + +
As Chl M Cyl S H A P Cyc An Cry St
* * ** *** **
Rank correlation coefficient
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
(b)
0 -1 -2 -3 -4
Yield exponent

FIGURE 6: Standardized fraction (observed/expected relative fraction) of *Cylindrospermopsis raciborskii* and the other individual species in mixtures depending on their growth rates (excluding *Stephanodiscus minutulus* which went extinct in 10 mixtures).

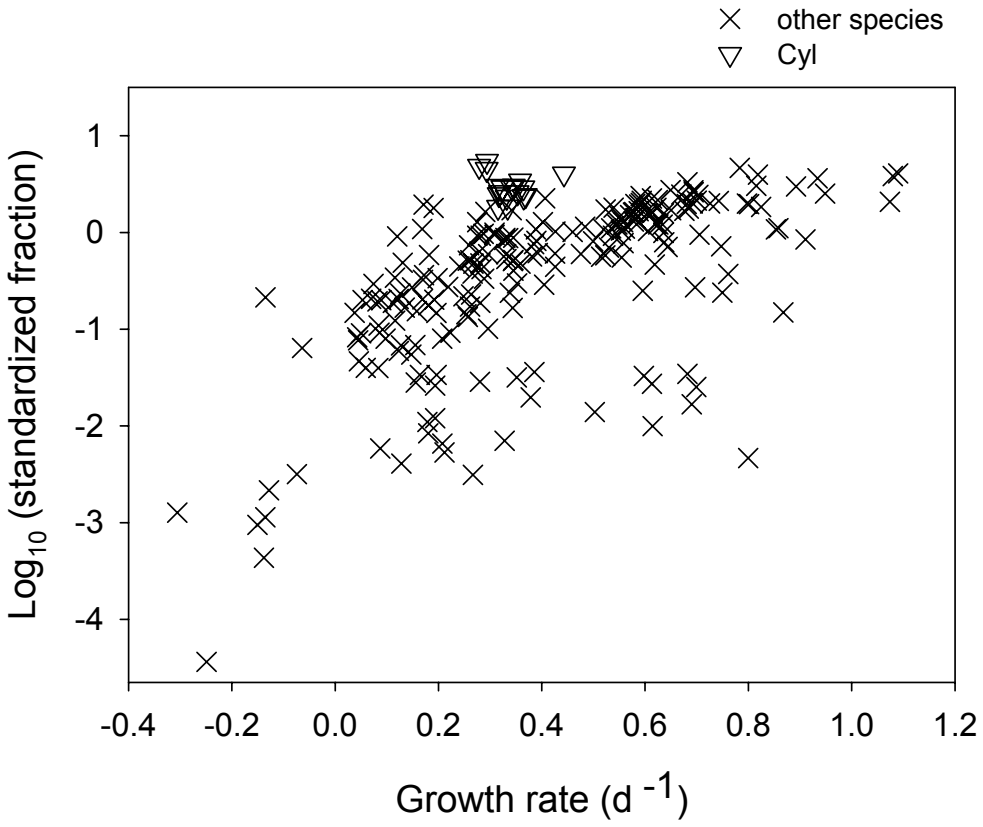
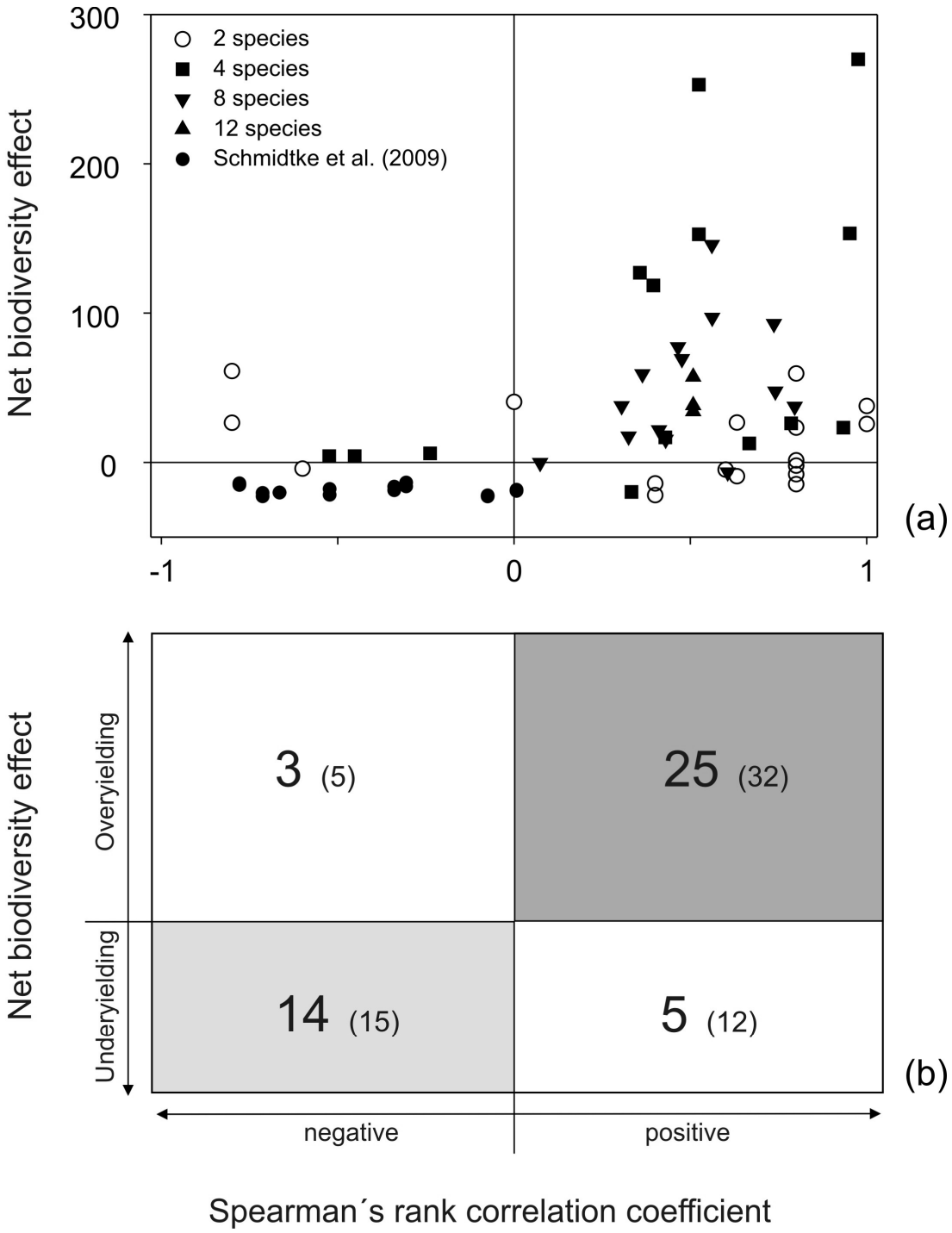


FIGURE 7: (a) Relationship between net biodiversity effect and Spearman´s rank correlation coefficient (correlation between the end biovolumes of the component species and their growth rates in monoculture). In the dataset of Schmidtke et al. (2009), all phytoplankton communities consisting of 1-4 functional groups and 5-8 species showed underyielding. (b) Scheme presenting a framework for the occurrence of community overyielding and underyielding. The numbers in the four quadrants provide the number of the respective communities based on the dataset of Fig 7a excluding the two species mixtures (numbers in brackets include all communities). The relationship between the end biovolumes of the component species and their growth rate in monoculture can promote community overyielding and underyielding, respectively. When fast-growing species reached high biovolumes in monoculture (positive Spearman´s rank correlation coefficient) communities tended to overyield. Community underyielding is promoted when fast-growing species build up low biovolumes in monoculture (negative Spearman´s rank correlation coefficient).


300
200
100
0
-1
0
1
2 species
4 species
8 species
12 species
Schmidtke et al. (2009)
Net biodiversity effect
(a)
Overyielding
Underyielding
3 (5)
25 (32)
14 (15)
5 (12)
negative
positive
Net biodiversity effect
(b)
Spearman´s rank correlation coefficient

3.9. Appendix

TABLE 1: Species compositions of the different species diversity and functional diversity (FD) levels. Spe=species (M=*Monoraphidium minutum*, A=*Ankistrodesmus gracilis*, S=*Scenedesmus obliquus*, Cry=*Cryptomonas* sp., Chl=*Chlamydomonas reinhardtii*, H=*Haematococcus pluvalis*, Cyc=*Cyclotella meneghiniana*, St=*Stephanodiscus minutulus*, As=*Asterionella formosa*, P=*Planktothrix agardhii*, An=*Anabaena flos-aquae*, Cyl=*Cylindrospermopsis raciborskii*). FG= functional group (gre=green algae, flag=phytoflagellates, dia=diatoms, cya=cyanobacteria).

Spe	FG	2 species mixture																4 species mixture														8 species mixture													
M	gre	x		x									x					x		x			x			x	x					x		x	x			x	x	x	x			x	x	x
A		x	x											x				x	x					x								x	x	x	x			x			x	x			x
S			x	x											x				x	x				x								x	x	x	x			x	x	x		x	x	x	
Cry	flag				x		x						x					x			x		x			x					x	x	x		x	x			x	x		x	x	
Chl					x	x										x		x		x		x	x			x		x		x	x	x	x	x	x				x	x	x		x	
H						x	x										x			x	x			x				x		x	x	x	x	x	x			x		x		x	x	
Cyc	dia							x		x				x				x		x			x			x					x	x		x	x		x	x	x			x	x	
St								x	x							x		x			x		x			x					x	x		x	x	x	x		x	x	x		x	
As									x	x										x		x		x	x			x				x		x	x	x		x	x	x			
P	cya										x		x			x				x		x		x									x	x		x	x	x	x	x		x	x	
An											x	x					x			x			x	x		x		x				x	x	x	x	x	x		x	x		x	x	
Cyl												x	x					x	x			x			x			x					x	x	x	x	x	x		x	x			x	
	FD	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	4	4	4	4	3	3	3	3	3	3	3	3	4	4	4	4	4	4

Chapter IV

Productivity, herbivory and species' traits and identity rather than diversity influence the invasibility of phytoplankton communities

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4.1. Abstract

Biological invasions are a major threat to natural biodiversity; hence, understanding the mechanisms underlying invasibility (i.e., the susceptibility of a community to invasion by new species) is crucial. Invasibility may be affected by a complex but hitherto hardly understood interplay of 1) productivity, 2) herbivory, 3) diversity, and 4) the characteristics of the invasive and resident species. Using semi-continuous microcosms, we investigated the effect of nutrient supply and diversity on the invasibility of phytoplankton communities in the presence or absence of an herbivore by introducing two functionally different algal species. With increasing nutrient supply, the productivity of microcosms increased resulting in higher herbivore abundances. Along this gradient, the invasibility for both invaders showed a unimodal pattern. At low productivity (i.e., very low influence of herbivory), the invasibility depended mainly on the competitive abilities of the invaders, whereas at high productivity the susceptibility to herbivory dominated. This resulted in different maxima of the unimodal pattern along the nutrient gradient of the two invading species due to their different functional traits. To test the effect of diversity on invasibility, a diversity gradient was generated by random selection of species from a resident species pool at an intermediate nutrient level. Invasibility was not affected by diversity; instead, it was driven by the functional traits of the resident and/or invasive species mediated by herbivore density. Our results suggest that the strength of herbivory mediated by productivity has a major impact on the invasibility of phytoplankton communities in conjunction with the functional traits of both the resident and invasive species, while diversity plays a minor role.

4.2. Introduction

Biological invasions are an important aspect of human-caused global environmental change (Vitousek et al. 1997). After habitat loss, invasive species are considered as the most important threat to biodiversity for terrestrial and freshwater ecosystems (Wilcove et al. 1998) and may alter the functioning of these ecosystems with potentially large negative impacts, both environmentally and economically (Mack et al. 2000). Communities differ in their susceptibility to invasions and the reasons for these differences have been intensely investigated in the past decade (Levine et al. 2004; Fridley et al. 2007). An understanding of the underlying mechanisms is crucial for the development of management strategies to control invasions (Huston 2004) which holds true, in particular for lakes, where the greatest impact of introduced species on diversity is expected (Sala et al. 2000).

Three main factors have been described to drive invasions of species, 1) the number of propagules arriving at the new habitat (propagule pressure), 2) the characteristics of the invading species, and 3) the susceptibility of the community to invasions by new species which is termed invasibility (Lonsdale 1999). The invasibility of a community is affected by many factors, such as resource availability and productivity (Davis and Pelsor 2001; Jiang and Morin 2004), herbivory and predation (Maron and Vilá 2001; Shea and Chesson 2002), presence of facilitative species (Maron and Conners 1996) and the competitive abilities of the resident species (Kennedy et al. 2002). Most of these factors may also influence the diversity of communities which can lead to positive invasibility-diversity-relationships at a broad spatial scale (Levine 2000; Naeem et al. 2000; Foster et al. 2002). At smaller scale, high diversity may reduce the invasibility via an increased probability for the occurrence of highly competitive resident species (sampling/selection effect) or an enhanced resource use complementarity of the resident community (Wardle 2001), leading to negative invasibility-diversity-relationships (Kennedy et al. 2002; Fargione and Tilman 2005).

We hypothesize that the invasibility of phytoplankton communities increases with increasing productivity of a community, since enhanced resource supply or a reduced resource uptake mediated by consumers can promote the necessary resource availability for invading species (Davis et al. 2000). If the community diversity exhibits a similar response to productivity as the invasibility, than a positive invasibility-diversity-relationship emerge. Contrary, we expect that invasibility decreases with increasing diversity due to stronger resource use of the resident community with increasing diversity (Naeem et al. 2000; Fargione and Tilman 2005) leading to a negative invasibility-diversity-relationship.

There are variable relationships between productivity and diversity in natural communities (positive, negative, unimodal, u-shaped, none) and these patterns differ depending on habitat type, taxonomic group and spatial scale (Waide et al. 1999; Chase and Leibold 2002). For example, in lake communities unimodal relationships dominated (Dodson et al. 2000), whereas in terrestrial plant communities positive relationships are likely to prevail (Gillman and Wright 2006). Factors that influence diversity and interact with productivity, such as disturbance (Huston 2004) or consumption (Worm et al. 2002), may differentially influence the productivity-diversity-relationships and especially in pelagic food webs consumption plays a leading role. Hence, we ask how consumption is influenced by productivity and how this dependency shapes the productivity-diversity-relationship.

Many experimental studies examined the effects of productivity and diversity on invasibility in the absence of herbivores, although herbivory

may have strong impacts on diversity and/or invasibility (Proulx and Mazumder 1998; Sommer 1999; Maron and Vilá 2001). Since productivity and herbivory may have opposing effects on diversity (Hillebrand 2003) and, therefore, potentially also on invasibility, the productivity-diversity (invasibility)-relationships may vary depending on the abundance, efficiency, selectivity and functional or numerical response of the herbivores (Maron and Vilá 2001). Individual factors (productivity, herbivory, diversity) do not only directly influence invasibility but potentially interact with each other, e.g., productivity typically enhances herbivore abundance. This, in turn, may alter the observed response of invasibility to these factors. To further improve our knowledge about potentially co-varying factors influencing invasibility, we need experiments in which these factors are varied in a broad range of reasonable combinations.

In the present study, we examined the influence of nutrient supply, diversity and herbivory on the invasibility of phytoplankton communities in semi-continuous microcosms by introducing two functionally different invaders. The aim of our study was to assess the effects of these three factors potentially driving the invasibility in a pelagic environment for two invasive species strongly differing in their functional traits.

4.3. Methods

Experimental design and microcosm assembly

We designed two experimental series with herbivory, 1) a productivity experiment by varying the nutrient supply and 2) a diversity experiment by varying the number and composition of resident species. Additional experiments without herbivores were designed to assess the invasibility of communities, when competition for resources plays the dominant role. The experiments were run in the same manner: We established aquatic microcosms by inoculating phytoplankton species, the key primary producers in most lakes and oceans, in the presence or absence of a generalist herbivore. Erlenmeyer flasks (300 ml) were filled with 100 ml of modified sterile freshwater medium, WC (Nichols 1973; buffered with 0.476 g l^{-1} HEPES), and inoculated immediately with a target phytoplankton community (day 0). The community was composed from a pool of 10 species of different phyla and with widely differing functional traits such as maximum growth rate, susceptibility to grazing, affinity to nutrients, silicate demand, ability to fix nitrogen and motility: *Navicula pelliculosa* (Bacillariophyta), *Scenedesmus obliquus* (Chlorophyta), *Ankistrodesmus gracilis* (Chlorophyta), *Oocystis marsonii* (Chlorophyta), *Monoraphidium minutum* (Chlorophyta), *Chlamydomonas reinhardtii* (Chlorophyta), *Chlorella vulgaris* (Chlorophyta), *Anabaena flos-aquae* (Cyanobacteria) all from Göttinger Culture Collection (Göttingen/Germany), *Planktothrix agardhii*

(Cyanobacteria, from Norwegian Institute for Water Research, Oslo/Norway) and *Asterionella formosa* (Bacillariophyta, provided by A. Nicklisch, Humboldt-University of Berlin/Germany). The resident communities started with a relatively small inoculum (1.1 µg fresh weight ml^{-1}, calculated from the biovolume of each phytoplankton species, see below) with an equal proportion of the selected species. Treatments with herbivory were subsequently inoculated with the filter feeding rotifer *Brachionus calyciflorus*, which feeds albeit on all phytoplankton species used with different efficiency including the filamentous cyanobacteria (Weithoff and Walz 1995). The experiments were run at 20°C, at a photosynthetic photon flux density (400–700 nm) of 130 µmol m^{-2} s^{-1} and at a light: dark cycle of 14:10 hours. All microcosms were manually shaken twice a day to keep phytoplankton in suspension. Every second day, 20% of the medium was replaced (dilution rate = 0.1 d^{-1}) and the relative fluorescence as an approximation of the algal biomass was fluorometrically measured using a Turner Designs TD700 fluorometer with a 436 nm excitation and 680 nm emission filter set. Furthermore, at all sampling days the density of herbivores was determined with a stereo microscope (ZEISS Stemi 2000).

In treatments with herbivory, the initial peak of algal biomass was followed by a high peak in herbivore density (see Appendix). To prevent invasive species from extinction due to transient high grazing pressure during the first two weeks of the experiment, the invaders were introduced at day 14 when algal biomass increased again after the decline of the herbivores (i.e., when transient dynamics were attenuated). During the invasion period, i.e., from the day when the invaders were introduced (day 14) to the end of the experiment (day 36), the strength of herbivory was assessed as the $\log_{10}$ of the mean density of *B. calyciflorus* (individuals ml^{-1}) at the 12 sampling days (i).

$$\text{mean herbivore density} = \log_{10}\left(\frac{1}{12}\sum_{i=14}^{36}(B.\,calyciflorus\ \text{ml}^{-1}\ \text{at sampling day}\ i)_i\right) \qquad (1)$$

After the introduction of the invaders at day 14, all experiments were terminated at day 36 resulting in an invasion period of 22 days, allowing for up to 20 generations of the invaders. The biomass of all phytoplankton species was determined as fresh weight at day 14 and day 36 by counting and measuring the cells using an inverted microscope (Thalheim Spezial-Optik) with a computer-aided measuring device. The Shannon-Wiener diversity index (H') of the resident community, which will be named in the following as species diversity and the species richness (S) of the resident community were determined at day 14 and 36. The species diversity (H') considers both the number of species and the evenness in the resident community, whereas the species richness (S) only reflects the species pool.

Invasive species and their traits

As invaders, two functionally different phytoplankton species, *Cylindrospermopsis raciborskii* (Cyanobacteria, provided by C. Wiedner, Institute of Freshwater Ecology and Inland Fisheries in Berlin/Germany) and *Cryptomonas* sp. (Cryptophycophyta, from the Göttinger Culture Collection, Göttingen/Germany), were introduced together at day 14 into all microcosms with relatively small biomasses (0.08 µg fresh weight ml^{-1} of each species) compared to the resident community which ranged from 0.7 – 145 µg fresh weight ml^{-1} in the productivity experiment. *C. raciborskii* is an invasive cyanobacterium in the temperate regions of Europe originating from tropical areas (Padisák 1997). Because of its potential toxicity, it deteriorated the water quality in countries of its origin and is probably less-edible for herbivorous zooplankton due to its filamentous phenotype (Hawkins and Lampert 1989). *C. raciborskii* is characterized by moderate growth rates of 0.41–0.45 d^{-1} in the laboratory at 77.5 µg P l^{-1} (unpublished data) and of 0.15–0.28 d^{-1} in temperate lakes (Wiedner et al. 2007), as well as strong competitive abilities for phosphorus and nitrogen (Istvánovics et al. 2000; Burford et al. 2006). In contrast, species of the genus *Cryptomonas* are fast growing flagellates (growth rate of 0.50-0.77 d^{-1} in the laboratory at 77.5 µg P l^{-1}, unpublished data) that are well-edible for most herbivorous zooplankton species and relatively poor competitors for nutrients (Sommer 1985). *Cryptomonas* sp. is common in temperate lakes and was chosen because of its trait complementarity to *C. raciborskii* (Weithoff 2003) to evaluate the importance of species characteristics/traits for invasibility. Previous competition experiments at 80 µg P l^{-1} starting with a small inoculum of both invaders nearly equal in biomass yielded a dominance of *Cryptomonas* sp. under permanent herbivory of *B. calyciflorus*, whereas without herbivory *C. raciborskii* prevailed after 36 days (see Appendix). This confirms the assumed trait complementarity of the two invaders (see below).

Productivity experiment

In the productivity experiment with herbivory we tested the impact of nutrient supply on the herbivore density, the invasibility and the diversity of phytoplankton communities by generating a gradient of seven levels in nutrient concentration. The nutrient ratios, N:P = 16 and Si:P = 30, were kept constant at all levels and the concentration was increased at an exponential scale ranging from 10 to 640 µg P l^{-1}. Three replicates were run for each nutrient supply level with the whole resident community comprising the ten phytoplankton species described above. The herbivore was introduced at day one with abundances adapted to the respective nutrient supply levels (10 µg P l^{-1}: 33, 20 µg P l^{-1}: 55, 40 µg P l^{-1}: 110, 80 µg P l^{-1}: 220, 160 µg P l^{-1}: 440, 320 µg P l^{-1}: 880, 640 µg P l^{-1}: 1500 *B. calyciflorus* per microcosm) to accelerate the adjustment of consumer consumption to prey production and thereby, attenuate transient high

herbivore densities. *B. calyciflorus* went extinct at low and intermediate nutrient supply levels (10-160 µg P l^{-1}) between days 14 and 20. Therefore, all microcosms were inoculated again with *B. calyciflorus* at day 21 with abundances described above. However, the herbivore failed to establish successfully and disappeared until day 30 again in almost all microcosms of low and intermediate nutrient supply levels. Nevertheless, the used nutrient supply range, which covered the natural range from oligotrophic to hypertrophic lakes, was chosen to determine the supply level where herbivory starts to become important for our phytoplankton communities.

To assess the influence of herbivory on the invasibility of communities at different nutrient supply levels we ran an additional experiment without herbivores at intermediate and high nutrient supply (80 and 320 µg P l^{-1}, 3 replicates each). We excluded very low nutrient supply levels because the herbivore went extinct rapidly at these supply levels suggesting small effects of herbivory on these communities. Altogether, this resulted in 21 microcosms with herbivory and 6 microcosms without herbivory in the productivity experiments.

Diversity experiment

The diversity experiment with herbivory was run to investigate the influence of diversity on invasibility. We generated initially three levels of species richness by selecting ten times randomly 3, 4 or 6 of the 10 phytoplankton species as resident community at 80 µg P l^{-1} (for species composition see Appendix). We chose an intermediate nutrient supply level for the diversity experiment to enable both introduced species to invade successfully (see below). The microcosms were inoculated with the resident communities at the beginning of the experiment (day 0), and two days later, 200 individuals of *B. calyciflorus* were added to each microcosm. *B. calyciflorus* went extinct in 13 microcosms at different species richness levels and a repeated inoculation at day 21 was successful only in two microcosms. The stock culture of *B. calyciflorus* was fed with *C. reinhardtii* and despite carefully rinsing prior to inoculation of the herbivore the forage alga was accidentally introduced. Thus, in some microcosms species richness became higher than the initial species richness at day 0. However, the contribution of *C. reinhardtii* to total community biomass was mostly lower than 15% (no problems arose in the productivity experiment where *C. reinhardtii* belonged always to the resident community). Furthermore, resident species extinctions resulted in reduced species richness until the day of invasion (day 14). Therefore, we examined the dependencies of invasibility on the present species richness and the species diversity (H') at this day.

Additionally, the 10 microcosms with an initial species richness of 4 phytoplankton species were run without herbivores (see Appendix) to assess potential effects of herbivory on the assembly of phytoplankton

communities and their invasibility. This resulted in 30 microcosms with herbivory and 10 microcosms without herbivory in the diversity experiments.

Invasibility of the phytoplankton communities

We quantified the invasibility as the $\log_2$ of the ratio between the final and the initial invader biomass during the invasion period (day 14 until day 36) separately for both invaders (*i* = *C. raciborskii*, *Cryptomonas* sp.):

$$\text{invasibility}_i = \log_2\left(\frac{\textit{invader}\ \text{biomass}\ \textit{at day}\ 36}{\textit{invader}\ \text{biomass}\ \textit{at day}\ 14}\right) \quad (2)$$

We used the logarithm of this ratio to weight an increase or decrease of invader biomass equally. Thus, if the invasibility measure is greater than zero the invader increased in biomass, whereas negative values indicate a decrease in invader biomass. If the invader was not detected at day 36 its detection limit was estimated from the water volume counted to calculate a zero replacement value (ZRV) for its biomass:

$$\text{invasibility}_i(\text{ZRV}) = \log_2\left(\frac{\text{detection limit of}\ \textit{invader}\ \text{biomass}\ \textit{at day}\ 36}{\textit{invader}\ \text{biomass}\ \textit{at day}\ 14}\right) \quad (3)$$

The calculated ZRVs of invasibility were averaged for each invader separately both in the productivity and diversity experiment to receive one non-varying ZRV.

When the invaders were introduced (day 14), the resident communities were at different stages of their temporal dynamics as some communities were close to an equilibrium state, whereas others exhibited pronounced dynamics with either very low or high densities (see Appendix). Thus, we did not use the change in the relative contribution of the invaders to the community biomass during the invasion period as a measure of invasibility because it partly depended more strongly on the change in the resident community biomass than on a change in invader biomass.

Statistical analysis

The Kolmogorov-Smirnov-test was used to test for normal distribution of variables and residuals of regression models. Spearman rank correlation coefficients (r_S) were used to determine relationships among variables which were not normally distributed and of unclear dependency to each other. Mean values were compared using *t*-tests. All analyses including non-linear and (multiple) linear regressions were carried out using SPSS for Windows (version 12.0.1). For multiple regression analysis we used the stepwise

selection procedure (entry, $P \leq 0.1$; removal, $P \geq 0.05$) and only significant predictors were shown. For non-linear relationships we used polynomial equations with quadratic terms. The nutrient supply gradient in the productivity experiment was $\log_2$-transformed, which adjusts for the increasing intervals between the nutrient supply levels and prevents an overestimation of data at high nutrient supply levels.

Principal components analysis (PCA) visualized differences in invasibility and mean herbivore density among microcosms in relation to the realized species composition at the end of the productivity experiment (day 36) with herbivory. Another PCA was applied to identify potential relationships of the resident species composition to the invasibility and mean herbivore density at the day of invasion (day 14) in the diversity experiment with herbivory. The relative contributions of resident phytoplankton species to the community were used as a covariance matrix using the software Canoco for Windows (version 4.53). We applied untransformed relative contributions without standardization (i.e., no correlation matrix) to especially emphasize dominant species, which probably played the major role in community processes. Using other ordination methods, e.g., principal coordinates analysis (PCoA) which allow the choice of different distance measures (e.g., Bray-Curtis distance), resulted in a very similar order of microcosms along the ordination axes compared to the PCA. Thus, the problem of double zero counts that may arise by the usage of the Euclidean distance metric, which is the default for PCA, seems to be negligible in the present study.

4.4. Results

Productivity experiment

The mean herbivore density during the invasion period was strongly positively affected by nutrient supply (Fig. 1a; Table 1), whereas algal biomass remained low in microcosms with herbivory compared to microcosms without herbivory (Fig. 1a). This suggests that primary production was enhanced at high nutrient concentrations which resulted in high herbivore abundance. The invasibility for both invaders showed a unimodal pattern with respect to nutrient supply (Fig. 1b; Table 1). The maximum invasibility for *Cylindrospermopsis raciborskii* was at 40 µg P l^{-1} and thus, lower than for *Cryptomonas* sp., whose maximum of invasibility was between 80 and 160 µg P l^{-1}. Considering non-transformed nutrient supply levels, the invasibility for both invaders becomes more or less positively skewed. Species richness (S) was negatively affected by nutrient supply at the day of invasion (day 14, Fig. 1c; Tab. 1) and at the end of the experiment (day 36, Fig. 1c; Table 1). Species diversity (H') was unrelated to nutrient supply at day 14, whereas at day 36 a relatively weak negative relationship was found (Fig. 1d; Table 1). The very low species diversity at

80 µg P l^{-1} was caused by the dominance of *Ankistrodesmus gracilis* which contributed more than 90% to the community. Due to the unimodal relationship between invasibility and nutrient supply and the negative one between diversity and nutrient supply, no distinct diversity-invasibility relationship emerged, which depended on the invader species and the measure of diversity (Fig. 1b-d).

Based on the community composition at day 36, the PCA separated the microcosms with herbivores into two groups (except for one replicate at 160 µg P l^{-1}; Fig. 2a, 5 I). One group was dominated by the well-edible, fast growing flagellate *Chlamydomonas reinhardtii* and occurred at 320-640 µg P l^{-1} where the mean herbivore density was at its maximum (Fig. 2b). In one replicate of 160 µg P l^{-1} the mean herbivore density was also high but another well-edible, fast growing species, *Chlorella vulgaris*, dominated the resident community (Fig. 2a, 5 I). In the other group, the colony forming, fast growing *A. gracilis* or the well-edible, fast growing *Monoraphidium minutum* were dominant resident species (Fig. 2a). At 10-40 µg P l^{-1} the mean herbivore density was very low, whereas at 80 µg P l^{-1} and in two replicates of 160 µg P l^{-1} (Fig. 2a, 5 II and 5 III) there was an intermediate mean herbivore density (Fig. 2b) and a strong dominance of *A. gracilis* (Fig. 2a). The invasibility for the fast growing, well-edible, but competitively weak invader *Cryptomonas* sp. was not clear related to the resident species composition or mean herbivore density (Fig. 2a-c). The less-edible, slowly growing and competitively strong invader *C. raciborskii* increased in biomass only at low or intermediate mean herbivore density and was not detected at high mean herbivore density when *C. reinhardtii* or *C. vulgaris* dominated (Fig. 2a, b, d). These patterns also hold for the community composition at the day of invasion (day 14) but became more evident when considering the community at the end of the experiment (day 36).

Without herbivory, both invaders exhibited an opposite response during the invasion period, i.e., *C. raciborskii* increased in biomass whereas *Cryptomonas* sp. was not detected (Fig.3). The invasibility was not affected by the nutrient supply, since at both nutrient supply levels *Cryptomonas* sp. consistently failed to establish (Fig. 3a), whereas *C. raciborskii* had the same invasion success (Fig. 3b; t-test: $t = 1.8$, $df = 4$, $P = 0.16$). At 80 µg P l^{-1} the resident species *M. minutum* prevailed, whereas at 320 µg P l^{-1} *Scenedesmus obliquus, M. minutum* and *C. reinhardtii* were predominant species. Thus, the different resident species composition at both nutrient supply levels had only little influence on the invasibility. In contrast to the microcosms without herbivory, the respective microcosms with herbivory showed a similar pattern of invasibility for both invaders. At 80 µg P l^{-1} both invasive species increased in biomass and at 320 µg P l^{-1} both species showed negative values for invasibility (Fig. 3). However, herbivory seemed to promote the occurrence of *Cryptomonas* sp. even though at high nutrient

supply (i.e., also a high mean herbivore density) at which *C. raciborskii* failed to establish.

Diversity experiment

In the presence of herbivory, the invasibility for both invaders was unaffected by species richness (linear regression: *Cryptomonas* sp., t = 0.14, df = 28, P = 0.89, r^2 < 0.01; *C. raciborskii*, *t* = 1.36, df = 28, P = 0.18, r^2 = 0.06), and by species diversity (H') when regarding *C. raciborskii* (Fig. 4a; t = 0.87, df = 28, P = 0.39, r^2 = 0.03) at the day of the invasion. The invasibility for *Cryptomonas* sp. slightly increased with increasing species diversity (H') at the day of invasion (Fig. 4a; Table 1). Instead, there was a strong relationship between invasibility and mean herbivore density (Fig. 4b) which arose from the extinction of the herbivore in the presence of *A. gracilis*, a species that formed inedible colonies under herbivory. The extinction of the herbivore resulted always in an approximately equal increase of biomass of *C. raciborskii*, whereas *Cryptomonas* sp. mostly failed to establish (Fig. 5a, b, non-permanent herbivory). In microcosms with the absence of *A. gracilis* and permanent herbivory, *C. raciborskii* was never detected (Fig. 5b). Thus, the variability in invasibility for *C. raciborskii* is almost exclusively explained by the mode of herbivory, i.e., non-permanent or permanent herbivory. In contrast, *Cryptomonas* sp. more frequently increased (11 observations) than decreased (6 observations) in biomass under permanent herbivory leading to a positive relationship between invasibility and mean herbivore density (Fig. 4c; Table 1) explaining only 31% of the variance in invasibility. Therefore, the remained variability, especially at high mean herbivore density, could be explained by additional factors.

A multiple regression analysis of invasibility for *Cryptomonas* sp. including additionally the two significant factors, relative contribution of *C. reinhardtii* to the resident community and species diversity (H') at day 14, explained together 68% of the overall variance (Table 1). *C. reinhardtii* had a negative effect on *Cryptomonas* sp. indicating some competitive interactions among these functionally similar species. In this multiple regression, the variance of invasibility for *Cryptomonas* sp. explained by species diversity (6%) was clearly reduced compared to the regression with species diversity used as the only independent variable (20%; Table 1). This, and the fact that the invasibility for *C. raciborskii* was completely unrelated to species diversity (H'), indicates a weak direct influence of species diversity on the invasibility for both invaders.

A PCA based on the relative community composition of microcosms with herbivory separated three groups represented by different initial species richness levels (Fig. 6a). One group was dominated by the colony forming and therefore inedible, fast growing *A. gracilis* (Fig. 6a, positive PC1-axis) and was characterized by low mean herbivore density, whereas in the other

two groups mean herbivore density was high (Fig. 6b). In one of them the well-edible, fast growing *C. reinhardtii* was dominant (Fig. 6a, negative PC1- and positive PC2-axis), and in the other one either *M. minutum*, *C. vulgaris* or *P. agardhii* prevailed (Fig. 6a, negative PC1- and PC2-axis). Invasion of the well-edible, fast growing *Cryptomonas* sp. was often successful at high mean herbivore density when the functionally similar *C. reinhardtii* was not the dominant resident species (Fig. 6a-c). The less-edible, slowly growing invader *C. raciborskii* always increased in biomass at low mean herbivore density and a dominance of *A. gracilis* whereas it was not detected at high mean herbivore density (Fig. 4a, b, d).

In the ten microcosms without herbivory, the invader *Cryptomonas* sp. mostly was not detected leading to a strong negative mean of invasibility (Fig. 5a), whereas *C. raciborskii* always strongly increased in biomass (Fig. 5b). Both invaders responded similarly compared to their responses at non-permanent herbivory in microcosms with herbivores (Fig. 5a, b). The resident communities without herbivory were dominated by different fast growing green algae; mostly of *M. minutum*, but also by *S. obliquus*, *C. reinhardtii* or *A. gracilis*. Thus, in microcosms without herbivory the different resident species composition probably had a low effect on invasibility, as shown in the productivity experiment.

4.5. Discussion

Our study showed that the factors potentially influencing the invasibility of phytoplankton communities (nutrient supply, diversity, herbivory and species functional traits) were interrelated with each other. For example, nutrient supply and/or the presence of *Ankistrodesmus gracilis* in the resident community influenced the strength of herbivory which, in turn, influenced diversity and invasibility. Moreover, the functional traits of the invasive species had a strong effect on invasion success. Subsequently, the impact of the individual factors and their different interrelationships are discussed and synthesized.

Herbivory and traits of invaders

Generalist herbivory has a direct negative impact on both, resident and invasive primary producers, due to mortality. It may also have an indirect positive effect on invasive species due to a reduced competition for nutrients or a faster nutrient recycling increasing the resource availability for invasive species (Davis et al. 2000; Shea and Chesson 2002). The emergent effect of herbivory on invasive species is often negative in terrestrial plant communities (Levine et al. 2004) but little is known for plankton communities.

In contrast to our expectations, substantial herbivory prevented a successful invasion of the supposedly less-edible, filamentous cyanobacterium *Cylindrospermopsis raciborskii* but promoted that of the well-edible flagellate *Cryptomonas* sp. *Vice versa*, without herbivory *C. raciborskii* always invaded, whereas *Cryptomonas* sp. failed to establish a population (see Appendix). These different responses of the invaders emerged clearly from their different functional traits but edibility itself is an implausible explanation. A better explanation for the differences in invasibility may deliver the traits competitiveness and maximum gross growth rates. Without herbivory, strong competition for nutrients likely prevailed given the low dilution rate of 20% every second day. This favoured *C. raciborskii* which is known to be a strong competitor for nutrients (Burford et al. 2006) and hampered *Cryptomonas* sp. due to its inferior competitive strength under stable, highly competitive conditions (Sommer 1985). Under more or less unselective herbivory, as it was imposed by *Brachionus calyciflorus*, herbivore-mediated competition arises between the different algal species. This promotes those species with high gross growth rates (i.e., *Cryptomonas* sp.) when a sufficient amount of nutrients are available due to the nutrient recycling of the herbivore. A high co-consumption of less-edible and usually slower growing algal species like *C. raciborskii* is expected because the herbivore does not reduce its total food source when its grazing eliminates a particular species of the community. Rather, the herbivore can maintain high abundances due to high production of fast growing, well-edible species.

Effects of productivity/herbivory on invasibility

In our productivity experiment, productivity was not directly measured. However, mean herbivore density strongly increased with increasing nutrient supply, whereas the biomass of the primary producers remained low (Fig. 1a), which was confirmed by simple bitrophic food chain models (Oksanen et al. 1981; Vos et al. 2004). Thus, mean herbivore density can be used as an indirect estimate of productivity because a higher biomass production of the phytoplankton community at higher nutrient levels was converted into a higher number of herbivores. Furthermore, the invasion success was influenced by two counteracting processes along the nutrient gradient: At higher nutrient levels (i.e., higher productivity), a potentially increased nutrient availability is expected to facilitate invasions (Davis et al. 2000), whereas enhanced herbivory and thus, grazing mortality may hamper invasions of initially small populations. The invasibility for both invaders exhibited a unimodal relationship to nutrient supply. At low nutrient levels (implying low productivity/herbivory) the invasibility increased with increasing nutrient supply presumably due to the increasing resource availability for the invaders. In contrast, at high nutrient levels (implying high productivity/herbivory) the invasibility decreased suggesting that the direct negative effect of herbivory was stronger than the indirect

positive effect of enhanced resource availability. The higher gross growth rate of *Cryptomonas* sp. compared to *C. raciborskii* may explain why its maximum of invasibility occurred at a higher productivity/herbivory level because it can compensate higher loss rates at higher grazing pressure.

These findings are summarized in a conceptual model describing the potential interplay between resource supply, resource competition, generalist herbivory and invasibility (Fig. 7) and were partially confirmed by investigations of effects of either competition/resource availability or herbivory/consumption on invasive species. For instance, in several experimental studies invasibility increased with enhanced resource availability (Burke and Grime 1996; Jiang and Morin 2004; Romanuk and Kolasa 2005). Increasing resource availability might be responsible for the positive effect of herbivory on the invasibility for *Cryptomonas* sp. due to prevention of resource depletion caused by its competitors. In other studies a negative effect of consumers on particular invasive species was found (Miller et al. 2002; meta-analysis in Levine et al. 2004; DeRivera et al. 2005) as well as in our study for *C. raciborskii*. However, our conceptual model may be valid only for food chains with even-numbered length within a certain productivity range. Thus, generalizations to entire lake ecosystems should be handled with caution because at higher productivity the existence of food chains with odd-numbered trophic levels is allowed leading, for instance, to other productivity-herbivore density relationships (Oksanen et al. 1981). This may change the productivity-invasibility relationships depending on the traits of invasive species.

Effects of productivity/herbivory on diversity

Other experimental studies based on a manipulation of nutrient supply, but without consumption, reported positive (protist microcosms, Jiang and Morin 2004), negative (zooplankton mesocosms, Lennon et al. 2003) or unimodal (bacterial microcosms, Kassen et al. 2000) productivity-diversity relationships, which were attributed to mechanisms such as sufficient resource availability, strong competition or selection in a heterogeneous environment. Our study confirms that consumption influences the diversity of prey communities and may depend itself on the productivity of the system (Worm et al. 2002).

During our productivity experiment, the self-regulating, non-manipulated species richness and species diversity declined along the nutrient gradient. This may be explained by the increasing mean herbivore density with increasing nutrient supply, as slowly growing phytoplankton species could not compensate for the almost non-selective mortality of the generalist herbivore and fast growing species became dominant. At low nutrient supply levels where herbivory declined and competition was the driving factor, more species were able to compensate the grazing mortality resulting

in higher species richness and species diversity. The exclusion of species due to competition presumably requires more time than their elimination by herbivory. Thus, low species richness at low productivity and an emerging unimodal productivity-diversity relationship might be expected at longer time periods due to the temporally different responses of species richness to both drivers: competition and herbivory.

In the productivity experiment, no clear relationship between invasibility and diversity emerged due to the differently shaped patterns of the invasibility-productivity-relationship and the diversity-productivity-relationship. Furthermore, decreasing diversity did not enhance invasibility due to possible increased resource availability (i.e., release from the sampling or complementarity effect; Wardle 2001). Instead, increased nutrient supply and thus, herbivory led to a negative effect on both invaders and most resident species. Hence, the independent effect of diversity on invasibility can only be examined at constant nutrient supply by manipulating the community composition as it was done in the diversity experiment.

Effect of diversity on invasibility

The invasibility for both invaders showed no response to species richness and increased weakly for *Cryptomonas* sp. with increasing species diversity (H'). In contrast, in terrestrial or coastal marine studies which examined substrate-bound systems a negative diversity-invasibility relationship was observed frequently at small scale (Stachowicz et al. 1999; Stachowicz et al. 2002; Levine et al. 2004). Despite the same nutrient supply in our microcosms of the diversity experiment, mean herbivore density varied depending on the presence or absence of the resident species *Ankistrodesmus gracilis*. This resident species formed inedible colonies in the presence of the herbivore and caused its extinction. Both invaders responded strongly and contrarily to the permanence of herbivory mediated by the occurrence of *A. gracilis*. This species led to a low mean herbivore density (i.e., mostly an extinction of the herbivore), a condition that facilitated *C. raciborskii* and hampered *Cryptomonas* sp. as it was found in the productivity experiment. These results demonstrate the potential importance of the resident species composition at a certain nutrient supply in conjunction with the functional traits of the invasive species for the invasibility of a community.

The invasibility for *C. raciborskii* exclusively depended on the occurrence of *A. gracilis* in the resident community and no effect of species richness was detected for both invaders. A negative effect of species richness on invasibility may arise from resource use complementarity as it was shown for plant communities without herbivory implying strong competition for resources (Fargione and Tilman 2005). In our experimental system such an

effect is unlikely to occur because either herbivory reduced competition for nutrients or, when competition was more important (i.e., at non-permanent herbivory), a strong dominance of *A. gracilis* prevented complementary resource use.

The invasibility for *Cryptomonas* sp. was negatively influenced by the dominance of another resident species, *Chlamydomonas reinhardtii*, which has similar functional traits as the invader (Weithoff 2003). Thus, this resident species either caused unfavorable conditions for the invasion, e.g. extremely high herbivory, or had a direct negative impact on *Cryptomonas* sp. by competing for the available nutrients. This emphasizes again the potential relevance of particular species for the invasion resistance as found in another study with microbial communities (McGrady-Steed et al. 1997). In their study, invasion was more often successful at low species richness, but the abundance of distinct species explained more of the variance of invasibility than species richness.

Implications of the invasion potential of *C. raciborskii* for natural communities

In the last few decades *C. raciborskii* has spread from tropical to northern temperate zones (Padisák 1997). In some newly invaded regions *C. raciborskii* occurs mainly in eutrophic, polymictic lakes during summer (Stüken et al. 2006) and contributes up to 23% to the cyanobacterial biovolume (Wiedner et al. 2007). Field studies showed that light availability, temperature and to a lesser extent nutrient availability influenced the population dynamics of *C. raciborskii* (Mischke 2003; Wiedner et al. 2007). The question arises which circumstances allow a successful invasion into new environments and the development of such high abundances. *C. raciborskii* has a competitive advantage under nitrogen deficiency due to its high affinity for ammonium and its ability to fix atmospheric nitrogen using heterocysts (Présing et al. 1996). Moreover, the invasive cyanobacterium strongly competes for phosphorus, which often limits the growth of primary producers in lakes, due to high uptake affinity and storage capacity for this nutrient (Istvánovics et al. 2000). Our study confirmed the great competitive strength of *C. raciborskii* since its population always increased under nutrient depletion independent of the phytoplankton community composition.

It is assumed that most zooplankton species poorly ingest filamentous algae leading to decreased grazing pressure with increasing proportion of filamentous cyanobacteria to the community which was confirmed for *C. raciborskii* grazed by *Daphnia* (Cladocerean; Hawkins and Lampert 1989). We found that high abundances of a relative small zooplankton species prevented successful invasions but in lakes of the temperate zone *C. raciborskii* germinates from akinetes in the summer (Wiedner et al. 2007)

when cyanobacteria biovolume goes up and grazing declines. However, in situations where the introduction of *C. raciborskii* into a new lake or the annually initiating development of the population matches strong grazing, successful invasions or high abundances of *C. raciborskii* may be prevented.

Conclusions

The community composition in our diversity experiment strongly affected the permanence of herbivory which determined the invasibility, whereas species richness or species diversity *per se* had a small impact on community invasibility. The functional traits of resident species largely determined the conditions encountered by the invaders, and their response, in turn, depended on their own functional traits. This led to apparent facilitation of one invasive species (*C. raciborskii*) and suppression of the other one (*Cryptomonas* sp.) by a resident species (*A. gracilis*) via an indirect effect (herbivory) in the diversity experiment. However, if the influence of an extrinsic factor such as nutrient supply on invasibility was sufficiently strong, as shown in our productivity experiment, both types of invasive species showed similar responses along a gradient of this factor. Another key mechanism was the direct negative effect of the generalist herbivore on both invasive species which could outweigh the indirect positive effect of increasing resource availability, since herbivory strongly increased with increasing nutrient supply. Thus, herbivory may repel successful invasions especially in their initial phase even at high resource availability. The strength of this effect depends on the strength of herbivory and the functional traits of the invasive species; some species indirectly benefit from herbivory (e.g., *Cryptomonas* sp.), whereas others suffer more strongly from it (e.g., *C. raciborskii*).

4.6. Acknowledgement

We thank Melanie Hartwich and Angelika Wöhler for experimental assistance and Frank Schurr and Helmut Hillebrand for valuable comments on the manuscript. We also thank Claudia Wiedner for providing the strain of *C. raciborskii*. This study was supported by the German Research Foundation (DFG, GA 401/10-1).

4.7. Tables

TABLE 1: Summary of significant regression results in the productivity and diversity experiment. Coefficients describe the estimate of the slope for linear models and the estimate of the quadratic term for quadratic models.

Model	Dependent variable	Independent variable(s)	Coefficient ± SE	t	P	df	r^2
			Productivity experiment				
Linear	Mean herbivore density	Log_2(nutrient concentration)	0.59 ± 0.04	15.6	< 0.001	19	0.93
Qua-dratic	Invasibility *C. raciborskii*	Log_2(nutrient concentration)	-0.55 ± 0.15	-3.7	0.002	18	0.66
Qua-dratic	Invasibility *Cryptomonas*	Log_2(nutrient concentration)	-0.59 ± 0.13	-4.6	< 0.001	18	0.54
Linear	Species richness (S) day 14	Log_2(nutrient concentration)	-0.56 ± 0.09	-6.1	< 0.001	19	0.66
Linear	Species richness (S) day 36	Log_2(nutrient concentration)	-0.89 ± 0.07	-12.0	< 0.001	19	0.88
Linear	Species diversity (H') day 36	Log_2(nutrient concentration)	-0.06 ± 0.02	-4.0	< 0.001	19	0.46
			Diversity experiment				
Linear	Invasibility *Cryptomonas*	Species diversity (H') day 14	13.3 ± 5.0	2.7	0.013	28	0.20
Linear	Invasibility *Cryptomonas*	Mean herbivore density	3.4 ± 1.0	3.6	0.001	28	0.31
Multiple linear	Invasibility *Cryptomonas*	Mean herbivore density	4.1 ± 0.7	5.8	< 0.001	26	0.31
		p *C. reinhardtii* day 14	-5.6 ± 1.3	-4.2	< 0.001	26	0.31
		Species diversity (H') day 14	7.6 ± 3.4	2.2	0.035	26	0.06
							∑0.68

4.8. Figures

FIGURE 1: Relationships between a) mean herbivore density as an estimate for the strength of herbivory and mean relative fluorescence as an estimate for algal biomass (both averaged over the invasion period, day 14 to 36), b) invasibility for *Cryptomonas* sp. (dashed regression line) and *Cylindrospermopsis raciborskii* (solid regression line), c) species richness, and d) species diversity (H') at the day of invasion (day 14, solid regression line) and at the end of the experiment (day 36, dashed regression lines) and nutrient concentration (x-axis, note log_2-scale for the nutrient concentration gradient) in the productivity experiment with herbivory. Lines indicate significant regressions (n = 21, P < 0.01).

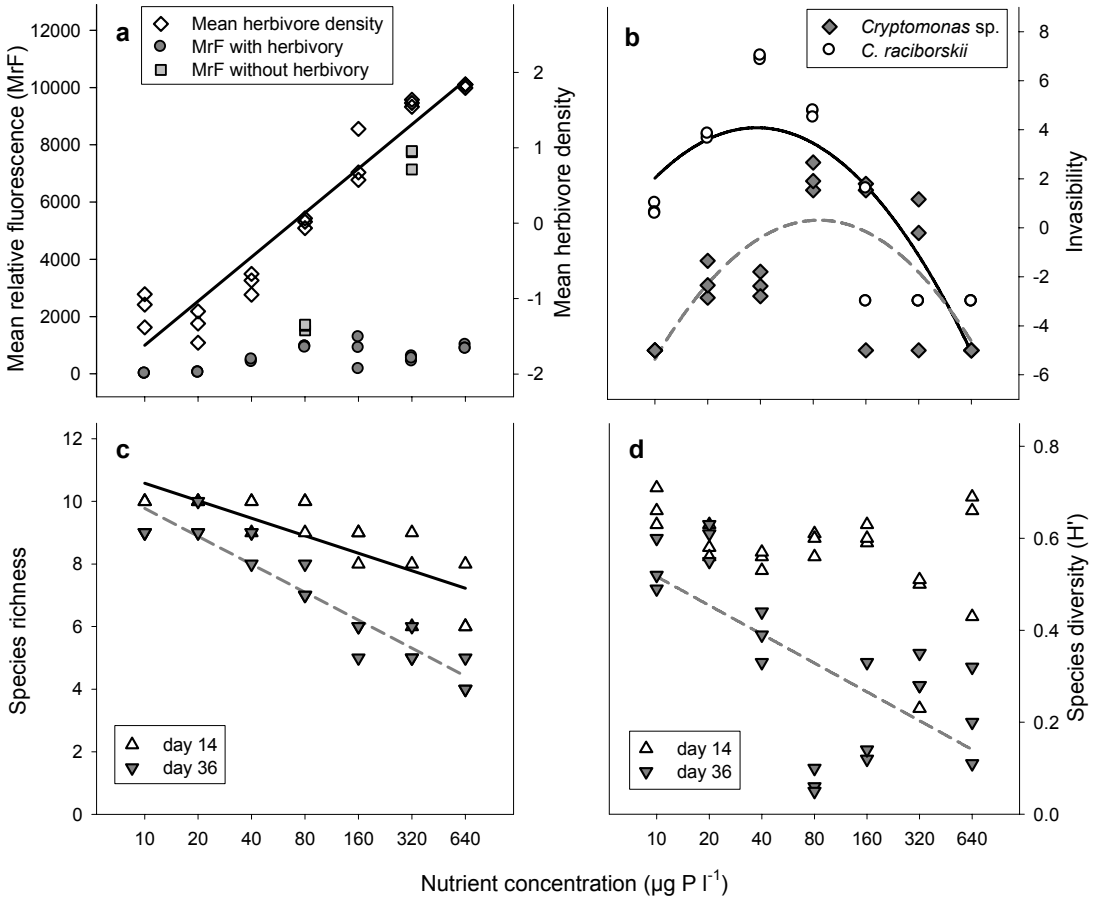


FIGURE 2: a) First two axes of the principal components analysis (PCA) based on the relative contribution of each resident species to the community in the productivity experiment with herbivory at the end of the experiment (day 36). Arabic numbers of the circles refer to the nutrient supply levels (1= 10 µg P l^{-1}, 2 = 20 µg P l^{-1}, 3 = 40 µg P l^{-1}, 4 = 80 µg P l^{-1}, 5 = 160 µg P l^{-1}, 6 = 320 µg P l^{-1}, 7 = 640 µg P l^{-1}) and the Romanic numbers indicate replicates. Percentages in brackets refer to the explained variance in species composition by the axis (principal component). The area of the circles represents b) the mean herbivore density and the extent of invasibility for c) *Cryptomonas* sp. and d) *C. raciborskii* (white: invader not detected, light grey: invader decreased in biomass, dark grey: invader increased in biomass).

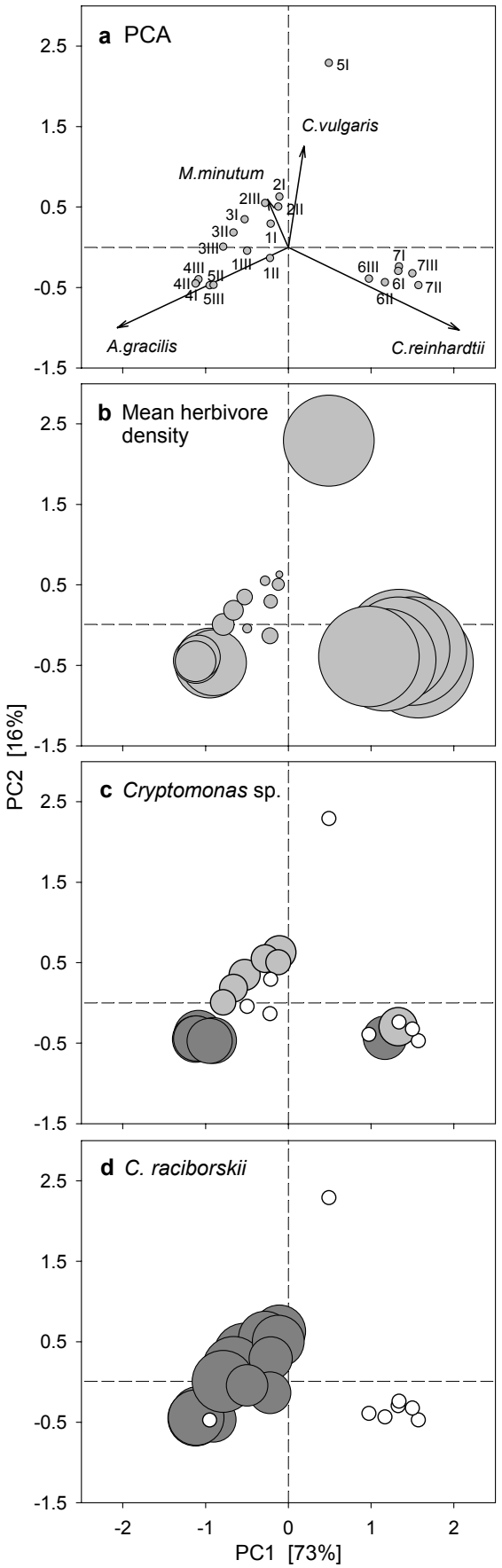

a PCA
5I
C.vulgaris
M.minutum
2I
2III
2II
3I
3II
1I
3III
1III
1II
4III
5II
4II
4I
5III
7I
7III
6III
6I
7II
6II
A.gracilis
C.reinhardtii
b Mean herbivore density
c Cryptomonas sp.
d C. raciborskii
PC2 [16%]
PC1 [73%]
2.5
1.5
0.5
-0.5
-1.5
-2
-1
0
1
2

FIGURE 3: Invasibility for a) *Cryptomonas* sp. and b) *C. raciborskii* in the productivity experiment at two nutrient supply levels (in µg P l^{-1}) with and without herbivory (mean ± SE, n = 3). *** denote significant differences between means within herbivory treatments (t-test, P < 0.001).

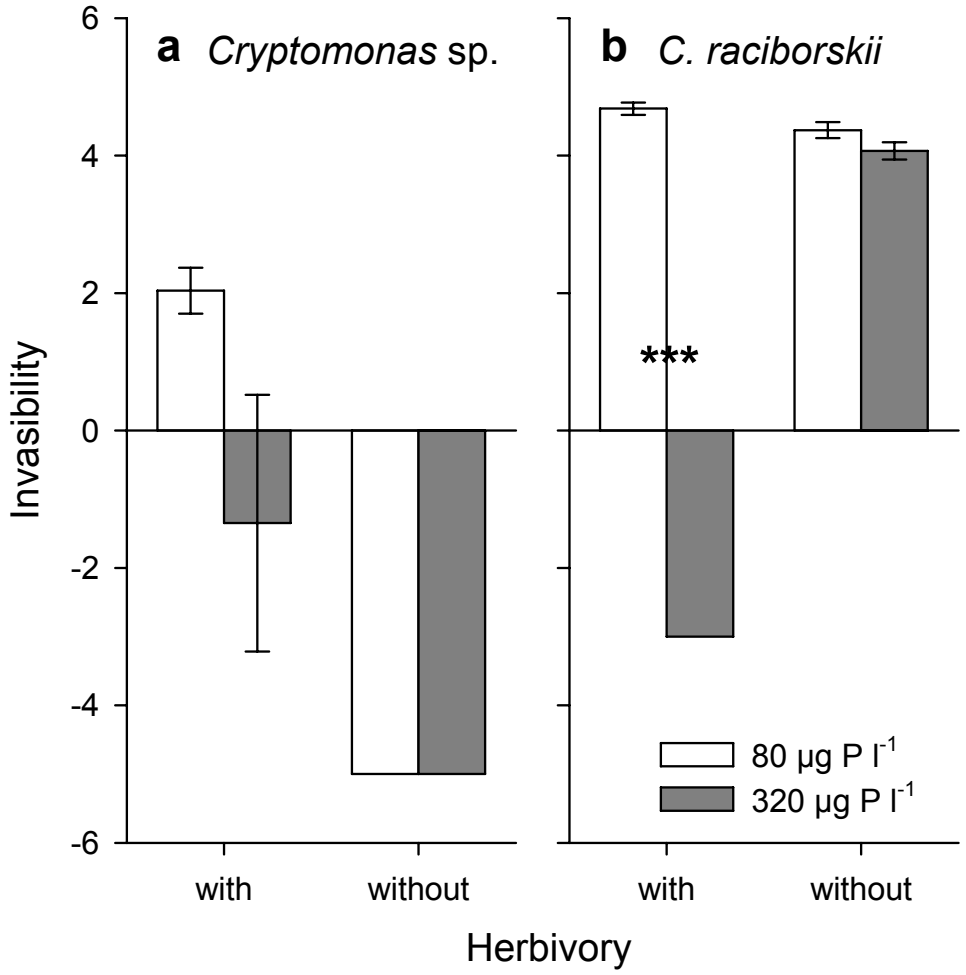


FIGURE 4: Relationships between invasibility for *Cryptomonas* sp. and *C. raciborskii* and a) species diversity (H') at the day of invasion (day 14) and b) mean herbivore density in the diversity experiment with herbivory. Lines indicate significant regressions (n = 30, P < 0.05). The vertical dashed line in b) separates microcosms with medium (generally permanent) herbivory from microcosms with weak (non-permanent) herbivory in the diversity experiment.

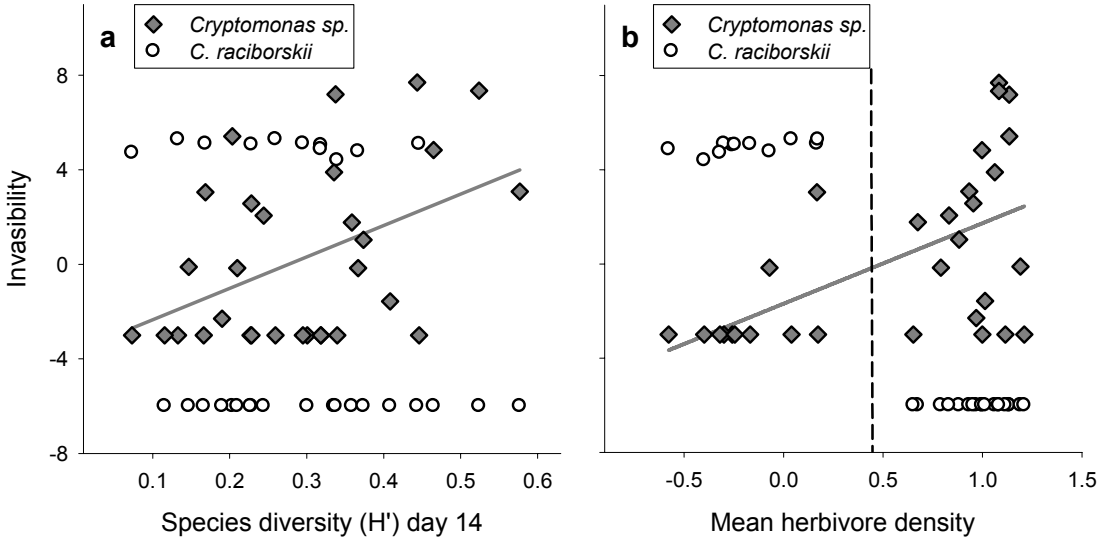


FIGURE 5: Invasibility for a) *Cryptomonas* sp. and b) *C. raciborskii* in the diversity experiment at three initial species richness levels without, with non-permanent and with permanent herbivory (mean ± SE). The number of observations is shown above or below the error bars.

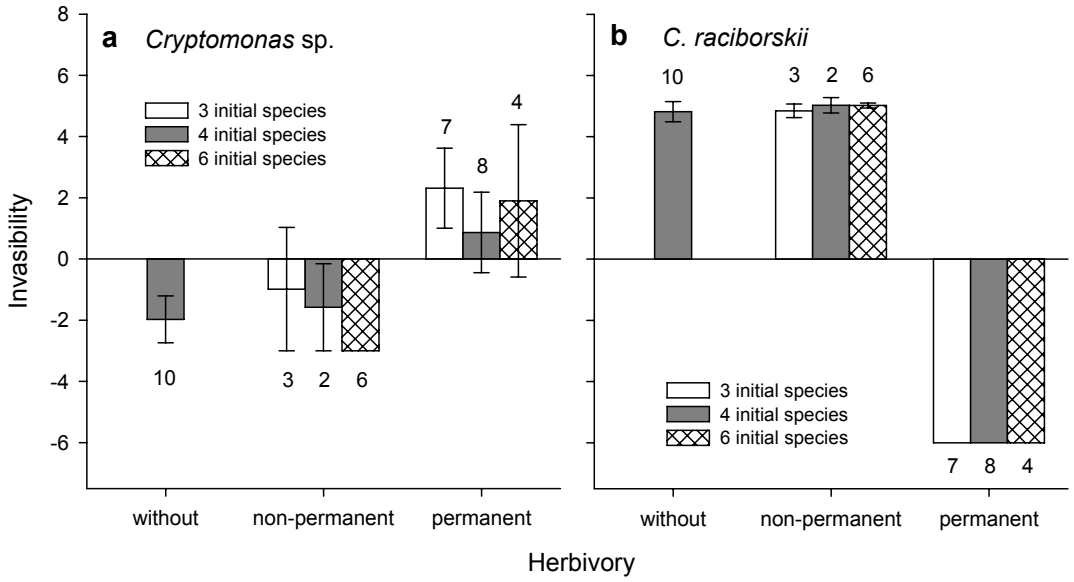


FIGURE 6: a) First two axes of the principal components analysis (PCA) based on the relative contribution of each resident species to the community in the diversity experiment with herbivory at the day of invasion (day 14). Arabic numbers of the circles refer to the initial species richness and the Romanic numbers indicate different species compositions. Percentages in brackets refer to the explained variance in species composition by the axis (principal component). The area of the circles represents b) the mean herbivore density and the extent of invasibility for c) *Cryptomonas* sp. and d) *C. raciborskii* (white: invader not detected, light grey: invader decreased in biomass, dark grey: invader increased in biomass).

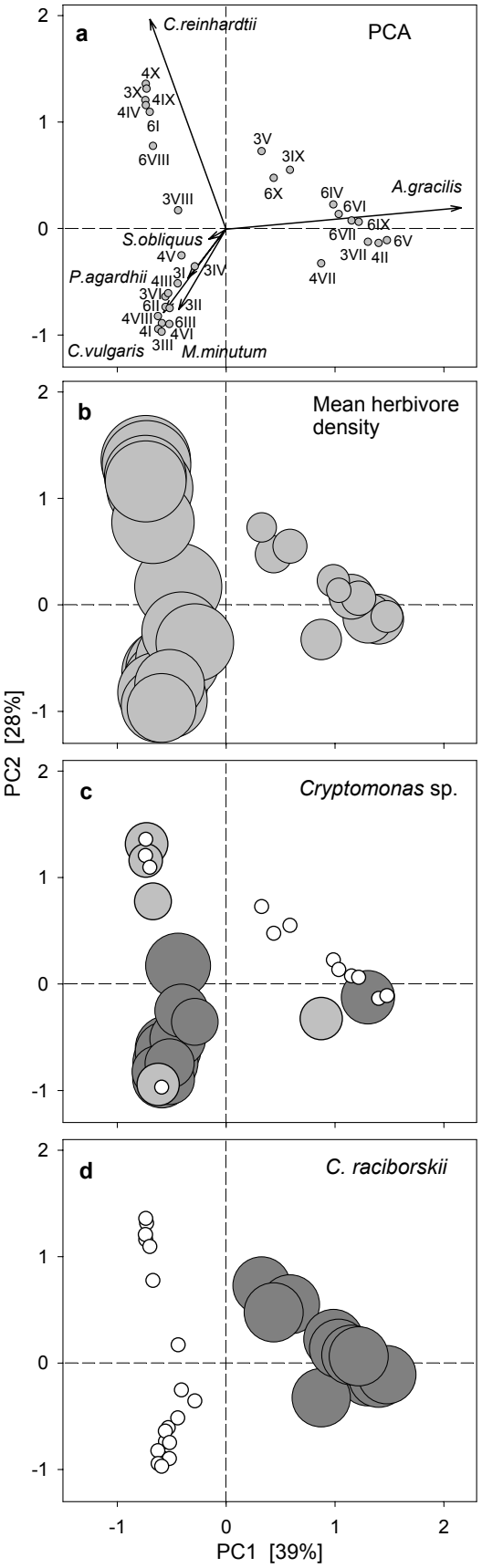
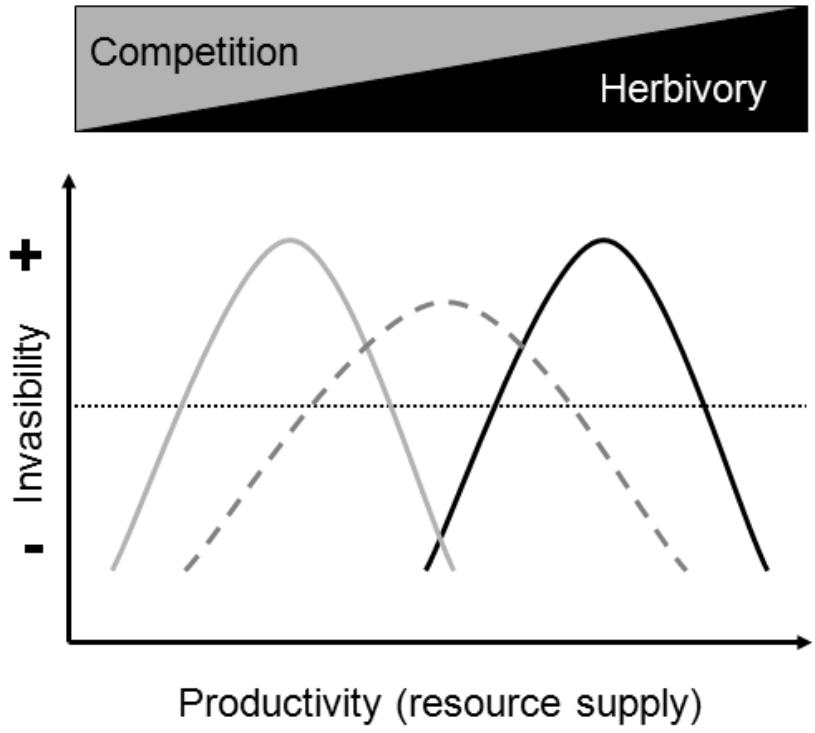
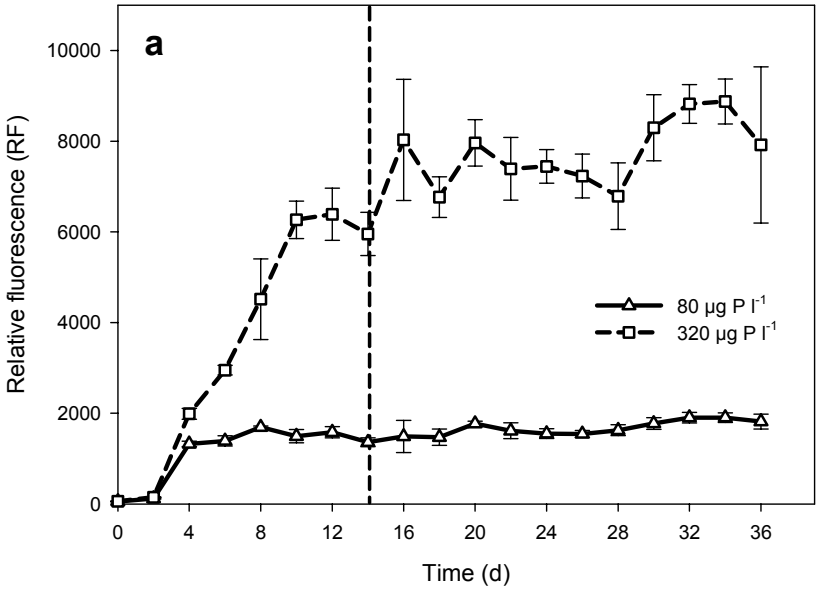

a
PCA
C.reinhardtii
A.gracilis
S.obliquus
P.agardhii
C.vulgaris
M.minutum
4X
3X
4IX
4IV
6I
6VIII
3V
3IX
6X
6IV
6VI
6IX
6VII
6V
3VII
4II
4VII
3VIII
4V
3I
3IV
4III
3VI
6II
3II
4VIII
6III
4I
4VI
3III
b
Mean herbivore density
c
Cryptomonas sp.
d
C. raciborskii
PC2 [28%]
PC1 [39%]
2
1
0
-1

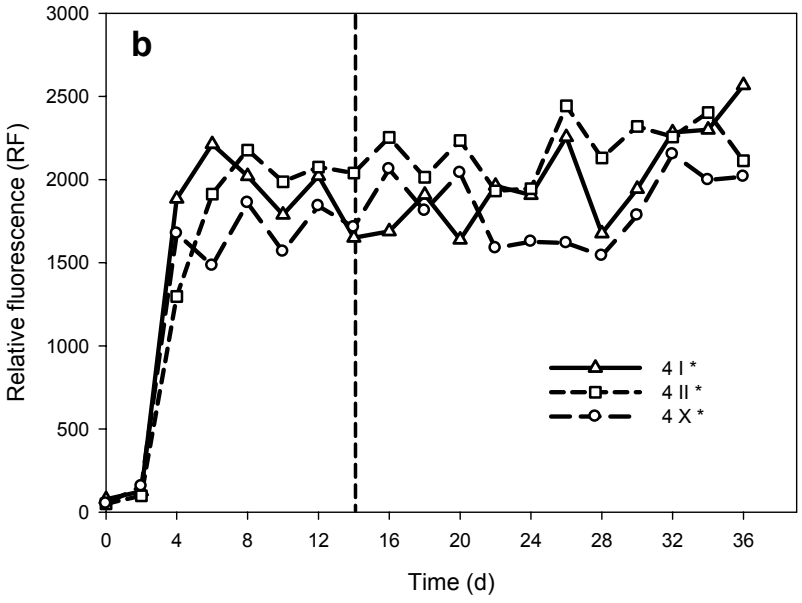
FIGURE 7: The potential influence of productivity (in terms of resource supply) on the invasion success of species which differ in their response to competition and herbivory due to their different functional traits (grey solid line: slowly growing, strong competitor, e.g., *C. raciborskii*; grey broken line: invader with intermediate growth rate and competitive abilities; black solid line: fast growing species with high resource requirements, e.g., *Cryptomonas* sp.), assuming that competition for resources decreases and generalist herbivory increases along the productivity/resource supply gradient.

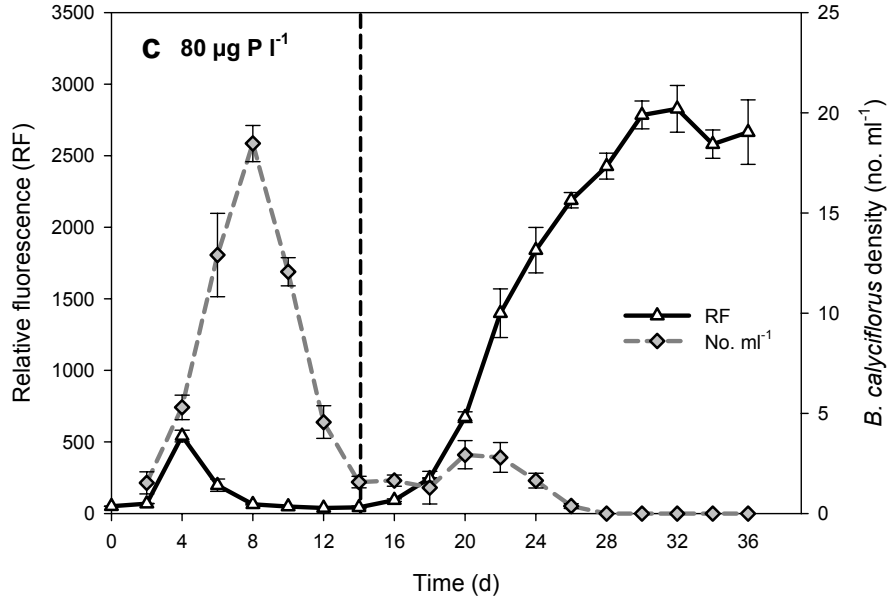


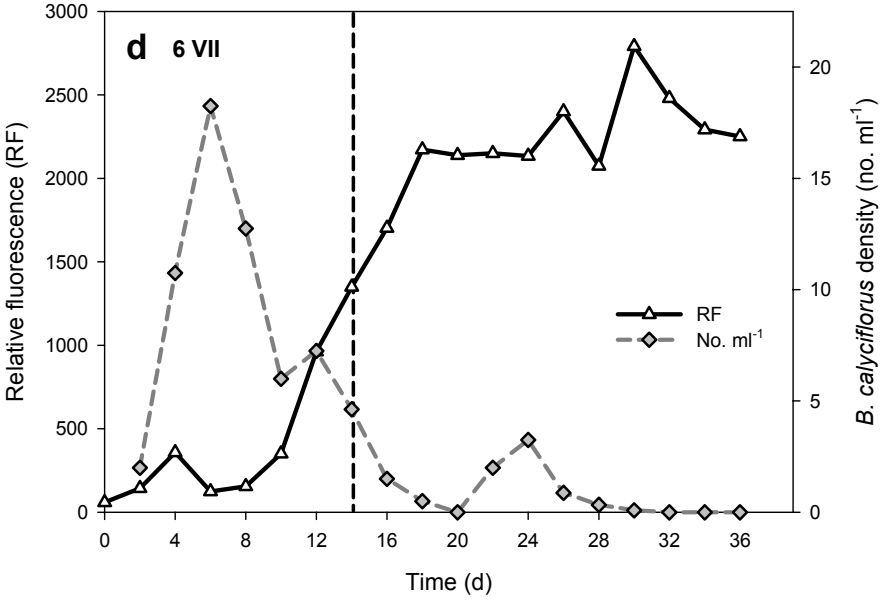
4.9. Appendix

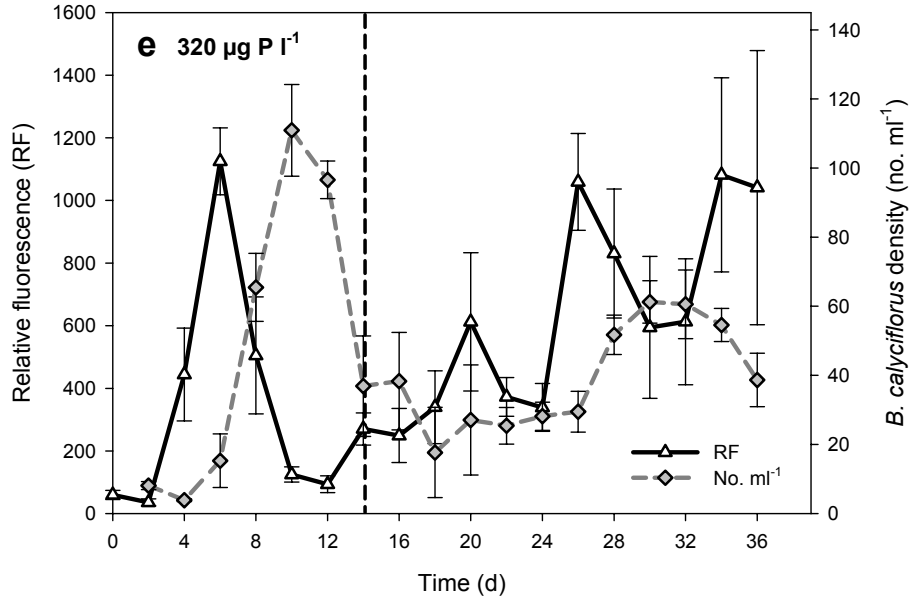
FIGURE 1: Examples of time-series data with estimated algal biomass (relative fluorescence) and density of *Brachionus calyciflorus* in microcosms of the productivity (a, c, e, n = 3) and the diversity (b, d, f) experiment without (a, b), with non-permanent (c, d) and with permanent (e, f) herbivory. For notation of microcosms of the diversity experiment see Table 1 in the Appendix. The vertical dashed line indicates the day of invasion.






c 80 µg P l-1
Relative fluorescence (RF)
B. calyciflorus density (no. ml-1)
Time (d)
RF
No. ml-1


d 6 VII
Relative fluorescence (RF)
B. calyciflorus density (no. ml-1)
Time (d)
RF
No. ml-1


e 320 µg P l-1
Relative fluorescence (RF)
B. calyciflorus density (no. ml-1)
Time (d)
RF
No. ml-1

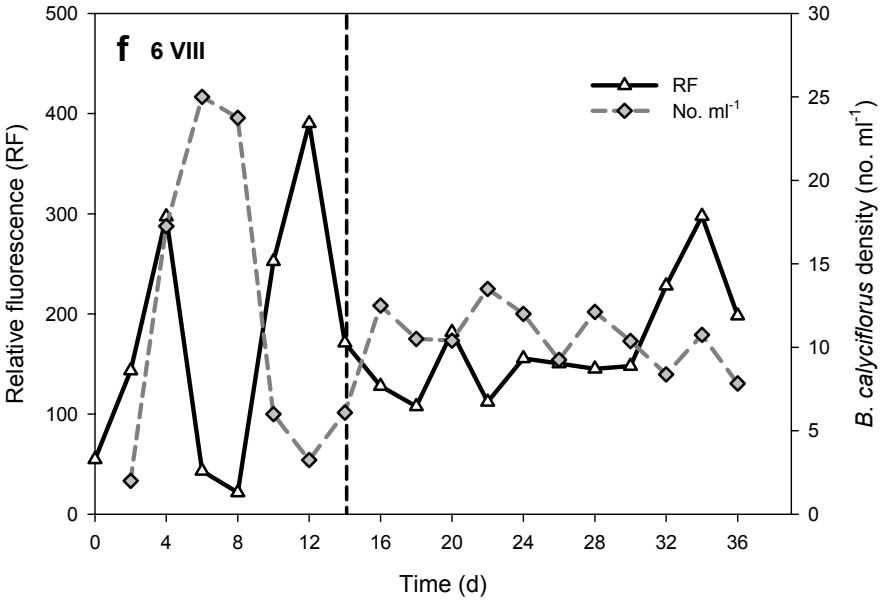

f 6 VIII
Relative fluorescence (RF)
B. calyciflorus density (no. ml-1)
Time (d)
RF
No. ml-1

FIGURE 2: Proportion of species, used as invaders in the main experiments (*Cryptomonas* sp. and *Cylindrospermopsis raciborskii*), reared together in separate microcosms with permanent and without herbivory. In the treatment with herbivory *Brachionus calyciflorus* was introduced at day two (with 2 individuals ml^{-1}). Thereby, its forage algae *Chlamydomonas reinhardtii* was accidentally introduced reaching a final proportion of 6.6% to the community. The experiment with the invader mixtures was finished after 36 days.

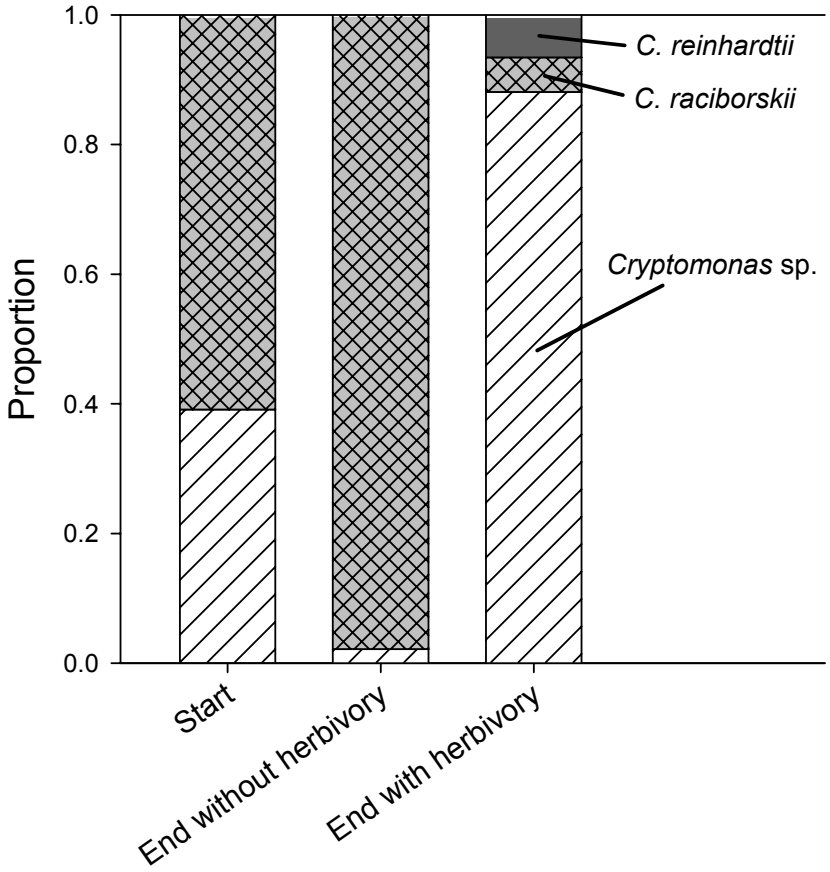


TABLE 1: Randomly selected species compositions of the diversity experiment with initial species richness level and species abbreviations. Asterisks denote microcosms without herbivory. Species abbreviations: *A.f.=Asterionella formosa, N.p.=Navicula pelliculosa, S.o.=Scenedesmus obliquus, A.g.=Ankistrodesmus gracilis, O.m.=Oocystis marsonii, M.m.=Monoraphidium minutum, C.r.=Chlamydomonas reinhardtii, C.v.=Chlorella vulgaris, P.a.=Planktothrix agardhii* and *A.f-a.=Anabaena flos-aquae.*

Species richness	Species compos.		Species									
			A.f.	*N.p.*	*S.o.*	*A.g.*	*O.m.*	*M.m.*	*C.r.*	*C.v.*	*P.a.*	*A.f-a.*
3	I				X		X				X	
3	II			X						X	X	
3	III						X	X		X		
3	IV			X	X		X					
3	V					X			X			X
3	VI		X				X	X				
3	VII			X		X						X
3	VIII		X		X		X					
3	IX					X			X		X	
3	X							X	X			X
4	I	*		X			X	X		X		
4	II	*	X			X				X	X	
4	III	*	X					X			X	X
4	IV	*			X		X		X	X		
4	V	*		X	X		X				X	
4	VI	*					X	X			X	X
4	VII	*	X		X	X		X				
4	VIII	*	X		X		X			X		
4	IX	*					X		X	X		X
4	X	*	X		X			X	X			
6	I		X	X					X	X	X	X
6	II		X				X	X		X	X	X
6	III			X	X			X		X	X	X
6	IV		X	X		X		X	X	X		
6	V			X	X	X	X			X		X
6	VI		X	X	X	X		X	X			
6	VII		X			X	X		X	X	X	
6	VIII			X			X	X	X	X		X
6	IX				X	X	X	X	X	X		
6	X		X		X	X		X	X		X	

General Discussion

In general, biodiversity effects on ecosystem processes and functions have been studied for different types of ecosystems, but frequently more for grasslands than other ecosystems such as freshwater and marine ones (Figure 1). This is surprising since aquatic microcosm studies offer a unique insight into the role of diversity that cannot be obtained from terrestrial experiments with their predominantly long-lived organisms (Giller et al. 2004, Gessner et al. 2004). Since primary producers provide the basis for higher trophic levels and contribute most to the total global biomass, changes to varying diversity were frequently investigated at the level of primary producers (Figure 1) and most of the measured ecosystem processes include their community biomass and their invasion resistance (Balvanera et al. 2006). In particular, experiments considering diversity effects on ecosystem processes have been mostly considered at the level of entire communities (Figure 2) even though community responses to diversity changes can depend on the performance of its component species (e.g., Dimitrakopoulos and Schmid 2004). As a consequence, analyses of biodiversity effects at the level of species and individuals are still missing, especially in grasslands, and biodiversity experiments are generally neglected for aquatic communities such as phytoplankton assemblages.

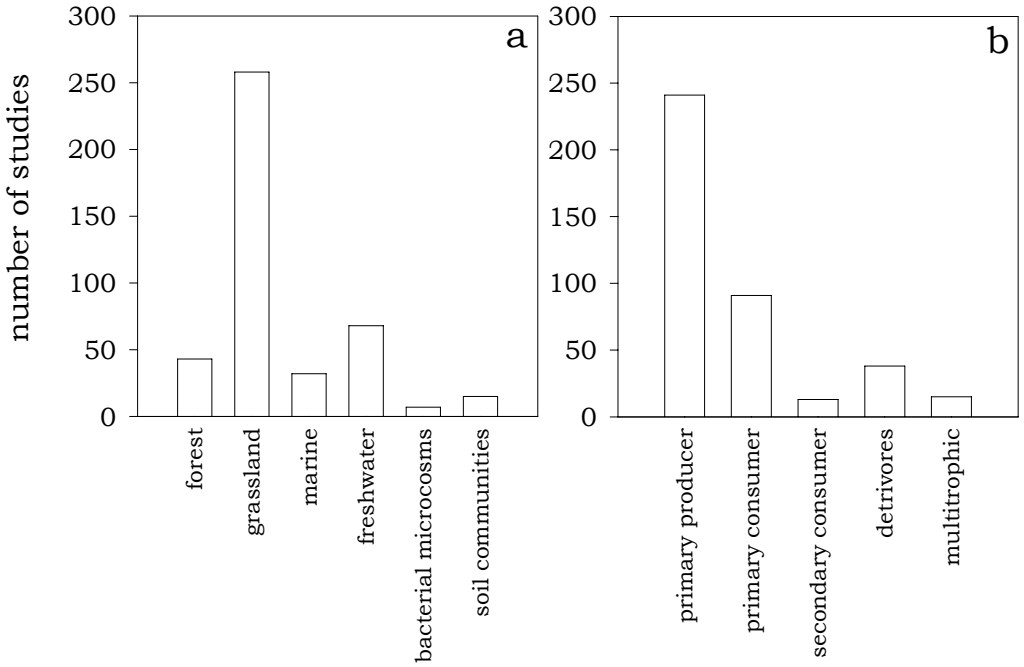


Figure 1: Number of studies that tested diversity effects on diverse ecosystem processes for different (a) ecosystem types and (b) trophic levels according to Balvanera et al. (2006). Multitrophic refers to studies where ecosystem processes involves more than one trophic level.

In general, the present thesis generally aimed to getting more insight into the open issues of biodiversity experiments by focusing down to individuals of terrestrial plants (Figure 2, green arrow) and down to species of phytoplankton communities (Figure 2, blue arrow) to better understand the underlying mechanisms behind the biodiversity-ecosystem functioning context.

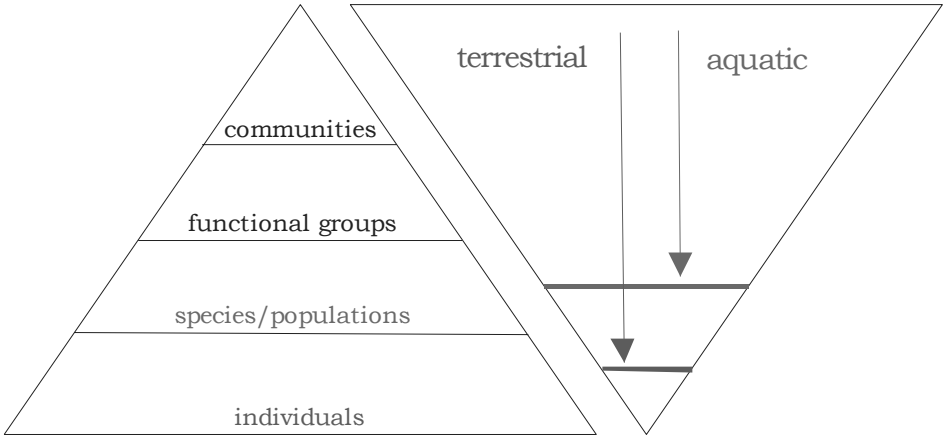


Figure 2: Scheme demonstrating a decline of emerging synthesis of biodiversity research (triangle, right) from the level of communities over functional groups and species/populations to individuals (triangle, left). The horizontal lines (green: terrestrial study, blue: aquatic studies) represent the integration of this thesis into the biodiversity-ecosystem functioning context. Please note that there are more biodiversity studies in terrestrial ecosystems than in aquatic ones.

Diversity effects at the community level

So far, positive relationships between diversity and community biomass have been found for terrestrial and aquatic ecosystems (reviewed by Cardinale et al. 2006, 2007). In particular, 78% of 44 reviewed biodiversity experiments showed overyielding but only 12% of those exhibited transgressive overyielding (Cardinale et al. 2007). In this thesis, both community overyielding and even transgressive overyielding were observed in two of three relevant studies (Table 1). This overyielding of the communities consisting of either terrestrial plants or algal species was mainly explained by a positive dominance and/or a positive complementarity effect (Table 1). Complementarity among species is thought to reflect species-specific differences in the spatio-temporal use of resources, the requirements of resources, or the ratios of resource demands. Moreover, the complementarity effect indicates facilitative interactions among species of a community. Terrestrial and other substrate-bound plants have different rooting architectures and depths permitting spatial complementarity in resource use. In contrast, algal species appear to belong to one meta

functional group with respect to spatial use of resources since they are free-floating species without roots. Their resource partitioning may have only occurred in time or as a function of resource type, and thus complementarity among substrate-bound species seems to be higher than for phytoplankton species. This contrasts with the fact that the proportions of non-transgressive and transgressive overyielding were slightly higher for the phytoplankton communities than for the terrestrial plants of the Jena Experiment (Table 1). Cardinale et al. (2007) showed that the probability for transgressive overyielding increases as experiments are run for longer time periods since complementarity among species grows stronger over time (e.g., Fargione et al. 2007, van Ruijven and Berendse 2005). Experiments conducted with phytoplankton communities offered approximately five generations of the species in monoculture and mixture whereas the annual, biennial or perennial plants of the Jena Experiment, which were sown in spring 2002, had approximately only two generations until transgressive overyielding was detected (Table 1). Therefore, the Jena Experiment has been performed for fewer generations of the focal organisms than the microcosm experiments with phytoplankton. This might give an explanation for the slightly higher proportion of both non-transgressive and transgressive overyielding for the phytoplankton communities, even though their resource use complementarity was assumed to be lower than that of terrestrial plants. However, overyielding of the terrestrial plant communities in the Jena Experiment and of the phytoplankton communities used in Chapter III was attributed largely to the complementarity effect, even though the underlying mechanisms for complementarity and facilitation are less clear for free-floating algal species than for substrate-bound plants.

Nevertheless, resource use complementarity among phytoplankton species was not a common finding in this thesis. The total biomass (also referred as to biovolume in this thesis) of the phytoplankton communities used in Chapter II were lower than the expected ones from monocultures, indicating community underyielding (Table 1). However, calculating the relative yield total (RYT), 13% of the communities achieved a value around one which is typically interpreted as non-transgressive overyielding due to complementarity among species. This pattern reflects a well-known limitation of the RYT method (Loreau 1998, Fridley 2001). For example, RYT values higher than one can be calculated when a low-productive species reaches a higher than expected yield in mixture while the other species maintain lower yields than expected from monoculture. In this case, the low-productive species becomes dominant in the mixture at the expense of other species which can lead to community underyielding due to a negative selection effect. This pattern was obvious in Chapter II and here, RYT values higher than one did not indicate community overyielding. The calculation of the RYT based on the relative yields of the species appears inappropriate for the detection of non-transgressive overyielding due to complementarity.

Instead, resource use complementarity among the phytoplankton species of Chapter II is not assumed. This is supported by the fact that all communities underyielded in this experiment.

Table 1: Occurrence of community overyielding according to the net biodiversity effect, the proportion of non-transgressive overyielding (relative yield total>1) and transgressive overyielding (D_{max}>0) and the underlying mechanisms causing community overyielding or underyielding in the Jena Experiment (Chapter I) and in the phytoplankton communities used in Chapters II and III. OY indicates overyielding.

	Jena Experiment (Roscher et al. 2005)	Phytoplankton communities (Chapter III)	Phytoplankton communities (Chapter II)
Overyielding (net biodiversity effect>0)	yes	yes	no
Non-transgressive OY	73%	81%	13%
Transgressive OY	23%	31%	0%
Mechanism	positive selection and complementarity effect	positive complementarity effect	negative selection effect

As mentioned above, underlying mechanisms for complementarity are less clear for free-floating algal species than for substrate-bound plants. Complementarity among species can depend on functional traits of species (Hooper and Vitousek 1997, Tilman et al. 1997, Hooper 1998, Mikola and Setälä 1998) and thus, the division of species into functional groups can lead to a better understanding of the complementarity effect. In this case, a positive relationship between the number of functional groups (functional diversity) and the community biomass will be observed when species diversity does not strongly change. However, although in Chapter III a high complementarity effect was detected according to the tripartite portioning method (Fox 2005), functional diversity did not positively affect the biomass of these phytoplankton communities. In Chapter II, the number of functional groups also did not influence the phytoplankton biomass, but here complementarity among the species was not found. *A priori* classifications of algal species into functional groups are often correlated to morphological traits (e.g., cell size, motility) and physiological traits (e.g., demand for silica, potential for N fixation). This classification might disregard traits that are relevant for e.g., competitive abilities and biomass production of the phytoplankton species. Therefore, functional diversity related to this classification can be a poor predictor for resource use complementarity among phytoplankton species, at least in the present thesis. However, the effect of functional diversity generally seems to be

outweighed by large differences in species-specific rates of productivity (Bruno et al. 2005, 2006, Griffin et al. 2009) since the phytoplankton species used in Chapters II and III differed greatly in their carrying capacities and growth rates. These differences tended to be higher within than among functional groups which can explain the lack of a functional diversity effect although a high complementarity effect was found in Chapter III.

However, the complementarity effect also indicates positive interactions among species (facilitation) since plant communities can benefit from nitrogen-fixing species such as legumes (Roscher et al. 2005, Spehn et al. 2005, Temperton et al. 2007) and cyanobacteria (Présing et al. 1996, Herrero et al. 2001). In the Jena Experiment (Chapter I) the presence of legumes enhanced the individual aboveground biomasses of other plant individuals because non-legumes weigh more when legumes are present in the community (facilitative interactions). In addition, the individuals of the legumes themselves weigh more than non-legumes leading to a higher aboveground biomass when legumes are present in the community. This effect corresponds with the positive effect of the cyanobacterium *Cylindrospermopsis raciborskii* on the phytoplankton community biomass in Chapter III. Contrary to the legumes in the Jena Experiment, the presence of *C. raciborskii* did not enhance the biomasses of other species and thus, facilitation by this species played a minor role in these phytoplankton communities. *C. raciborskii* was the most productive species in monoculture and increased the community biomass directly by its very high biomass in these mixtures.

Diversity effects at the species level

Diversity effects were mainly investigated at the level of entire communities and less at the species level although their response to changing diversity can be very different (Hector et al. 1999, Troumbis et al. 2000). In the experiments described in this thesis, the individual functional groups consisting of either terrestrial plants (Chapter I) or phytoplankton species (Chapters II and III) responded differently to changes in diversity. In the Jena Experiment, grasses and legumes had the tallest individuals and showed a stronger positive response in individual plant height with increasing species richness than small and tall herbs. Thus, they can be responsible for the average increase of individual plant height with increasing species richness across all species. The greater height of the grasses and legumes in more diverse communities corresponds with the fact that plastic responses to shading of smaller plants growing constantly under canopy shade are less pronounced than that of larger plants growing under sunny conditions (McLaren and Smith 1978), and that larger and smaller plants have different mechanisms to capture or use light (Werger et al. 2002, Anten 2005). Considering the yield exponent of the phytoplankton

species used in Chapter II (page 51) and Chapter III (Figure 3), the individual functional groups also responded differently to varying species diversity. For example, diatoms tended to exhibit a positive (Figure 3) or a negative (Chapter II) diversity effect on their yield exponent while green algae and phytoflagellates showed a less pronounced species diversity effect on their yield exponents (Figure 3 and Chapter II). Moreover, the green algae reached high relative yields in mixtures and thus, they contributed most to the community response. On the contrary, diatoms played only a minor role explaining community underyielding or overyielding although their yield exponent was positively affected by species diversity in Chapter III (Figure 3). These different responses of the individual functional groups of terrestrial plant and phytoplankton communities can be attributed to traits or characteristics which are more similar within than between functional groups. For example, the taller grasses and legumes responded more positively in their height to increasing diversity than the smaller herbs.

However, species within the same functional group also responded differently to changes in diversity. Thus, the response of some species can be accountable for the response across species of the same functional group. In the Jena Experiment, the relatively tall legume *Onobrychis viciifolia* showed the strongest positive response in its aboveground biomass to increasing species richness while the biomass of some other legumes decreased with increasing diversity. The same pattern was also found for the diatoms in Chapter III; the yield exponent of the mostly overyielding species *Asterionella formosa* was negatively affected by species diversity. On the contrary, species diversity had a positive impact on the yield exponent of *Stephanodiscuss minutulus* and *Cyclotella meneghiniana* which were both underyielding species. The classifications into functional groups can be very coarse (Lavorel et al. 1997) and therefore, species of the same functional group can still differ markedly in characteristics relevant for plant performance and yield exponent. This may lead to these different responses of individual species within the same functional group to varying diversity.

A similar pattern was also found in the study of Chapter IV where the invasibility of phytoplankton communities was investigated by using two functional different invader species: the less-edible, medium fast-growing species cyanobacterium *Cylindrospermopsis raciborskii* and the highly edible, fast-growing phytoflagellate *Cryptomonas* sp. The substantial herbivory by the generalist grazer *Brachionus calyciflorus* prevented a successful invasion of *C. raciborskii* but promoted that of *Cryptomonas* sp. and v*ice versa*. Thus, the functional traits of the invasive species had a strong effect on invasion success. Moreover, the species composition of the resident community, especially the presence of the green algae *Ankistrodesmus gracilis* (leading to a lower grazing intensity) and *Chlamydomonas reinhardtii* (similar functional traits as Cryptomonas sp.),

strongly influenced the invasibility of the phytoplankton communities. These results support the overall findings of the present thesis that both functional and species-specific traits can play an important role in the biodiversity-ecosystem functioning context.

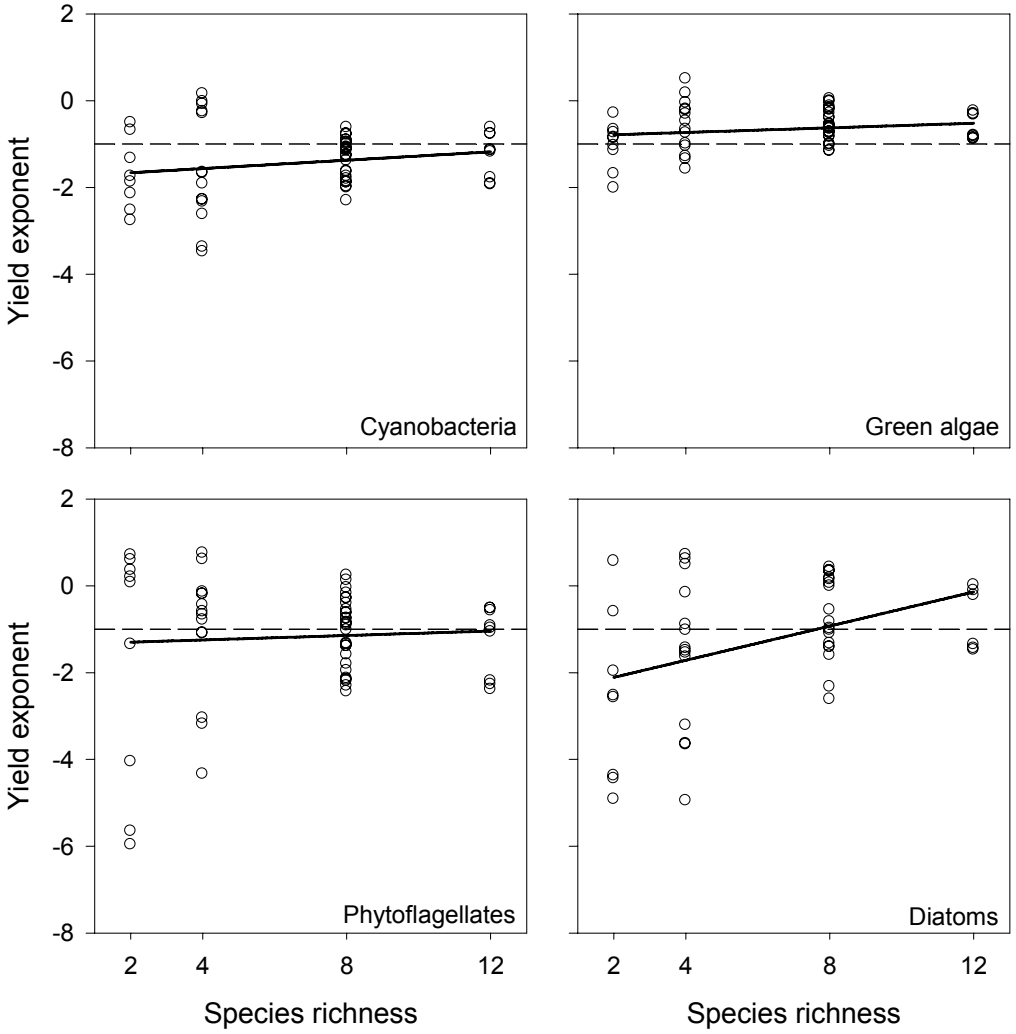


Figure 3: The effect of species richness on the yield exponents of the individual functional groups cyanobacteria, green algae, phytoflagellates, and diatoms used in Chapter III. Dashed horizontal lines represent the yield exponent values below which species are underyielding species. Solid lines present regression lines.

Diversity effects at the individual level

This thesis demonstrated that individual plant performance was affected by the diversity of the surrounding community (Chapter I). In particular, the average individual plant aboveground biomass decreased with increasing species richness. This provides evidence that the higher community biomass at higher species richness (Roscher et al. 2005) was observed due

to an increase in plant density in more species-rich plots (Marquard et al. 2009). Moreover, individual plant height increased with increasing species diversity indicating strong competition for light in more species-rich communities with a higher leaf area index. These findings at the level of individuals revealed underlying mechanisms at the community level in the biodiversity-ecosystem functioning context.

The present thesis did not aim to study diversity effects down to the level of algal individuals since their separation from communities seems to be experimentally difficult. Nevertheless, the cell size of algal species ranging from less than one µm up to several mm, seems to be a practical measurement at the level of individuals since it is a key trait that impacts e.g., growth and metabolism (Litchman et al. 2007). Diversity might have an impact on the individual cell size of algae due to the increasing interspecific competition in mixtures with increasing diversity. Contradictory to this hypothesis, functional diversity (Figure 4, r_S=-0.04, P=0.15) as well as species diversity (Figure 4, r_S=0.006, P=0.84) did not influence individual cell sizes among all species studied in this thesis (Chapters II and III). This suggests that the individual cell size is a poor parameter for investigating the effect of diversity on the performance of phytoplankton species, at least in the present thesis. However, organisms can respond at the cellular level to unfavorable conditions by a rapid acceleration in the rate of expression of a small number of specific genes. These gene products, the so-called heat shock proteins or stress proteins, which are also present under normal conditions but in lesser amounts, can increase and accumulate in cells to reach high concentrations under stressful situations. The estimation of such stress proteins in algal communities might demonstrate whether mixtures perform better than monocultures giving insights into the complementarity effect.

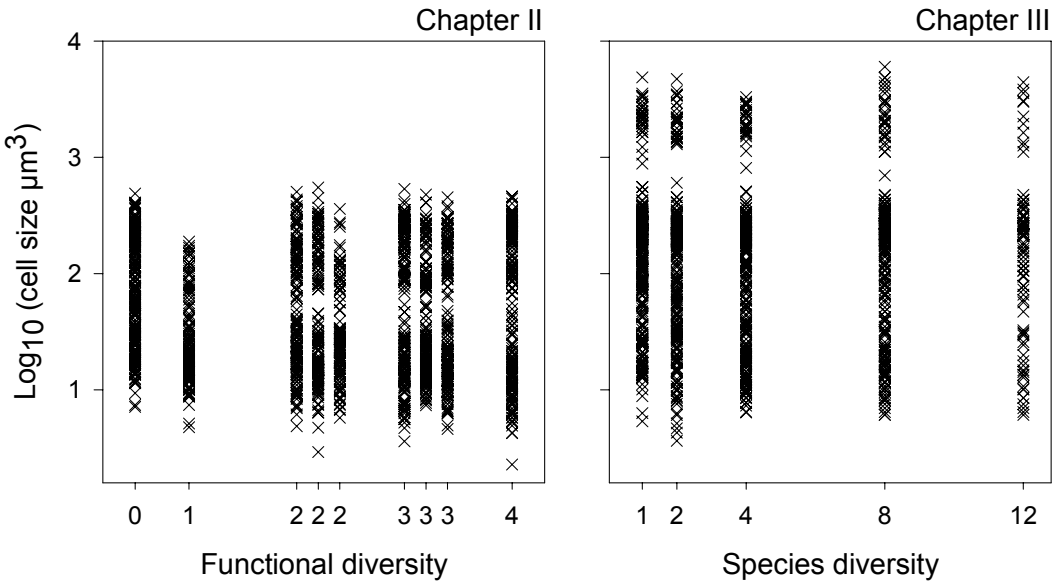


Figure 4: Cell size (µm³) of all algal species used in Chapters II (left) and III (right) depending on functional diversity (0=monoculture, 1-4 functional groups) and species diversity (1=monoculture, 2-4 species)

Conclusion

The present thesis contributes substantially to the understanding of open issues in both terrestrial and aquatic biodiversity experiments. To date, both research branches have reached different stages of development. The results of this thesis provide evidence for complementarity and facilitation among substrate-bound species and phytoplankton species but also show that resource use complementarity among free-floating species can be of minor importance. The underlying mechanisms for complementarity and facilitative interactions are less clear for algal communities than for substrate-bound species with different rooting architectures and depths. Thus, further research is required since the functional diversity of the phytoplankton communities seems to have little predictive power for the complementarity among algal species. Moreover, this thesis illustrates that it is important to separate contributions of the sheer presence of nitrogen-fixating species from their facilitative interactions with other plants and that the individual species responded differently to changing diversity, irrespective of whether they belong to one or different functional groups. The latter indicates that the response of both, certain functional groups and species, to varying species diversity can be responsible for the averaged community responses while functional and/or species-specific traits play a key role in explaining the different responses of individual species to diversity changes.

Summary

During the last decades, the potential consequences of human-caused species loss for ecosystem functioning have received considerable attention. To date, positive relationships between diversity (species richness, functional richness and composition of the community) and community biomass have been mainly found, especially in terrestrial ecosystems due to the complementarity and/or dominance effect. In this thesis, the effect of diversity on the performance of terrestrial plant and free-floating algal (phytoplankton) communities was investigated to get a better understanding of the underlying mechanisms in the biodiversity-ecosystem functioning context.

Community responses depend on the performance of component species since their responses to a changing diversity can be very different. In a large grassland biodiversity experiment, the Jena Experiment, the effect of community diversity on the individual plant performance was investigated by measuring the height, aboveground biomass, and inflorescence production of individual plants of all species. The species pool consisted of 60 plant species common to Central European mesophilic grassland of the *Arrhenateretum* type belonging to four functional groups (grasses, small herbs, tall herbs, and legumes). The Jena Experiment included 82 large plots (20x20m each) which differed in species richness (1-60), functional richness (1-4), and community composition. Individual plant height increased with increasing species richness suggesting stronger competition for light in more diverse communities. The aboveground biomass of the individual plants decreased with increasing species richness indicating stronger competition in more species-rich communities, which contrasts with the positive diversity effect on the community biomass in the Jena Experiment. Moreover, in more species-rich communities plant individuals were less likely to flower out and had fewer inflorescences which may be resulting from a trade-off between resource allocation to vegetative height growth and to reproduction. The individual plant performance was less affected by functional richness and the presence of legumes and grasses. Responses to changing species richness differed strongly between functional groups and between species of similar functional groups. To conclude, individual plant performance can largely depend on the diversity of the surrounding community.

As mentioned above, positive diversity effects on community biomass have been mainly found for substrate-bound plant communities. To test whether these findings can be generalised for free-floating algal communities, the effect of diversity on the biomass of phytoplankton was studied using microcosms. The communities consisted of eight algal species belonging to

four functional groups (green algae, diatoms, cyanobacteria, and phytoflagellates) and were grown at different functional richness levels (1-4). Functional richness and community biomass were negatively correlated and all community biomasses were lower than their average monoculture biomasses of the component species, revealing community underyielding. This was mainly caused by the dominance of a fast-growing species which built up low biomasses in monoculture and mixture (negative dominance effect). A trade-off between biomass and growth rate in monoculture was found for all species, and thus fast-growing species built up low biomasses and slow-growing species reached high biomasses in monoculture. As the fast-growing, low-productive species monopolised nutrients in the mixtures, they became the dominant species resulting in the observed community underyielding. As a consequence, diversity effects on community biomass may not be easily generalisable from substrate-bound plants to phytoplankton communities and *vice versa*. However, this study demonstrated that community underyielding can be caused by a negative relationship between biomass and growth rate of the individual species in monoculture.

It has been shown that numerous grassland and some freshwater communities tended to overyield (community performs better than its component monocultures). However, some experiments also provide evidence for community underyielding, which gives rise to the question when diversity causes community underyielding and overyielding. As mentioned by the study above, community underyielding can result from a negative relationship between biomass of the component species and their biomass in monoculture. These findings suggest community overyielding when biomasses of the component species are positively correlated with their growth rates in monocultures. In this case, fast-growing and high-productive species will be dominant while slow-growing and slow-productive species will be less abundant in mixtures. Aquatic microcosm experiments with an extensive design were performed to get a broad range of community responses. The phytoplankton communities differed in species diversity (1, 2, 4, 8, and 12), functional diversity (1, 2, 3, and 4) and community compositions. It was found that the species/functional diversity positively affected community biomass, revealing overyielding in most of the communities. This was mainly caused by a positive complementarity effect which can be attributed to resource use complementarity and/or facilitative interaction among the species. Overyielding of more diverse communities occurred when the biomass of the component species was correlated positively with their growth rates in monoculture. Thus, more diverse phytoplankton communities were dominated by fast-growing and high-productive species. Moreover, the cyanobacterium *Cylindrospermopsis raciborskii* enhanced community biomasses by its high biomass contribution rather than by its potential for nitrogen fixation. This and the

study mentioned above generated an emergent pattern for community overyielding and underyielding from the relationship between biomass and growth rate in monoculture as long as the initial community structure prevailed.

Invasive species like e.g., *Cylindrospermopsis raciborskii* which successfully invaded temperate regions of Europe and originated from tropical areas, can largely affect ecosystem processes, whereas species invasion is also influenced by community diversity. To date, studies revealed negative and positive diversity effects on the invasibility (susceptibility of a community to the invasion by new species). However, the invasibility is affected by a complex interplay of many factors such as e.g., nutrient availability and predation. Therefore, the effect of productivity (nutrient concentration ranging from 10 to 640 µg P L^{-1}), herbivory (presence/absence of the generalist feeder *Brachionus calyciflorus*) and diversity (3, 4 and 6 species were randomly chosen from the resident species pool) on the invasibility of phytoplankton communities consisting of 10 resident species was investigated using semi-continuous microcosms. Two functionally diverse invaders were chosen: the filamentous and less-edible cynaobacterium *C. raciborskii* and the unicellular and well-edible phytoflagellate *Cryptomonas* sp. Under grazing, the invasibility for both invaders were highest at medium productivity levels. The maxima of the unimodal pattern along the nutrient concentration were different for the two invading species due to their different functional traits. *Cryptomonas* sp. indirectly benefited from grazing pressure of herbivores whereas *C. raciborskii* suffered more from it. Diversity did not affect the invasibility of the phytoplankton communities. Rather, it was strongly influenced by the functional traits of the resident and invasive species which were mediated by grazing pressure.

Zusammenfassung

Die Ökosysteme unserer Erde sind durch das rasante Artensterben infolge von Umweltveränderungen durch den Menschen und des globalen Klimawandels stark betroffen. Mit den Auswirkungen dieses Artenverlustes und der damit einhergehenden Veränderung der Diversität (Anzahl von Arten, funktionellen Gruppen und die Artenzusammensetzung von Gemeinschaften) beschäftigt sich die heutige Biodiversitätsforschung. Spezieller wird der Effekt der Diversität auf Ökosystemprozesse wie beispielsweise den Biomasseaufbau von Primärproduzenten (grünen Pflanzen) oder der Resistenz einer Gemeinschaft gegen die Einwanderung neuer Arten untersucht. Primärproduzenten bilden in ihren jeweiligen Ökosystemen die Nahrungsgrundlage für die anderen Ebenen im Nahrungsnetz. Die Quantifizierung des Einflusses der Diversität auf die Primärproduktion und das Verständnis der zugrunde liegenden Mechanismen ist daher von besonderer Wichtigkeit. In terrestrischen Pflanzengemeinschaften wurde bereits ein positiver Diversitätseffekt auf die Gemeinschaftsbiomasse beobachtet. Dies wird hauptsächlich durch den Komplementaritäts- und/oder den Dominanzeffekt erklärt. Die Komplementarität zwischen Arten ist beispielsweise bei Unterschieden in der Ressourcenausnutzung gegeben (z.B. unterschiedliche Wurzeltiefen bei terrestrischen Pflanzen). Diese kann zu einer besseren Nährstoffausnutzung in diverseren Gemeinschaften führen, die letztlich deren höhere Biomassen erklärt. Der Dominanzeffekt hingegen beruht auf der in diverseren Gemeinschaften höheren Wahrscheinlichkeit, eine hochproduktive Art anzutreffen, was letztlich die höhere Biomasse der Gemeinschaft verursacht.

Diversitätseffekte auf Ökosystemprozesse wurden bisher hauptsächlich auf der Gemeinschaftsebene untersucht. Einige Studien zeigen jedoch, dass die einzelnen Arten einer Gemeinschaft unterschiedlich auf Diversitätsveränderungen reagieren können. Analysen über die Reaktionen, die alle Arten einer Gemeinschaft einschließen, fehlen bisher. Daher wurde der Einfluss der Diversität auf die individuelle Fitness von Pflanzenarten innerhalb des Biodiversitätsprojektes „Das Jena Experiment“ untersucht. Dieses Experiment umfasst 60 Arten, die charakteristisch für Mitteleuropäische Graslandschaften sind. Diese Arten wurden in die vier funktionellen Gruppen Gräser, kleine Kräuter, große Kräuter und Leguminosen eingeteilt. Im Freilandversuch zeigte sich, dass mit steigender Artenzahl die individuelle Pflanzenhöhe zunahm, während die individuelle oberirdische Biomasse sank. Der positive Diversitätseffekt auf die pflanzliche Gemeinschaftsbiomasse kann folglich nicht auf der individuellen oberirdischen Biomassezunahme beruhen. Überdies reagierten die einzelnen funktionellen Gruppen und sogar die einzelnen Arten innerhalb einer funktionellen Gruppe unterschiedlich auf Diversitätsveränderungen.

Folglich ist zu vermuten, dass einige Ökosystemprozesse auf Gemeinschaftsebene durch die Reaktionen von bestimmten funktionellen Gruppen bzw. Arten hervorgerufen werden.

Diversitätseffekte auf Gemeinschaftsbiomassen wurden bislang hauptsächlich mit terrestrischen Pflanzen und weniger mit frei-schwebenden Algenarten (Phytoplankton) erforscht. Demzufolge wurde der Einfluss der Diversität auf die Biomasse von Phytoplankton-Gemeinschaften experimentell untersucht, wobei es sowohl zu negativen als auch positiven Diversitätseffekten kam. Eine negative Beziehung zwischen Diversität und Gemeinschaftsbiomasse zeigte sich, wenn schnell-wüchsige Algenarten nur geringe Biomassen in Mono- und Mischkultur aufbauten. Die vorhandenen Nährstoffe in der Mischkultur wurden von den schnell-wüchsigen Arten monopolisiert und folglich standen sie den langsam-wüchsigen Algenarten, welche viel Biomasse in Monokultur aufbauten, nicht mehr zur Verfügung. Zu einem positiven Diversitätseffekt auf die Gemeinschaftsbiomasse kam es, wenn die Artengemeinschaft eine positive Beziehung zwischen Wachstumsrate und Biomasse in Monokultur zeigte, sodass die schnell-wüchsige Algenarten viel Biomasse aufbauten. Da diese schnell-wüchsigen Algen in der Mischkultur dominant wurden, bestand die Gemeinschaft letztlich aus hoch-produktiven Algenarten, was zu einer erhöhten Gesamtbiomasse führte. Diese beiden Versuchsansätze verdeutlichen Mechanismen für die unterschiedlichen Reaktionen der Gemeinschaften auf Diversitätsveränderungen, welche auch für terrestrische Pflanzengemeinschaften gefunden wurden.

Ein anderer wichtiger Ökosystemprozess, der von der Diversität beeinflusst wird, ist die Anfälligkeit von Gemeinschaften gegenüber invasiven Arten (Invasibilität). Die Invasibilität wird von einer Vielzahl von Faktoren beeinflusst und demzufolge wurde der Effekt der Diversität und der Produktivität (Nährstoffgehalt) auf die Invasibilität von Phytoplankton-Gemeinschaften in An- und Abwesenheit eines Herbivoren (Pflanzenfresser, Rädertier) untersucht. Die zwei funktionell unterschiedlichen invasiven Arten waren die Blaualge *Cylindrospermopsis raciborskii* (schlecht fressbar) und der Phytoflagellat *Cryptomonas* sp. (gut fressbar). Es zeigte sich, dass der Fraßdruck, welcher selber durch die Produktivität beeinflusst wurde, einen bedeutenden Effekt auf die Invasibilität von Phytoplankton-Gemeinschaften hat. Die funktionellen Eigenschaften der invasiven und residenten Arten waren zudem bedeutender als die Artenzahl.

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Declaration

This thesis includes one terrestrial and three aquatic manuscripts which I prepared either in cooperation with co-authors (Chapter I-III) or as co-author (Chapter IV).

Chapter I: The initial ideas were conceived by Prof. Dr. Markus Fischer who also contributed to the written form and content of the manuscript. With the help of Tanja Rottstock I developed the experimental setup and collected the data. I personally wrote the manuscript including data-analyses, figures and tables and corresponded to editors and referees during the publication process. Prof. Dr. Ursula Gaedke contributed to the written form and content of the manuscript.

Chapter II: My ideas and the setup of this experiment arose from discussions with Prof. Dr. Ursula Gaedke and PD Dr. Guntram Weithoff. I conducted the microcosm experiments, analyzed the data, personally wrote the manuscript and corresponded to editors and referees during the publication process. Prof. Dr. Ursula Gaedke and PD Dr. Guntram Weithoff contributed to the written form and content of the manuscript.

Chapter III: This manuscript emerged from findings of Chapter II. My ideas and the experimental setup arose from discussions with PD Dr. Guntram Weithoff, Prof. Dr. Markus Fischer and Prof. Dr. Ursula Gaedke. I performed the microcosm experiments, analyzed the data and personally wrote the manuscript. Prof. Dr. Ursula Gaedke and PD Dr. Guntram Weithoff contributed to the written form and content of the manuscript.

Chapter IV: This manuscript arose from the diploma thesis of Erik Sperfeld which was supervised by Prof. Dr. Ursula Gaedke and PD Dr. Guntram Weithoff. Erik Sperfeld performed the experiments and wrote the manuscript including data analyses, figures and tables. I contributed with my practical expertise to the overall ideas, the experimental setup, the performance of this study and to the written form and content of the manuscript.

Erklärung

Die geltende Promotionsordnung der Mathematisch- Naturwissenschaftlichen Fakultät der Universität Potsdam ist mir bekannt.

Die vorliegende Dissertation habe ich selbständig angefertigt und hierbei alle verwendeten Hilfsmittel, persönlichen Mitteilungen und Quellen angegeben.

Ich habe die Dissertation noch nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung eingereicht. Ferner habe ich nicht die gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei einer anderen Hochschule als Dissertation eingereicht.

Potsdam, den 27. November 2009

Andrea Schmidtke

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