Diversity Effects on Ecosystem Processes: a mechanistic Approach using Plankton Communities

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'Value is an intrinsic part of diversity; it does not depend on the properties of the species in question, the uses to which particular species may or may not be put, or their alleged role in the balance of global ecosystems. For biological diversity, value is. Nothing more and nothing less.'

David Ehrenfeld, 1988

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SUMMARY

Phytoplankton communities are among the most species-rich compartments of marine and limnic ecosystems and their primary production provides the basis for nearly all aquatic food webs. Although factors that shape and maintain the puzzling diversity of phytoplankton organisms have long been the subject of scientific research, the consequences of diversity for aquatic ecosystem processes have not so far been thoroughly explored. Ecosystem processes, such as primary production or transfer dynamics between trophic levels, have repeatedly been shown to be positively affected by species richness, but the underlying reasons for these positive correlations are still largely unclear. Recently, the focus has been directed towards functional trait diversity rather than to the actual number of species, because functional diversity is based on a strictly mechanistic (ecophysiological) point of view. This approach promises a deeper understanding of diversity-ecosystem process relationships, and thus a higher predictive accuracy of the consequences of ongoing, accelerating biodiversity loss.

I investigated the link between diversity, productivity and food web dynamics in a series of laboratory and field experiments, using artificially assembled and natural plankton communities. Importantly, my experiments were grounded on the hypothesis that algal diversity and productivity are positively linked via complementary use of light among phytoplankton species. This link should be mediated through complementary spectral light absorption by photosynthetic pigment complexes. Resulting higher resource (light) use efficiency could allow higher productivity of more diverse primary producer communities, and affect adjacent trophic levels (herbivore consumers).

Experiments showed increasing primary productivity (determined as biomass accrual, oxygen production, or ^{14}C-uptake) in more diverse phytoplankton communities, which was consistently detectable on a scale ranging from 100 ml freshwater microcosms to open ocean areas. Surveys of several laboratory and natural communities revealed that more diverse algal communities contain more diverse sets of photosynthetic pigments, and that higher pigment richness and diversity was reflected in higher specific light absorbance and spectral light use efficiency. Accordingly, greater pigment diversity correlated with higher community biomass accrual, which in most cases was attributable to the complementarity effect (positive species interactions), rather than to the selection effect (dominance of highly productive species). Hence, my results suggest that spectral partitioning of the light spectrum, based on individual

pigment composition (identity and frequency), can provide a mechanistic, trait-based explanation for positive diversity-productivity relationships in phytoplankton communities.

Moreover, I conducted experiments to examine how such positive diversity-productivity relationships in phytoplankton communities transfer to the next trophic level (herbivorous zooplankton). Higher resource use efficiency in diverse primary producer communities can lead to higher prey community biomass, presumably yielding beneficial effects on zooplankton. On the other hand, these positive diversity effects could be cancelled out by poorer food quality, due to the presence of inedible algal species, or stoichiometric constraints. My experiments, conducted in laboratory freshwater systems, revealed strong positive effects of producer diversity on consumer biomass, survival, reproduction, and population stability on a short-term (two weeks), and on a long-term (up to 35 weeks, equalling up to 100 phytoplankton generations) scale. Stoichiometric or species-specific negative effects turned out to be of minor importance. The net biodiversity effect on zooplankton growth was considerably strong and quantitatively comparable to that of substantial light enrichment.

In summary my results show that light partitioning can be an ecophysiological mechanism underlying positive biodiversity – ecosystem functioning patterns in phototroph communities. Furthermore, enhanced resource use efficiency, resulting from diversity-dependent niche partitioning, can positively affect further food web compartments.

1. GENERAL INTRODUCTION

1.1 Biodiversity, species loss and the functioning of ecosystems

Whilst the term 'biodiversity' has become an inherent part of everyday language in science as well as for the general public and in politics, there is a notable and somewhat surprising lack of a universal definition for that term. Ecologists complain of a growing 'terminological confusion around the concept diversity' (Tuomisto 2010) and its misuse as an umbrella term for a wide array of conceptually different phenomena, demanding a mathematically well-defined approach (Moreno & Rodríguez 2011). Others argue that it is precisely this diversity in definitions that is an inherent feature of biodiversity (Begon et al. 2006, Gorelick 2011).

A widely accepted though rather broad definition of biodiversity was given in the Convention on Biological Diversity in 1993, which defined biodiversity as 'the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.' (Mace et al. 2012).

Hence, biodiversity can be defined as a 'collective term for all biological differences at scales ranging from genes to ecosystems' (Harper & Hawksworth 1994), including variability among cells, individuals, races, species, populations, communities, and ecosystems. Most commonly, this variability is measured in terms of simple counts (e.g., number of different species: 'species richness'), relative abundance (e.g., distribution of biomass among different species in a community: 'evenness'), or is expressed by means of a diversity index (e.g., Shannon diversity index, H; Simpson index, D), mathematically combining both absolute numbers and relative distributions (Begon et al. 2006, Hillebrand et al. 2008, Soininen et al. 2011).

These basic and widespread measures of diversity have been extended by a recently emerging approach arguing that in a given environment, rather than the number and relative abundance of species, it is the presence and distribution of context-dependent 'functional traits' that determine a community's performance (Naeem & Wright 2003, Mouillot et al. 2005, Hillebrand & Matthiessen 2009). A functional trait can be any property of organisms that 'strongly influences organismal performance' (McGill et al. 2006), such as characteristic physiology, morphology, or life history. This concept is called 'functional diversity' and is

considered to provide a more mechanistic and thus more predictive understanding of how diversity influences community / ecosystem properties (Díaz & Cabido 2001, Lavorel & Garnier 2002, McGill et al. 2006, Petchey & Gaston 2006, Reiss et al. 2009).

Early naturalists such as C. Linnæus or A. v. Humboldt were already fascinated and puzzled by the sheer endless diversity of life forms on earth, but their main scientific purpose was to collect, sort and classify species (Linnæus 1758, von Humboldt 1849). Today, biodiversity research has again become a major topic of scientific interest, generated by the widespread and accelerating loss of species, populations and habitats (Balmford & Bond 2005, Butchart et al. 2010), occasionally denoted as 'earth's sixth mass extinction' (Barnosky et al. 2011). This decline in biological variety has also evoked broad public and political interest, because of its feared socio-economic consequences (Chapin et al. 2000, Tilman 2000, Loreau et al. 2006, Brauman et al. 2007). Rockström and co-workers numbered biodiversity loss as one of the key 'earth-system processes' (beside ocean acidification, consumption of freshwater, atmospheric CO_2 concentration) that are likely to pose substantial and far-reaching threats to human welfare in the future (Rockström et al. 2009).

Obviously, human societies have always been reliant (and dependent) on a multitude of so-called ecosystem services, meaning all kinds of goods and services provided by ecosystems (Díaz & Cabido 2001, Mace et al. 2012), such as food species, water purification, oxygen generation, or soil nutrient recycling (Balmford & Bond 2005, Balvanera et al. 2006, Worm et al. 2006). Nevertheless, it was not before the early 1990s that ecologists made the first efforts to reveal the fundamental relationships between biodiversity and 'ecosystem functioning' (whereby ecosystem functioning is supposed to be a requirement for use of ecosystem services; Reiss et al. 2009).

The first series of biodiversity – ecosystem functioning (BEF) experiments focused mainly on terrestrial vascular plant communities ('grassland experiments'; e.g., Tilman et al. 1996, 1997, Hooper & Vitousek 1997, Hector et al. 1999), measuring surrogates of primary productivity (above / below ground biomass production, or standing stock biomass) along artificially created gradients of species richness or functional group richness. Since then, experimental and theoretical work has proposed and tested various hypotheses, concentrating mainly on the relationships between diversity as an independent variable, and productivity (most frequently), respiration rates, temporal stability / variability in standing stocks or

productivity, nutrient cycling, and resilience / resistance to perturbation (Balvanera et al. 2006). These experiments were performed in a multitude of terrestrial and aquatic communities and ecosystems (see reviews by Díaz & Cabido 2001, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Cadotte et al. 2008, Cardinale et al. 2011).

Although the generality of patterns and processes observed in individual studies has been the subject of considerable debate (including experimental designs, diversity measures, or statistical methods, e.g., Wardle 1999, Petchey 2004, Wright et al. 2006, Jiang et al. 2009), the large majority of studies (and various meta-analyses performed thereof) point towards the existence of a generally positive but decelerating, i.e., saturating effect of diversity on most ecosystem processes (Cardinale et al. 2011).

1.2 Niche differentiation as a general explanatory approach for positive biodiversity effects on productivity

The remarkable and widespread correlations described between ecosystem processes such as primary productivity and the biological diversity of the system under examination are well documented. However, the underlying mechanisms are not yet fully understood (Loreau et al. 2001, Cardinale et al. 2011).

Most explanatory approaches are based on the ecological niche concept, elaborated by Hutchinson (1957), which states that 'each species is most suitably adapted to a particular, unique multidimensional combination of abiotic and biotic environmental factors' (Falkowski & Raven 2007). Therefore, a niche is an attribute of a species (or population), defined by a potentially infinite number of niche dimensions (such as temperature range, resource supply, predation pressure), that reciprocally corresponds with the physical space in which a species lives (Hutchinson 1957, Colwell & Rangel 2009).

In an ecological context, each species can be defined as a combination of (evolving) traits, which can be related to life history or resource uptake, and thus tightly coupled with the ecological demands of a species. Consequently, a species-rich (diverse) community should consist of a greater number of different traits, as a result of niche differentiation processes among coexisting species (Tilman 2000, Hooper & Dukes 2004, Levine & HilleRisLambers 2009). Compared to less diverse communities, a higher degree of niche differentiation (which may occur in space, time or resource type) can enable more diverse communities to more

completely (i.e., more efficiently) exploit limiting resources, such as light or nutrients. For example, the total nitrogen (N) pool in a water column can be specifically taken up as molecular nitrogen (N_2), nitrate (NO_3^-) or free amino acids by different phytoplankton species or (functional) groups, where each species / group may be restricted to the uptake of one particular nitrogen compound (Lampert & Sommer 2007). Likewise, algal species differ in their abilities to use different parts of the underwater light spectrum, depending on their individual pigment composition (Stomp et al. 2004, 2007, Falkowski & Raven 2007, Kirk 2011). Further examples of niche differentiation include varying root morphologies or adaptations to different light intensities in vascular plants.

Such complementary resource use ('niche complementarity') is assumed to be a major underlying reason of positive biodiversity-productivity relationships (Tilman et al. 1997, Fridley 2001, Loreau et al. 2001, Hooper & Dukes 2004, Vanelslander et al. 2009), although experiments explicitly addressing the physiological basis of complementary resource use have been rare (Cardinale 2011).

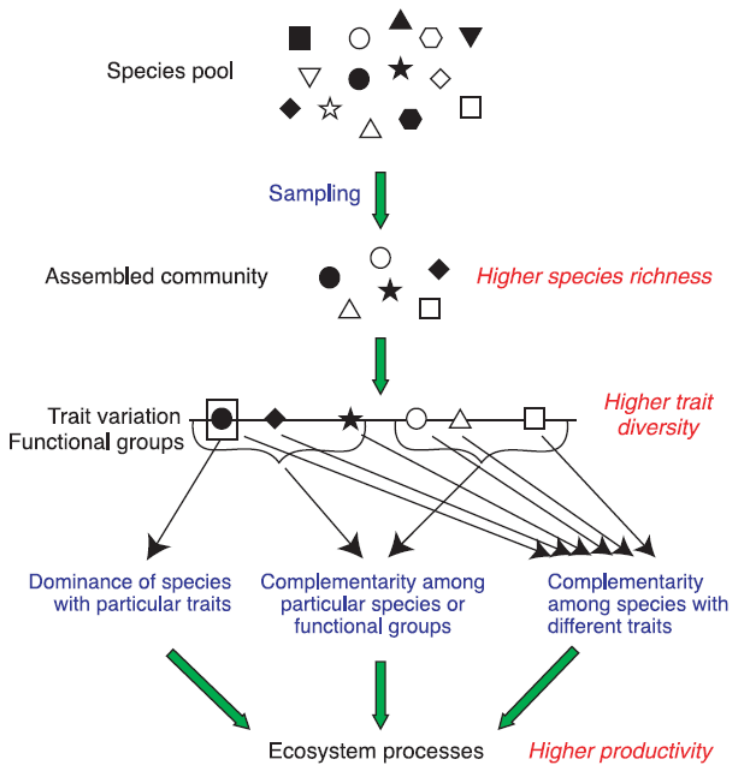

Fig 1. Processes supposed to underlie diversity effects in BEF experiments. Experimental communities usually represent artificial species combinations, being randomly assembled from a predefined species pool. Increasing species richness implies an increasing number of functional traits. However, positive diversity effects such as enhanced productivity may be attributed to both complementarity between different species / functional groups / traits, and the dominance of a particular species. (Figure from Loreau et al. 2001).

An alternative explanation attributes the positive relations between biodiversity and productivity to the occurrence of sampling or selection probability effects (Loreau 1998,

Fridley 2001, Hector et al. 2002, Hooper & Dukes 2004), meaning that more diverse communities are more likely to contain and become dominated by a species with particularly important traits (e.g., a particularly high growth rate). However, it is likely that in natural communities both aspects, i.e., both niche complementarity and species identity, are drivers of aggregate productivity, with varying relative importance (Fig. 1; Loreau et al. 2001). The potential degree of niche complementarity obviously depends on the number and identity (i.e., diversity) of both species-specific traits and on environmental heterogeneity (Hutchinson 1961, Harpole & Tilman 2007, Ptacnik et al. 2010).

Loreau & Hector (2001) introduced a mathematical method that allows *post hoc* distinction between the relative importance of 'complementarity effects' and 'selection effects' in multispecies experiments, based on monoculture and polyculture yields. The complementarity effect measures any (positive or negative) change in the average relative yield in a mixture, where positive changes may result from resource partitioning or facilitation, and negative effects may result from physical or chemical interference. The selection effect occurs when changes in the relative yields of species in a mixture are non-randomly related to their traits (yields) in monoculture and is measured by a covariance function. The sum of these two effects (the net biodiversity effect) measures deviation of the mixture yield from its expected value on the basis of monoculture yields and the relative abundance of species in the mixtures (Loreau & Hector 2001). This deviation from the expected value (the net biodiversity effect) is qualitatively equal to another well-established measure in BEF experiments, which is called overyielding (if more than expected), or underyielding (if less than expected). Complementary resource use and facilitation among species are discussed as two primary mechanisms leading to community overyielding (Loreau 1998, Hooper & Dukes 2004).

Loreau and Hector's method is widely used and accepted as a tool to better understand the often somewhat indistinct description of 'biodiversity effects'. However, it is applicable only to experimental communities and, due to its purely statistical nature, does not contribute to identification of the underlying ecophysiological mechanisms / traits that ultimately support biodiversity effects.

1.3 Complementary use of light: a possible mechanism for diversity effects in phytoplankton communities

Light is the primary source of energy on earth, driving directly or indirectly all major ecosystems through its conversion to chemical bond energy in photosynthesis. Light absorption is the initial step in photosynthesis. While the principal functioning of the photosynthetic apparatus is similar among most phototrophic organisms (as a result of joint evolution; Barsanti & Gualtieri 2006, Falkowski & Raven 2007), there is remarkable variation in the nature and composition of light-absorbing pigments. Beside chlorophyll (chl) *a*, which plays a key role in photosynthesis of all phototrophic eukaryotes and cyanobacteria, there exist a wealth of accessory pigments (located in antenna complexes) with distinct absorption maxima and absorption ranges in the spectrum of photosynthetically active radiation (PAR), ranging from 400-700 nm wavelength (Fig. 2; Rowan 1989, Jeffrey et al. 1997, Scheer 1999, Kirk 2011). While the specific absorption characteristics of each pigment also depend on its chemical structure (including associated proteins), the assembly of accessory pigments in antenna structures increases the effective absorption cross-section of photosystems by one to two orders of magnitude (Renger 1999, Blankenship 2002). Photons, captured by antenna pigments, are transferred to the photosynthetic reaction centres, where the primary photochemical redox reactions take place.

In contrast to vascular plants, algae consistently show a much greater variety of accessory pigments, including chlorophylls *c* and *d*, several types of phycobilins, and a generally high abundance of different carotenoids. The identity and combination of accessory pigments are highly specific to distinct algal groups (e.g., peridinin and chl *c* in dinoflagellates, fucoxanthin and chl *c* in diatoms, lutein and chl *b* in chlorophytes, phycobilins and myxoxanthophyll in cyanobacteria, etc.) and are therefore often used as 'marker pigments' for phytoplankton identification (Wilhelm 1999, Schlüter et al. 2006). Since pigment composition and plastid structure of phytoplankton is considered to reflect very well its evolutionary history, algal taxonomy is historically largely built upon the presence of such marker pigments (Falkowski et al. 2004a).

While the existence of large differences in pigment composition among phytoplankton has long been recognized, its ecological significance is still a topic of considerable research (Falkowski & Raven 2007, Dubinsky & Schofield 2010, Zohary et al. 2010). Phytoplankton

experience enormous changes in light supply when transported through a mixed water layer. With increasing depth, not only light intensity decreases exponentially (as described by the Lambert-Beer law, see e.g., Kirk 2011), but also the spectral composition of light changes as a result of wavelength-specific scattering and absorption of light by particles, water molecules, or phototrophic organisms (Kirk 2011).

In contrast to many terrestrial habitats, where water supply (accompanied by nutrient uptake) rather than light confines primary production, aquatic phototrophs live in an optically dense medium where light availability often becomes limiting (van Oijen et al. 2004, Dubinsky & Schofield 2010, Kirk 2011). This frequent shortage of irradiance, together with unpredictable shifts in spectral composition that are unavoidable for a passively drifting organism, has been suggested to serve as an explanation for the high variety of photosynthetic (and photo-protective) pigments present in phytoplankton (Scheer 1999, Falkowski et al. 2004b).

Wavelength-specific absorption of light by photosynthetic pigments, coupled with heterogeneity in the spectral distribution of light in aquatic habitats, yields the potential for diversity effects based on light quality. Compared with species-poor communities or monocultures, more diverse algal communities should exhibit a higher variety of photosynthetically active pigments. The pigments' absorption spectra should be less redundant and thus cover the available light spectrum more evenly (completely). Such niche complementarity would provide a possible ecophysiological mechanism for diversity effects in phytoplankton communities based on complementary resource (i.e., light) use.

A higher variety of functional traits (wavelength-specific absorption) can cause higher resource use efficiency and thus a positive relationship between (functional) diversity and ecosystem processes.

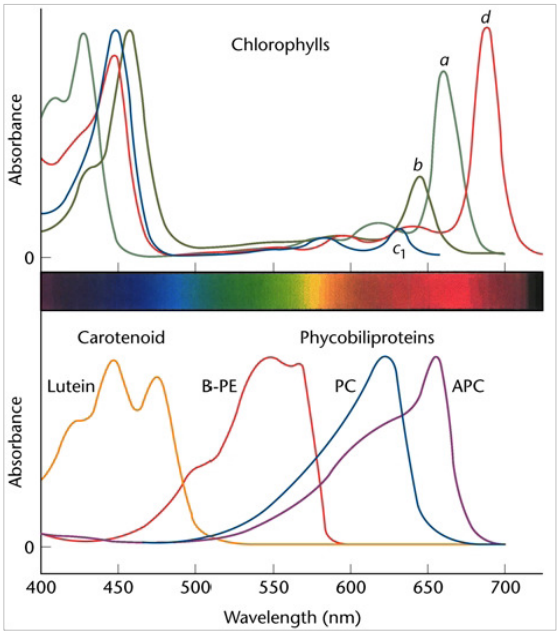

Fig. 2. Qualitative absorption spectra of some major photosynthetic pigments commonly found in algae: chlorophylls (*a, b, c_1, d*), phycobiliproteins (APC: allophycocyanin, PC: phycocyanin, B-PE: phycoerythrin), and the carotenoid lutein. While chlorophylls capture photons mainly in the blue and red range of the visible light spectrum, phycobilins and carotenoids effectively cover the 'green gap' in between. (Figure from Gantt, E. & Cunningham, F. X. Jr. 2001.)

1.4 Diversity and trophic interactions

Most biodiversity – ecosystem functioning studies have focused on the primary producer level (Balvanera et al. 2006, Cardinale et al. 2011). This is partly due to the fact that experimental two-level systems (resources–primary producers) are generally easier to manage and results are easier to interpret than three- (or more) level systems (resources–primary producers–consumers) with various interactions and feed-back mechanisms (Duffy 2002, Duffy et al. 2007). The main reason, however, is that primary producers represent the basal component of most ecosystems, which make them a logical starting point from which to begin detailed studies on biodiversity-ecosystem functional relationships (Loreau et al. 2001).

Traditionally, studies of trophic interactions and food web dynamics have focused on total trophic level biomass and on total nutrient pools, often irrespective of species composition or trait diversity related to nutrient (resource) uptake (e.g., Carpenter et al. 1985, Sommer et al. 1986, Carpenter & Kitchell 1993, Sarnelle 1993). Clearly, total food web production (and also the possible length of food chains) is ultimately limited by the amount of available resources at the bottom of the food web (Carpenter et al. 1985, Persson et al. 1992). However, recent experiments and theoretical considerations demonstrated that species or trait diversity can enhance resource-use efficiency of primary producer communities, meaning that

a given amount of resource can be exploited more completely, through complementary resource use (Ptacnik et al. 2008, Cardinale 2011). The question of how this effect of diversity that is emerging at the basic trophic level affects adjacent or further trophic levels is vital to a better understanding of the role of biodiversity in natural food webs.

Although higher resource use efficiency can result in higher primary productivity, its effects on herbivores remain unclear. Beside enhancing secondary production, higher primary production can paradoxically also evoke constraints to herbivores: higher primary productivity can be accompanied by a change in nutritional quality, i.e., the stoichiometric composition of biomass, with respect to essential elements or macromolecules (e.g., phosphorus, nitrogen, vitamins, fatty acids). Stoichiometric mismatches between consumers and prey biomass was repeatedly demonstrated to potentially impair herbivore growth (e.g., Urabe & Sterner 1996, DeMott 1998, Hessen et al. 2002, Andersen et al. 2007, Müller-Navarra 2008).

Additionally, higher primary productivity does not necessarily increase the abundance of edible prey species. It has been suggested that in phytoplankton a trade-off exists between a species' resistance to grazing and its maximum growth rate, where resistance may result from inappropriate size and morphology, or from toxicity (Sarnelle 1993, Agrawal 1998, Steiner 2001). Given that a more diverse community is more likely to contain such inedible species, diversity-related positive effects on primary production may not translate to the next trophic level (herbivores) because of overriding negative effects, resulting from inedible prey species, which may dominate the community under grazing pressure (Steiner 2001, Duffy 2002, Edwards et al. 2010).

It has been shown that diversity effects tend to dampen with increasing trophic distance, i.e., the number of trophic levels between the 'manipulated' and the measured community (Balvanera et al. 2006, Scherber et al. 2010). However, precisely evaluating if and how diversity-borne effects travel through complex food webs is still a major challenge to understanding the role of diversity in 'real-world ecosystems' and to predicting the possible constraints arising from species loss (Duffy & Stachowicz 2006, Duffy 2009).

2. THE CENTRAL SCIENTIFIC QUESTIONS OF THIS THESIS

From the above it follows that, besides the considerable progress that has already been made in promoting knowledge about how biodiversity drives ecosystem dynamics, there exists a number of central scientific questions, which are either still poorly understood or have not so far been investigated. In my thesis, I explore several of these issues by addressing the following scientific questions, clustered into four central aspects:

A) Biodiversity – ecosystem functioning in phytoplankton communities

1) Does phytoplankton diversity affect pelagic ecosystem processes, especially primary productivity?
2) Are the strength and the shape of this relationship dependent on the different measures that are usually used to determine diversity?
3) Is this relationship dependent on the presence of particular species, or does it arise from complementary resource use / facilitation among species?

B) Mechanistic investigations of biodiversity – ecosystem functioning relationships in phytoplankton communities

1) Is spectral niche differentiation in the use of light a possible mechanism underlying diversity–productivity relationships in phytoplankton communities?
2) Is spectral niche differentiation in the use of light mediated by species-specific pigment composition and absorption characteristics?
3) Does this possible mechanism, other than affecting primary production and carbon accrual, also affect elemental biomass composition (stoichiometry) of phytoplankton?

C) Multi-trophic diversity effects in pelagic food webs

1) Do biodiversity effects emerging at the primary producer level travel up the food chain?
2) Do herbivorous consumers show any positive or negative response to algal diversity in growth or demography?

D) General validity and global importance of diversity – ecosystem functioning relationships in pelagic environments

1) Are diversity–productivity relationships, the hypothesized underlying mechanism, and multi-trophic effects which may be identified in synthetic (laboratory) communities, applicable to natural plankton communities, including freshwater and marine pelagic systems?
2) Do diversity–productivity relationships, the hypothesized underlying mechanism, and multi-trophic effects occur at larger scales in time (generations) and space?
3) Do diversity effects significantly influence community processes, in particular relative to strong environmental factors (e.g., the effects of varying resource supply)?

In the following, I present the results of my experimental work investigating these questions. The work has led to the preparation of five papers, two of them published (Publications I & II), and three submitted (Manuscripts I, II & III).

PUBLICATION I

SPECTRAL NICHE COMPLEMENTARITY AND CARBON DYNAMICS IN PELAGIC ECOSYSTEMS

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Notes and Comments

Spectral Niche Complementarity and Carbon Dynamics in Pelagic Ecosystems

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ABSTRACT: Positive effects of biodiversity on ecosystem function are described from an increasing number of systems, but the underlying mechanisms frequently remain elusive. A truly predictive understanding of biodiversity–ecosystem function relationships requires the a priori identification of traits conferring specific (and possibly complementary) functions to individual species. Although planktonic organisms are responsible for approximately half of the world's primary production, few studies have reported on the relationship between phytoplankton biodiversity and planktonic primary production. We argue that taxon-specific differential equipment with photosynthetically active pigments provides a biochemical mechanism of resource use complementarity among phototrophic microorganisms, enabling more diverse communities to more completely harvest the light spectrum. In line with this, more diverse phytoplankton communities showed higher pigment diversity, higher biomass-specific light absorbance, and higher rates of primary production and biomass accrual.

Keywords: biodiversity, carbon dynamics, pelagic ecosystems, ecosystem function, phytoplankton, complementarity.

Introduction

There is growing concern that the worldwide loss of biodiversity may impair the functioning and stability of ecosystems and, thus, the ability of the biosphere to provide critical ecosystem services to the human population (Balmford et al. 2002; Worm et al. 2006). The study of relationships between biodiversity and ecosystem function has therefore become a priority in ecology (Loreau and Hector 2001). Particularly well studied to date is the relationship between plant species richness and primary production, which has been found to be positive in an overwhelming majority of experimental studies (Balvanera et al. 2006; Cardinale et al. 2006). In contrast, observational studies in unmanipulated ecosystems showed inconclusive evidence of the effect of plant species richness on primary production (Thompson et al. 2005; Grace et al. 2007). The empirical evidence is strongly biased toward temperate grassland systems, which are responsible for only a minor fraction of global primary production; studies from other terrestrial biomes and from aquatic systems are still rare. Also, very few studies have conclusively documented the mechanisms mediating diversity effects. It therefore remains an open question whether positive plant diversity–primary productivity relationships are a truly general phenomenon; whether the phenomenon applies to unmanipulated, natural communities; and, if so, what are its underlying mechanisms?

Generally, two types of nonexclusive mechanisms have been made responsible for positive diversity-productivity relationships: the selection effect (also called sampling effect), where more diverse communities are more likely to contain and become dominated by inherently more productive species; and the complementarity effect, where resource partitioning and/or facilitation among species leads to increased resource use and productivity in more diverse communities (Loreau and Hector 2001; Cardinale et al. 2006; Tilman et al. 2006). In experimental studies, it is now standard to assess the relative contributions of the complementarity and selection effects to total biodiversity effects by additive variance partitioning (Loreau and Hector 2001). Many of these studies have identified complementarity as the main mechanism underlying positive relationships between terrestrial plant species richness and primary production (Loreau and Hector 2001; Flombaum and Sala 2008). Partitioning of the physical niche space (e.g., nutrient and water uptake in different soil compartments, light harvesting in different canopy layers) among higher plants with complex morphologies has been suggested ad hoc to explain this pattern (Hooper 1998). Similarly, variance partitioning can only separate the contributions of selection and complementarity ad hoc. Prediction of the consequences of biodiversity loss requires, however, yet a deeper understanding of the mechanisms that mediate biodiversity effects. In particular, the a priori

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identification of species traits that promote selection, niche complementarity, and/or facilitation is called for.

Phytoplankton in lakes and oceans is responsible for approximately half of the world's annual primary production and is thus a major component of the global carbon cycle (Field et al. 1998). A recent study compiling >3,000 samples from Scandinavian lakes and the Baltic Sea revealed that resource use efficiency (the biomass produced per unit of nutrient) and phytoplankton taxonomic diversity are positively linked. Specifically, the amount of algal carbon per unit total phosphorus was positively related to genus richness of the phytoplankton communities (Ptacnik et al. 2008). These data are the first evidence suggesting that positive diversity-productivity relationships may be a general phenomenon extending to pelagic aquatic communities. But how is this possible? Compared with the physical complexity provided by most terrestrial environments, permanent mixing and a rather simple physical structure seem to strongly limit opportunities for niche complementarity among planktonic primary producers (Hutchinson 1961). Still, data suggest that strong and appropriately timed temporal variability is required to maintain even low to moderate levels of phytoplankton biodiversity (Sommer 1985, 1994; Passarge et al. 2006).

Because of its strong vertical attenuation, light often (co)limits the production and biomass of aquatic primary producers (Boyd 2002; Berger et al. 2006). A hitherto largely neglected aspect of algal resource partitioning is complementarity in the use of different spectral components of the photosynthetically active radiation (PAR). In addition to chlorophyll *a*, most phytoplankton species possess other photosynthetic pigments in taxon-specific combinations and quantities (Rowan 1989). Complementarity effects within phytoplankton communities could then result from more diverse communities using a broader range of wavelengths and thereby increasing the effectiveness of light harvesting (Barsanti and Gualtieri 2006; Stomp et al. 2007*a*, 2007*b*).

On the basis of these arguments, a positive relationship between phytoplankton diversity and primary production could at least partly be explained by the following suite of mechanistic hypotheses. (1) Taxonomically, more diverse phytoplankton communities possess a more diverse array of photosynthetically active pigments. (2) Communities with higher pigment diversity make more efficient use of the PAR spectrum; specific absorbance (the proportion of PAR energy absorbed per unit of community biomass) should then increase with increasing taxonomic diversity. (3) Higher specific absorbance yields higher specific primary production and thus an increase in phytoplankton biomass accrual with increasing diversity, at least in underwater climates where phytoplankton production is light limited. We investigated this suite of hypotheses with a combination of highly controlled laboratory experiments with assembled algal communities and a comparative survey of natural phytoplankton communities in the field.

Methods

Experiments with Assembled Algal Communities

Communities were assembled from 12 algal strains representing the major classes of freshwater algae (see tables A1, A2 in the appendix in the online edition of the *American Naturalist*). We precultured all 12 strains in monoculture in a common growth medium (after Guillard and Lorenzen [1972], with the phosphorus content reduced to 3.1 μg P L^{-1}) over a period of several months and used this medium in all subsequent experiments. In the main experiment, termed "biomass accrual experiment," we established monocultures of all 12 algal strains as well as polycultures at five levels of taxon richness (2, 3, 5, 7, and 10 species). For polycultures, five different communities (each being a unique, random draw from the available pool of strains) were established at each level of taxon richness, yielding a total of 37 different experimental communities (12 monocultures and 25 polycultures; for taxonomic composition, see tables A1, A2). All communities were started with the same initial total algal biovolume, and different species contributed to polycultures with equal initial biovolume. All communities were kept in 1-L translucent polyethylene flasks in a climate chamber at 20°C and exposed to continuous irradiance with 100 μmol quanta of PAR m^{-2} s^{-1}. At this irradiance, photosynthesis of our algal strains is not yet light saturated (M. Striebel, S. Behl, S. Diehl, and H. Stibor, unpublished data; see also Kirk 1994). The experiment was conducted in semibatch culture with a daily replacement of 10% of the culture volume by fresh medium.

At the start of the experiment, pigment analyses (described in detail in "Pigment Analyses") were conducted on three randomly chosen communities from each diversity level ($n = 18$; pigment composition in tables A1, A2). We also determined the in vitro and in vivo biomass-specific PAR absorbance of all polycultures and of five monocultures ($n = 30$; see tables A1, A2) at the start of the experiment. For the in vitro analysis, we filtered equal aliquots of the initial phytoplankton communities (with identical concentrations of algal wet biomass) onto glass fiber filters (Whatman GF/F). The filters were extracted in 95% acetone, sonicated, mixed on a vortex mixer, and allowed to extract at 4°C. To remove cell and filter debris, extracts were centrifuged, and subsequently PAR absorbance by the pigment extract was measured in steps of 1 nm over the range 400–700 nm on a Shimadzu UV-1700 spectrophotometer (Shimadzu Europe). In vivo PAR ab-

sorbance was measured directly on aliquots of the initial phytoplankton communities suspended in their growth medium. Absorbance spectra from both in vitro and in vivo measurements were then integrated to calculate average PAR absorbance per nanometer and milligram phytoplankton carbon biomass. In vivo and in vitro absorbances were similar and showed identical trends in all analyses. We therefore show only results based on in vitro absorbances, which had slightly less scatter (because extraction of pigments from a larger sampling volume gave higher measurement precision).

At the end of the experiment after 2 weeks of incubation (corresponding to ~10 generation times), we filtered water from all polycultures and five monocultures ($n = 30$) onto precombusted, acid-washed glass fiber filters (Whatman GF/F) and determined the particulate organic carbon content on an elemental analyzer (CE Instruments, Milan). For all experimental communities ($n = 37$), we determined final total phytoplankton wet biomass, and the contribution of each taxon to it, from microscopic counts. Algae in samples fixed with Lugol's iodine were counted and measured in an inverted microscope using Utermöhl chambers (Utermöhl 1958). The biovolume of each algal taxon was subsequently calculated according to Hillebrand et al. (1999) and converted to wet biomass assuming a wet mass of 1 fg μm^{-3} of biovolume. We used the wet biomass data to calculate the contributions of the selection and complementarity effects to the total biodiversity effect on community biomass according to the additive variance partitioning suggested by Loreau and Hector (2001). We were unable to calculate selection and complementarity effects for the communities with 10 species, because they were all contaminated by one or two species (*Desmodesmus* sp. or *Tetraedron* sp.) that were not grown in monoculture. Apart from these contaminations, treatments were very well maintained throughout the experiment (correlation final vs. initial taxon richness, Pearson's $r = 0.99$). Our choice to present response variables as functions of initial rather than final taxon richness therefore does not influence the conclusions.

In a separate experiment, termed "short-term incubation," we established five monocultures and 20 polycultures ($n = 25$) at five levels of taxon richness (1, 2, 3, 5, and 7 species; the taxonomic composition is given in table A3 in the appendix in the online edition of the *American Naturalist*). For each of these 25 communities, we measured the specific rates of net primary production (sNNP) during 4 h of incubation at 20°C and 100 μmol quanta of PAR m^{-2} s^{-1}. The net rate of carbon fixation by each algal community was measured as the rate of oxygen evolution according to Wetzel and Likens (1991).

Data from Natural Algal Communities

We sampled water from 46 lakes in southern Bavaria and Austria (47°–48°N, 12°–14°E). Twenty-eight of the lakes were oligotrophic (total phosphorous [TP] < 10 $\mu g\ L^{-1}$), 15 were mesotrophic (10–25 μg TP L^{-1}), and three were eutrophic (TP > 25 $\mu g\ L^{-1}$). From each lake we took a water sample from the mixed surface layer and filtered it through a 200-μm mesh to remove crustacean zooplankton. Samples were stored cold and dark for a maximum of 4 h during transport. We determined total phosphorus content (after sulphuric digestion), particulate organic carbon content (as described above), and the content of 26 different algal pigments from aliquots of the lake samples. We also determined the absolute and relative contributions of different algal taxa to phytoplankton wet biomass from microscopic counts and measurements as described above. Estimates of wet biomass were converted to algal carbon biomass assuming a carbon content of 0.14 fg C μm^{-3} algal biovolume (Rocha and Ducan 1985; Vadstein et al. 1988).

Pigment Analyses

Samples from assembled and natural phytoplankton communities were filtered onto glass fiber filters (Whatman GF/F) and stored at −80°C until analysis. The filters were extracted, filtered through 0.2-μm Teflon syringe filters to remove cell and filter debris, transferred to high performance liquid chromatography (HPLC) vials, and injected (with buffer) on an HPLC system (Shimadzu LC-10A HPLC system with LC Solution software, Shimadzu Europe). HPLC analyses were performed by DHI Water and Environment (Hørsholm).

It should be noted that several pigments included in our analysis may perform other functions in addition to being photosynthetically active. Conversely, the HPLC analysis misses a few important pigments, notably the hydrophilic phycobilins. Concerning pigment functionality, only one of the 26 analyzed pigments (the photoprotective pigment zeaxanthin) is currently suspected to be truly photosynthetically inactive (Goss 2005; R. Goss, personal communication). The inclusion of zeaxanthin did not, however, bias the results, because this pigment was present in all but one of our 76 communities. As for the phycobilins, they are the major photosynthetically active pigments in cyanobacteria. Cyanobacteria were, however, of very minor quantitative importance in the field samples (their contribution to total biomass was on average <4%). Moreover, only two of the 12 phytoplankton taxa in the assembled communities were cyanobacteria. This allowed us to assess whether the results from the laboratory experiments were biased by the inclusion of cyanobacteria. To do so, we analyzed all data from

assembled communities twice, that is, with the treatments containing cyanobacteria either excluded or included.

Results

Laboratory Experiments

The experiments with assembled communities support our suite of hypotheses. First, there was a positive relationship between taxon richness and pigment richness in assembled communities (fig. 1*A*). Second, biomass-specific PAR absorbance increased with taxon richness (fig. 1*B*) and was positively related to pigment richness (fig. 1*C*). The residuals of the latter regression were unrelated to taxon richness ($P = .44$), suggesting that higher pigment diversity was indeed the primary mechanism allowing more diverse communities to harvest PAR more effectively. Third, the specific rate of net primary production increased with taxon richness (fig. 1*D*). Finally, phytoplankton biomass accrual after 2 weeks of incubation measured both as particulate organic carbon (POC) concentration and as wet mass was positively related to taxon richness (fig. 1*E*), pigment richness ($\ln \text{POC} = -0.25 + 0.06 \times$ pigment richness, $r^2 = 0.43$, $P = .0035$; $\ln$ wet mass $= 0.18 + 0.15 \times$ pigment richness, $r^2 = 0.41$, $P = .007$; $n = 18$; data not shown), and absorbance (fig. 1*F*). The residuals of the latter regression were positively related to taxon richness (residual $\ln \text{POC} = -0.16 + 0.13 \times$ in vitro

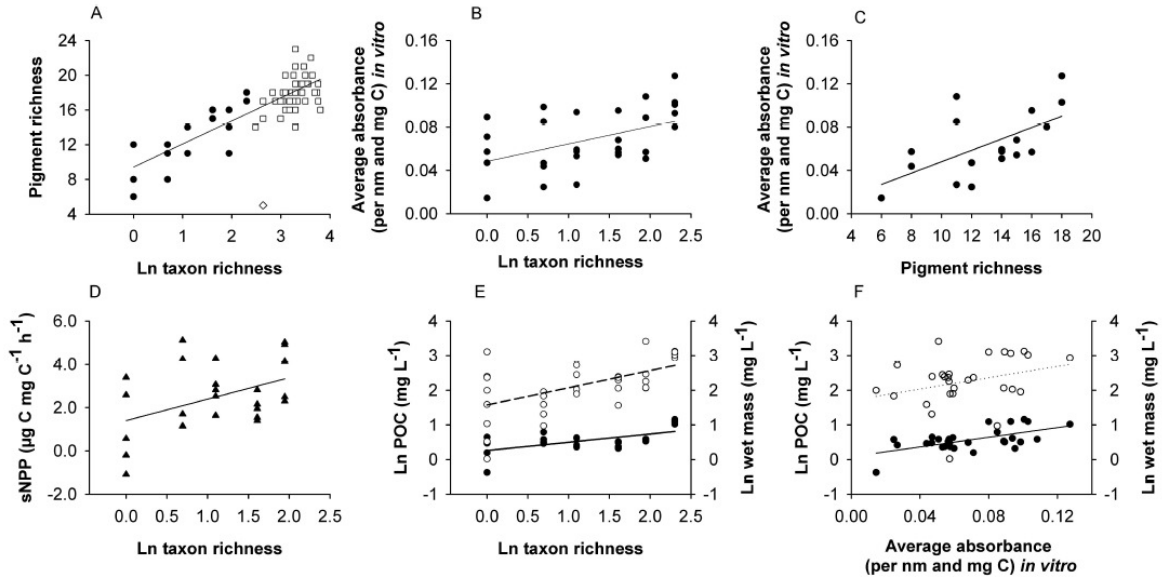

Figure 1: Data from the biomass accrual experiment (*circles*), short-term incubation experiment (*triangles*), and field sampling (*squares and diamond*). *A*, Relationship between taxon richness (number of phytoplankton taxa) and pigment richness (number of photosynthetically active pigments) in assembled (*circles*) and natural (*squares*) algal communities. Linear regression statistics: (1) assembled communities: pigment richness $= 8.49 + 3.63 \times \ln$ taxon richness, $r^2 = 0.69$, $P < .0001$, $n = 18$; (2) natural communities: pigment richness $= 9.2 + 2.69 \times \ln$ taxon richness, $r^2 = 0.17$, $P = .0045$, $n = 45$; outlier (*diamond*) excluded; (3) assembled and natural communities combined: pigment richness $= 9.43 + 2.66 \times \ln$ taxon richness, $r^2 = 0.68$, $P < .0001$, $n = 63$; outlier (*diamond*) excluded. Relationships are similar and statistically significant whether the outlier is excluded or not. Shown is the common regression line for the combined assembled and natural communities. *B*, Relationship between taxon richness and biomass-specific average in vitro PAR absorbance (per nm and mg C) of assembled communities. Linear regression statistics: average absorbance $= 0.048 + 0.016 \times \ln$ taxon richness, $r^2 = 0.22$, $P = .0085$, $n = 30$. *C*, Relationship between pigments richness and biomass-specific average in vitro PAR absorbance (per nm and mg C) of assembled communities. Linear regression statistics: average absorbance $= -0.005 + 0.005 \times \ln$ pigment richness, $r^2 = 0.37$, $P = .0077$, $n = 18$. *D*, Relationship between taxon richness and specific net primary production (sNPP; μg C mg C^{-1} h^{-1}) of assembled algal communities during the short-term (4 h) incubation experiment. Linear regression statistics: sNPP $= 1.4 + 0.99 \times \ln$ taxon richness, $r^2 = 0.19$, $P = .03$, $n = 25$. *E*, Relationship between taxon richness and particulate organic carbon concentration (POC; mg L^{-1}; *solid circles and solid line*) and phytoplankton wet mass concentration (mg L^{-1}; *open circles and dashed line*) of assembled communities after 2 weeks of incubation. Linear regression statistics: (1) $\ln \text{POC} = 0.26 + 0.24 \times \ln$ taxon richness, $r^2 = 0.37$, $P = .0004$, $n = 30$; (2) $\ln$ wet mass $= 1.58 + 0.5 \times \ln$ taxon richness, $r^2 = 0.27$, $P = .0009$, $n = 37$. *F*, Relationship between biomass-specific average in vitro PAR absorbance (per nm and mg C) and POC (mg L^{-1}; *solid circles and solid line*) and phytoplankton wet mass concentration (mg L^{-1}; *open circles and dotted line*) of assembled communities after 2 weeks of incubation. Linear regression statistics: (2) $\ln \text{POC} = 0.09 + 6.98 \times \ln$ average absorbance, $r^2 = 0.37$, $P = .0004$, $n = 30$; (2) $\ln$ wet mass $= 1.7 + 8.2 \times$ average absorbance, $r^2 = 0.09$, $P = .13$, $n = 30$.

absorbance, $r^2 = 0.16$, $P = .028$; residual ln wet mass = 0.48 + 0.39 × in vitro absorbance, $r^2 = 0.2$, $P = .017$; $n = 30$), suggesting that increased light harvesting by communities with a higher pigment diversity was not the only mechanism contributing to the higher biomass accrual of more diverse communities. The above results are robust against the exclusion of treatments with cyanobacteria from the analyses: pigment richness, PAR absorbance, specific net primary production, and phytoplankton biomass accrual all remain significantly positively related to taxon richness when treatments containing cyanobacteria are excluded (data not shown).

Collectively, these results suggest that the observed positive relationship between phytoplankton diversity and primary production is at least in part a consequence of algal niche complementarity with respect to the use of different spectral components of the PAR supply. Additive variance partitioning supports this interpretation. The selection effect was 0 on average (mean = −0.04 mg wet mass L^{-1}, SE = 0.75) and unrelated to taxon richness (fig. 2*A*). In contrast, the complementarity effect was positive on average (mean = 2.27 mg wet mass L^{-1}, SE = 1.41) and increased with taxon richness (fig. 2*B*).

Field Data

Our survey of 46 German and Austrian lakes (47°–48°N, 12°–14°E) shows that the above results extend to natural communities with shared evolutionary histories. The relationship between taxon richness and pigment richness was similar and positive in assembled and natural communities and is well described by a common regression line (fig. 1*A*). Because phytoplankton biomass in freshwater lakes strongly correlates with TP concentration (Schindler 1978; Berger et al. 2006), we used TP as an additional predictor variable when assessing the contribution of taxonomic diversity to phytoplankton biomass in the field samples. Similar to the assembled lab communities, both particulate organic carbon and algal wet mass were positively related to algal taxon richness also in the lake samples (table 1, A and B). Standard partial regression coefficients (SPRCs) indicated that, over the ranges of taxon richness and TP encountered in the field, the positive impact of taxon richness on carbon biomass was more than 10 times higher than the positive impact of TP (SPRC = 0.57 vs. 0.05, all variables in ln-transformed units).

A clear, positive effect of biodiversity on carbon biomass in the field samples is also indicated by the positive relationship between resource use efficiency and taxon richness (table 1, C and D). We calculated resource use efficiency in two independent ways, that is, based on POC (which includes nonalgal particulate organic material) and on algal carbon (estimated from microscopically derived algal biovolume). The relationship based on algal carbon (intercept = −1.3, slope = 1.35; table 1, D) is very similar to the relationship reported by Ptacnik et al. (2008; intercept = −0.96, slope = 1.12), who used the same method to estimate algal carbon.

Discussion

The idea that more diverse plant communities are more productive than less diverse ones dates back to Darwin (McNaughton 1993; Loreau 2000). While experiments with assembled communities have frequently supported this idea, the relevance of these experiments to natural communities

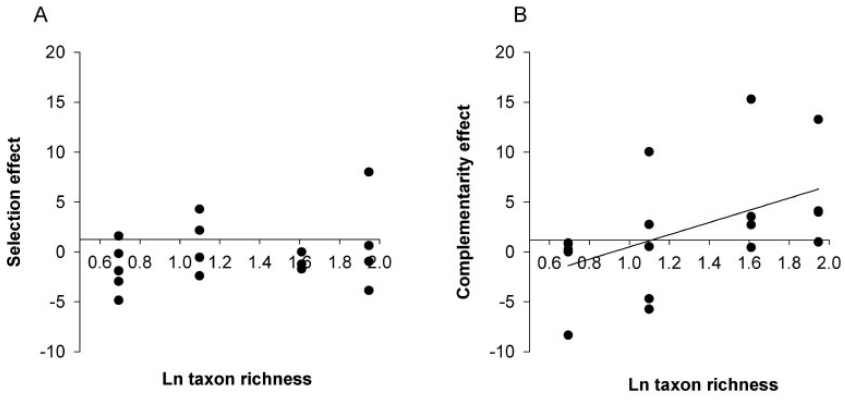

Figure 2: Relationship between taxon richness and the selection effect (*A*) and the complementarity effect (*B*; mg phytoplankton wet mass L^{-1} for both *A* and *B*) in the biomass accrual experiment after 2 weeks of incubation. Linear regression statistics: selection effect = −1.5 + 1.13 × ln taxon richness, $r^2 = 0.03$, $P = .48$, $n = 20$; complementarity effect = −5.6 + 6.1 × ln taxon richness, $r^2 = 0.25$, $P = .03$, $n = 20$.

Table 1: Regression statistics describing the relationships between phytoplankton taxon richness (TR) and measures of production and resource use efficiency (RUE) in 46 natural lakes

		Overall regression		Regression parameters					
				Coefficient		SE		*P*	
	Equation	r^2	*P*	TR	TP	TR	TP	TR	TP
A	$\ln \text{POC (mg L}^{-1}) = -5.6 + 1.3 \times \ln \text{TR} + 0.24 \times \ln \text{TP}$	.51	<.0001	1.3	.24	.28	.12	<.0001	.05
B	$\ln \text{wet mass (mg L}^{-1}) = -4.7 + 1.0 \times \ln \text{TR} + 0.38 \times \ln \text{TP}$	.29	.0006	1.0	.38	.43	.19	.02	.05
C	$\ln \text{RUE}_{\text{POC}} = 1.85 + 0.9 \times \ln \text{TR}$	.1	.03	.9		.42		.03	
D	$\ln \text{RUE}_{\text{biovolume}} = -1.3 + 1.35 \times \ln \text{TR}$	.14	.01	1.35		.5		.01	

Note: RUE_{POC} is defined as particulate organic carbon (POC; μmol L^{-1}) per unit total phosphorus (TP; μmol L^{-1}), and $\text{RUE}_{\text{biovolume}}$ is defined as algal carbon (μmol L^{-1}; calculated from microscopic counts) per unit TP (μmol L^{-1}).

is a matter of debate. A crucial, missing link in the quest for a conclusive, mechanistic understanding of the influence of biodiversity on ecosystem function has been the a priori identification of species traits conveying complementarity in resource use. We have argued that the differential equipment with photosynthetically active pigments provides a biochemical mechanism of resource use complementarity among phototrophic microorganisms, enabling more diverse communities to more completely harvest the spectrum of solar energy, thus creating a positive relationship between phytoplankton diversity and primary production.

Our data from both assembled and natural communities are in congruence with the above chain of reasoning. We therefore propose that pigment complementarity is likely to contribute to the recently described positive relationship between phytoplankton diversity and resource use efficiency in Scandinavian lakes and the Baltic Sea (Ptacnik et al. 2008). Interestingly, in the Scandinavian data set, diversity effects on resource use efficiency were stronger in less diverse communities (Ptacnik et al. 2008). The latter would be expected under the pigment complementarity hypothesis because, as absorption spectra of different pigments fill up the available spectral niche space, the gain in total PAR harvesting with the addition of new pigments to the community becomes increasingly marginal. This should have constrained the evolution of pigment diversity, yielding a saturating relationship between phytoplankton biodiversity and pigment diversity. The log-linear relationship in figure 1*A* does indeed imply that pigment richness increases most strongly with taxon richness in the least diverse communities.

Importantly, pigments and absorption spectra of different phototrophic microorganisms are relatively easy to measure, allowing the a priori prediction of spectral niche overlap among different taxa. The distribution of pigments among phytoplankton taxa is, in turn, phylogenetically constrained, and many pigments are used in the quantification of higher taxonomic algal units from bulk seston samples (Rowan 1989; Schlüter et al. 2006). Because of this hierarchical distribution of pigments among higher taxonomic units, it seems plausible to expect that spectral niche complementarity (and, consequently, light use efficiency) should be higher among species belonging to different algal classes than among species belonging to the same algal class. The experiments presented here do not lend themselves to an assessment of this hypothesis. We are therefore currently conducting additional experiments to explore this issue further.

While the spectral component of phytoplankton niche space has received relatively little attention, it was recently shown that pigment complementarity can facilitate stable coexistence of otherwise very similar taxa (Stomp et al. 2004, 2007*b*). The ecological consequences of photosynthetic pigment diversity may, however, extend beyond their impact on phytoplankton community structure and diversity-productivity relationships. In particular, increased resource use efficiency, as manifested by an increase in algal carbon fixation per unit of nutrient (table 1, C and D; Ptacnik et al. 2008), affects the carbon to nutrient stoichiometry of suspended particles, with consequences for ecosystem processes such as the sequestration and storage of atmospheric carbon dioxide and the transfer of energy and matter along the food chain (Hessen et al. 2004; Diehl et al. 2005; Striebel et al. 2008). Future studies on the ecological consequences of photosynthetic pigment diversity therefore hold promise to improve our understanding of the carbon dynamics of pelagic ecosystems, which cover 70% of the earth's surface.

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PUBLICATION II

THE RELATIVE IMPORTANCE OF SPECIES DIVERSITY AND FUNCTIONAL GROUP DIVERSITY ON CARBON UPTAKE IN PHYTOPLANKTON COMMUNITIES

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The relative importance of species diversity and functional group diversity on carbon uptake in phytoplankton communities

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Abstract

We conducted laboratory experiments with 85 assembled phytoplankton communities composed of species from four predefined functional groups (chlorophytes, diatoms, cyanobacteria, chrysophytes) to distinguish the relative importance of species diversity from functional group diversity on carbon uptake. We separated the observed diversity effects on carbon uptake into those caused by species with particularly important traits (selection effect) and those caused by positive interactions among species (e.g., complementary resource use or facilitation [complementarity effect]). Additionally, we measured the composition of photosynthetically active pigments and light absorbance in communities and monocultures, and related them to species and functional diversity effects on carbon accrual. Biodiversity effects were weak or even absent in pure cyanobacterial and diatom communities compared to strong effects in chlorophytes. Complementarity effects and light absorbance increased as functional (i.e., phylogenetic) diversity increased. There was a positive correlation between complementarity effects on carbon accrual and light absorbance. These findings support hypotheses regarding biodiversity–productivity relationships in phytoplankton communities based on niche separation along spectral light gradients.

During the last decade concern has been growing that biodiversity is declining from the local to global scale, which may affect resource sustainability, ecosystem functioning, and human welfare (Cardinale et al. 2006; Worm et al. 2006; Brauman et al. 2007). Public perception of the ongoing diversity loss is normally associated with the loss of a single species. However, diversity can be defined in terms of species number, allele frequency, or number of functional traits inherent in a community. Although 'functional trait' is, due to its intuitive applicability, a widespread term, an array of vague or specific definitions exists in the scientific literature (McGill et al. 2006; Petchey and Gaston 2006; Hillebrand and Matthiessen 2009). Generally speaking, this concept implies that ''species can be grouped according to common responses to the environment and/or common effects on ecosystem processes'' (Lavorel and Garnier 2002, p. 545). Specific functional traits, which might have been evolving for many generations, include characteristic physiology, morphology, or life-history properties of species such as resource use abilities, behavior, or reproduction. Hence, a loss of 'diversity' can have different implications depending on the definition of diversity (alleles, functional groups, traits, landscapes, etc.). The question arises whether the loss (or gain) of one particular species affects ecosystems to the same extent as the loss (gain) of a particular functional trait. This is a crucial point for our understanding of diversity effects, because one species with a unique trait (e.g., a 'keystone species') might have a stronger bearing on the whole system than several species with partly redundant traits. Most of the pioneering work dealing with 'functional groups' has been conducted in grassland communities (Díaz and Cabido 2001), but the concept has rapidly spread to marine and limnic systems, too (Downing 2005; Hood et al. 2006). However, the question of how to identify a truly functional group is still controversial. Petchey (2004) and Wright et al. (2006) demonstrated that those assignments have not always been justifiable, because a priori–characterized artificial functional groups may not match the real trait distribution of species in a community. Statistical reanalysis of such functional diversity vs. ecosystem property relationships revealed that random grouping of species would often have produced the same effect (Wright et al. 2006). This means that assigning functional species groups needs to be preceded by an identification of the trait that is thought to be crucial for the process of interest (Duffy and Harvilicz 2001). Then, lumping species into functional groups can be suitable to remove some complexity from the system and may, thus, help to better understand and predict ecosystem responses to changing environmental conditions.

In recent years, several experiments that aimed at describing the relationship between biodiversity and ecosystem properties (e.g., productivity, stability) revealed a predominantly positive but saturating connection (Cardinale et al. 2006; Loreau 2008). Two nonexclusive mechanisms have been identified and are thought to explain such positive connections: the selection effect, where more diverse communities are more likely to contain and become dominated by a species with particularly important traits; and the complementarity effect, where resource partitioning or facilitation among species leads to increased resource use and productivity in more diverse communities (Loreau and Hector 2001; Hector et al. 2002; Cardinale et al. 2007). However, differences between these mechanisms are difficult to address experimentally. Loreau and Hector (2001) introduced a mathematical method that

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allows distinction between complementarity and selection effects in multispecies experiments based on monoculture and polyculture yields.

So far, functional groups have mostly been assigned in terrestrial plant systems on the basis of different traits related to nutrient uptake, such as root morphology, growth period, or the ability for atmospheric nitrogen fixation (Tilman et al. 1997; Díaz and Cabido 2001; Fornara and Tilman 2008). However, besides nutrients, light is a major resource for all phototrophic organisms and is the most important source of energy for life on earth. Recently, competition for light was shown to cause a loss of diversity in nutrient-enriched terrestrial plant communities (Hautier et al. 2009), and overyielding in a terrestrial plant community was associated with higher light interception (Vojtech et al. 2008). This indicates that complementarity based on niche differentiation in terms of light use can be an important mechanism of biodiversity–productivity relationships in plant communities. The spatial and temporal availability of light in terms of quality (wavelength distribution) and quantity (light intensity) can be quite heterogeneous, even in an apparently homogenous environment such as the pelagic zone of oceans and lakes (Kirk 1994). Considering the light quality as one niche dimension, this heterogeneity may promote diversity via possible niche differentiation processes in phototrophic plankton organisms (Stomp et al. 2004, 2007; Striebel et al. 2009). In contrast to terrestrial vascular plants, the phytoplankton consists of different eukaryotic and prokaryotic groups, representing a large variety of different evolutionary lineages (Falkowski et al. 2004). Thus, algal species may show larger differences in their resource-use abilities, which reflect the physiological traits founding any diversity–productivity relationship in communities ('alga' hereafter is defined in an ecological sense, including eukaryotic and prokaryotic [i.e., cyanobacterial] species). Because algae are the predominant primary producers at the base of most marine and freshwater ecosystems, diversity effects on algal productivity would be affecting all important aquatic ecosystem services. This may include effects on fisheries yields, nutrient cycling, and carbon export fluxes and storage (Duffy and Stachowicz 2006).

One mechanism underlying such diversity–productivity relationships may be based on the high variety of photosynthetically active pigments in algae and the fact that different pigments have different absorption characteristics along the photosynthetically active radiation (PAR) light spectrum ranging from 400 nm to 700 nm: pigment composition, and therefore wavelength-dependent light absorption, is a distinctive characteristic of algal species. Moreover, certain pigments are also distinctive of whole algal groups (e.g., Chlorophyceae, Bacillariophyceae), because pigments are a major criterion for algae taxonomical classification above the species level (van den Hoek et al. 1995; Jeffrey et al. 1997). Interspecific differences in pigment composition are on average larger among species from different taxonomic groups (e.g., Chlorophyceae and Cyanobacteria) than among species from the same taxonomic group (e.g., Chlorophyceae only; own pigment data in Results [Scheer 1999; Schlüter et al. 2006]). Hence, we suggest that taxon-specific photosynthetically active pigments provide a biochemical mechanism of resource-use complementarity among phototrophic plankton microorganisms, enabling more diverse communities to more completely harvest the light spectrum. Species from different algal groups, which differ more in their pigment composition than species from the same algal group, should therefore have a higher probability for complementary light use. Accordingly, we propose that algal pigment composition may also be considered as a good determinant for light-use efficiency and biomass-specific carbon incorporation. Previous experimental results from field and laboratory experiments support this idea (Striebel et al. 2009). Because pigments underlie phototrophic energy absorption, we propose that phylogeny-based algal groups with different pigment compositions can simultaneously be considered true functional groups in terms of light use. In this sense, we will use both terms (functional diversity and phylogenetic diversity) as synonyms.

The above considerations lead to the following hypotheses regarding diversity–productivity relationships in phytoplankton communities: (1) biodiversity effects in communities with identical species richness will be larger in communities consisting of species from different algal groups; (2) pigment diversity, light-absorption efficiency, and carbon accrual will be higher in communities consisting of species from different algal groups compared to communities consisting of species from single algal groups, and they increase with increasing phylogenetic (functional) diversity; (3) complementarity effects of biodiversity should, therefore, be larger in communities with species from different algal groups than in communities consisting of single algal groups, and they increase with increasing phylogenetic (functional) diversity.

To address these hypotheses, we established laboratory experiments with artificially assembled phytoplankton communities, comparing pigment composition, light absorbance, carbon accrual, and biodiversity effects among communities consisting of species from only one algal group and communities consisting of species from different algal groups. Finally, we analyzed the development of these diversity gradients during the experiments.

Methods

Experimental set-up and response measurements—We used a set of 25 algal strains (Sammlung von Algenkulturen, Göttingen; Canadien Phycological Culture Centre; Table 1) that had been precultured for several weeks in phosphorus-deficient (30.9 μg P L^{-1}) freshwater algal growth medium (Woods Hole Combo [WC], modified after Guillard and Lorenzen [1972]). Algal strains belonged to the following four phylogenetic algal groups (each defined as one functional group in terms of light use): diatoms (dt), chlorophytes (ch), cyanobacteria (cy), and chrysophytes (chr). Within each algal group (except chrysophytes, due to a lack of different species growing in WC medium), we established a gradient of species diversity with four diversity levels consisting of all

Table 1. List of algal strains used for the laboratory experiment.

Chlorophytes	*Crucigenia tetrapedia* W. et G.S. West
	Desmondesmus subspicatus Hegewald et Schmidt
	Golenkinia brevispicula Hegewald et Schnepf
	Haematococcus pluvialis Flotow em. Wille
	Pediastrum simplex Meyen
	Scenedesmus obliquus Kützing
	Selenastrum capricornutum Printz
	Staurastrum tetracerum (Meyen) Ralfs
	Tetraedron minimum Hansgirg
Chrysophytes	*Dinobryon cylindricum* Ehrenberg
	Synura petersenii Korshikov
Cyanobacteria	*Anabaena cylindrica* Lemmermann
	Chroococcus minutus Kützing
	Merismopedia glauca Ehrenberg
	Microcystis wesenbergii Kützing
	Planktothrix rubescens Anagnostidis et Komárek
	Pseudoanabaena galeata Böcher
	Synechococcus sp.
Diatoms	*Asterionella formosa* Hassall
	Cyclotella meneghiniana Kützing
	Diatoma elongatum (Lyngbye) Agardh
	Fragilaria crotonensis Kiton
	Navicula pelliculosa Hilse
	Nitzschia palea Kützing
	Tabellaria flocculosa Kützing

monocultures and polycultures with two, three, and four different species each. Additionally, we established a gradient of algal group diversity (i.e., functional diversity), again with four diversity levels, each consisting of four species from one (four ch or four dt or four cy species), two (two ch and two dt species), three (two ch and one dt and one cy species), or four (one ch and one dt and one cy and one chr species) algal groups. Each diversity level (species diversity and algal group diversity) was replicated five times with different species compositions, resulting in 85 communities (Table 2). All communities were randomly composed from the respective species pool (nine chlorophytes, seven diatoms, seven cyanobacteria, and two chrysophytes; Table 1). Initial total algal biovolume was set identical in all treatments (5.26×10^6 μm^3 mL^{-1}), and different species contributed with equal initial biovolumes to communities with two or more species. In so doing, we created two diversity gradients by either increasing species diversity and simultaneously keeping algal group diversity constant or increasing algal group diversity and keeping species diversity constant (Table 2). Both gradients covered the same diversity range in terms of the (initial) Shannon Diversity Index H. For 21 d the communities (400 mL) were exposed in 650-mL cell culture flasks to 90 μmol quanta m^{-2} s^{-1} PAR with a daily medium exchange of 12.5% volume. All communities were stirred three times a day to prevent the algae from sinking and accumulating at the bottom. Algal biomass was measured as particulate organic carbon (POC) subsequent to filtration onto precombusted and acid-washed glass-fiber filters (Whatman GF/C; Whatman) by elemental analysis (Elemental Analyzer, EA 1110 CHNS; CE Instruments). In vivo PAR absorbance was measured in steps of 1 nm over the range 400–700 nm on a spectrophotometer (Uvikon 930; Kontron Instruments). Absorbance spectra were then integrated to calculate specific PAR absorbance per milligram phytoplankton carbon biomass. Of each algal community (i.e., experimental unit), an aliquot was fixed with Lugol's iodine for microscopic diversity analysis. All measurements were performed at the start and the end of the experiment.

Table 2. Number and design of experimental phytoplankton communities. Communities consist of one (monocultures), two, three, or four species from the same or from different algal groups, resulting in gradients of species diversity and algal group (i.e., functional group) diversity. The Shannon Diversity Index H is based on biovolumes.

No. of communities	No. of species per community	No. of algal groups per community	Initial diversity H	
			Species	Algal groups
25	1	1	0	0
15	2	1	0.69	0
15	3	1	1.04	0
15	4	1	1.39	0
5	4	2	1.39	0.69
5	4	3	1.39	1.04
5	4	4	1.39	1.39

Calculations—Relative biomass accrual in terms of particulate organic carbon (POC) was calculated as the natural logarithm (ln) of ending POC (mg L^{-1}) divided by starting POC (mg L^{-1}). The relative yield of POC is the ratio of the observed relative biomass accrual in terms of POC in the communities and the relative biomass accrual expected from the monocultures. Thus, overyielding occurs when this ratio is > 1, and underyielding when it is < 1. Overyielding can be split into nontransgressive overyielding and transgressive overyielding. The first occurs when the yield of a mixture is greater than expected based on a weighted average of the monoculture yields of the component species. Transgressive overyielding occurs when a mixture yields more than any monoculture of the component species (Hector et al. 2002). Complementarity effect (increased resource-use efficiency by resource partitioning or facilitation) and Selection effect (dominance of a high productive species) were calculated based on the relative biomass accrual POC by the additive partitioning method described in Loreau and Hector (2001): both effects can be negative or positive. The complementarity effect measures any change in the average relative yield $\overline{\Delta RY}$ in the mixture, compared to the weighted average monoculture yield $\overline{M}$ of the component species, where N is the number of species: ($N\,\overline{\Delta RY}\,\overline{M}$). The selection effect is measured by the covariance between the monoculture yield M of species and their change in relative yield ΔRY in the mixture: [N covariance (ΔRY, M)] (Loreau and Hector 2001). For this purpose, we counted the final algal composition of each community, determining the relative proportion of each species in terms of biovolume (*see* below). The specific PAR absorbance yield in vivo was calculated as the ratio of the

Table 3. Comparison of the coefficients of determination r^2 and p-values for linear regression models between initial H, mean H, final H diversity, and species richness (SR; or functional group richness [FGR] in fg-communities). Diversity as the predictor variable is calculated as species diversity H in diatom (dt), chlorophyte (ch), and cyanobacterial (cy) communities and as algal group diversity H in communities consisting of more than one algal group (fg). Values for r^2 are displayed only when the overall regression model is statistically significant. * $p<0.05$; ** $p<0.01$; *** $p<0.001$; ns=not significant.

		Initial H		Final H		Mean H		SR (FGR)	
Response variable	Communities	r^2	p	r^2	p	r^2	p	r^2	p
ln relative biomass accrual POC	fg (n=30)	0.40	***	0.37	***	0.43	***	0.35	***
	dt (n=22)	0.19	*	—	ns	0.19	*	0.19	*
	ch (n=24)	0.32	**	0.35	**	0.36	**	0.27	**
	cy (n=22)	—	ns		ns	—	ns	—	ns
Relative yield of POC	fg (n=30)	0.18	*	0.17	*	0.20	*	0.18	*
	dt (n=15)	—	ns	—	ns	—	ns	—	ns
	ch (n=15)	—	ns	—	ns	—	ns	—	ns
	cy (n=15)	—	ns	—	ns	—	ns	—	ns
Complementarity effect	fg (n=30)	0.35	***	0.37	***	0.40	***	0.35	***
	dt (n=15)	—	ns	—	ns	—	ns	—	ns
	ch (n=15)	—	ns	0.28	*	—	ns	—	ns
	cy (n=15)	—	ns	—	ns	—	ns	—	ns
Selection effect	fg (n=30)	—	ns	—	ns	—	ns	—	ns
	dt (n=15)	—	ns	—	ns	—	ns	—	ns
	ch (n=15)	—	ns	0.52	**	—	ns	—	ns
	cy (n=15)	—	ns	0.29	*	—	ns	—	ns

observed biomass-specific absorbance (400–700 nm) in the polycultures and the biomass-specific absorbance expected from the monocultures. Mean specific PAR absorbance yield in vivo is the arithmetic average of initial (day 1) and final (day 21) measurement values.

Microscopic counting, biovolume, and diversity determination—In order to examine the final species diversity and algal group (i.e., functional) diversity, algal species were counted from samples fixed with Lugol's iodine in an inverted microscope using Utermöhl chambers (Utermöhl 1958). At least 100 cells of every species were counted by scanning a minimum of five perpendicular transects or 20 randomly distributed, distinct fields so as to keep the counting error at < 10% (Lund et al. 1958). Biovolumes of cells were determined by measuring two-dimensional live pictures using analySIS software (Pro 2.11.006, Soft-Imaging Software GmbH) and subsequent biovolume calculation by defining geometric shapes and mathematical equations according to Hillebrand et al. (1999) or own our adjustments. Diversity was calculated at the beginning (initial diversity H) and the end (final diversity H) of the experimental period as Shannon Diversity Index H, using the measured biovolumes of the algal cells. From this, we calculated a mean diversity H by arithmetic averaging of the initial and final H. Finally, we compared the effects of the different diversity measurements (initial H, final H, and mean H) on the examined community parameters (Table 3).

Pigment analyses—One important assumption underlying our hypotheses was that pigment composition of species from the same algal (functional) group would be more similar to each other than pigment composition of species from different algal groups. In order to verify the accuracy of this assumption, 100-mL samples of initial communities from all phytoplankton monocultures and polycultures were filtered onto glass-fiber filters (Whatman GF/C) and stored at −80°C until analysis. The filters were extracted, filtered through 0.2-mm Teflon syringe filters to remove cell and filter debris, transferred to high-performance liquid chromatography (HPLC) vials, and injected on an HPLC system (Shimadzu LC-10A HPLC system with LC Solution software; Shimadzu). The HPLC system was calibrated with pigment standards (DHI Water and Environment). For further details on pigment analysis *see* Jeffrey et al. (1997). The relative pigment concentrations of eight pigments (Fucoxanthin: Fuco, Diatoxanthin: Diat, Allo-xanthin: Allo, Lutein: Lut, Zeaxanthine: Zea, Chlorophyll *b*: Chl *b*, Chlorophyll *a*: Chl *a*, β-Carotene: βCar) were used to calculate the similarities regarding pigment composition among communities, using Paleontological Statistics software (PAST) 2.01, Copyright Hammer and Harper 1999–2010.

Results

Relative biomass accrual and relative yield of POC—We found a statistically significant increase in relative carbon biomass accrual with increasing mean species diversity within chlorophytes (linear regression: $p = 0.002$, $r^2 = 0.36$; Fig. 1A) and diatoms ($p = 0.042$, $r^2 = 0.19$; Fig. 1B). In chlorophytes, this transferred to a net average increase of final biomass of 0.50 (± 0.10 SE) mg C L^{-1} per additional species under the assumption that species contributed equally to the communities' total biovolumes. In diatoms this transferred to an average increase of final biomass of 0.33 (± 0.24 SE) mg C L^{-1} per additional species. In the cyanobacterial communities, there was no significant change in relative biomass accrual with increasing mean

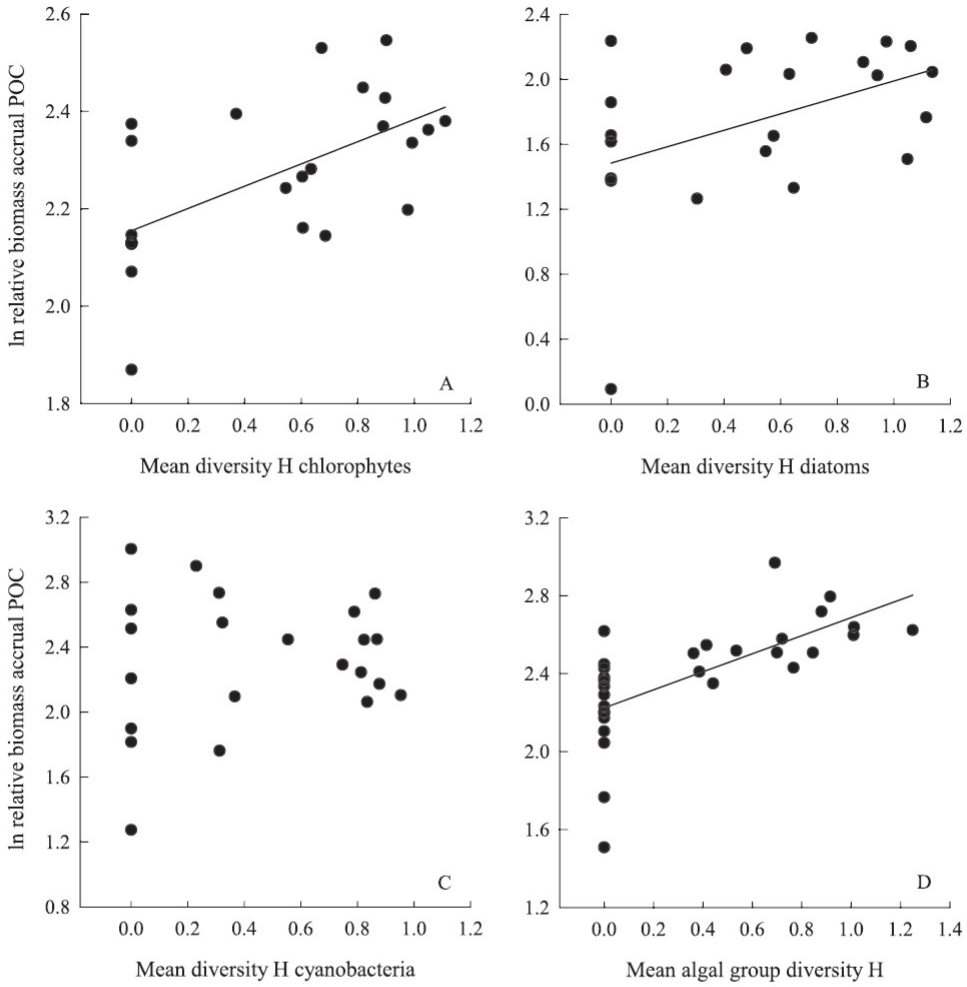

Fig. 1. Relationship between biovolume-based mean species-diversity H and relative biomass accrual in (A) chlorophyte communities, (B) diatom communities, and (C) cyanobacterial communities. (D) Displays the relationship between biovolume-based mean algal group diversity H and relative biomass accrual. Linear regression lines are displayed when statistically significant ($p < 0.05$). Linear regression statistics are: (A) ln relative biomass accrual POC = 2.15 + 0.23 × mean species diversity H, $r^2 = 0.36$, $p = 0.002$, $n = 24$; (B) ln relative biomass accrual POC = 1.48 + 0.51 × mean species diversity H, $r^2 = 0.19$, $p = 0.042$, $n = 22$; (C) not statistically significant; (D) ln relative biomass accrual POC = 2.22 + 0.46 × mean algal group diversity H, $r^2 = 0.43$, $p < 0.0001$, $n = 30$.

species diversity ($p = 0.62$, $r^2 = 0.01$; Fig. 1C). Increasing mean algal group diversity resulted in an increasing carbon biomass accrual ($p < 0.0001$, $r^2 = 0.43$; Fig. 1D) during the experimental period, which transferred to an increase of final biomass of 1.65 (± 0.59 SE) mg C L^{-1} per additional algal group. There was no increase of the relative yield of POC with increasing species diversity H within diatom communities, chlorophytes, and cyanobacteria (Fig. 2A–C). However, we found a positive relationship between increasing algal group diversity H and increasing relative yield of POC ($p = 0.017$, $r^2 = 0.20$; Fig. 2D). Overyielding occurred in 53.3% of cyanobacterial communities (6.7% transgressive overyielding [tr.ov.]), in 86.7% (40.0% tr.ov.) of the diatom communities, in 86.7% (73.3% tr.ov.) of chlorophyte communities, and in all (100%; 53.3% tr.ov.) communities with more than one algal group (Fig. 2A–D).

Complementarity and selection effect—Within diatom, chlorophyte, and cyanobacterial communities, no changes in the complementarity effect or in the selection effect with increasing mean species diversity H were observed (Table 3). However, with increasing mean algal group diversity H, the complementarity effect increased (linear regression, $p = 0.0002$, $r^2 = 0.40$; Fig. 3A), whilst the selection effect declined slightly (linear regression, $p = 0.09$, $r^2 = 0.10$; Fig. 3B). Under the assumption that species contributed equally to the communities' total biovolumes, the complementarity effect accounted for an average increase of 0.72

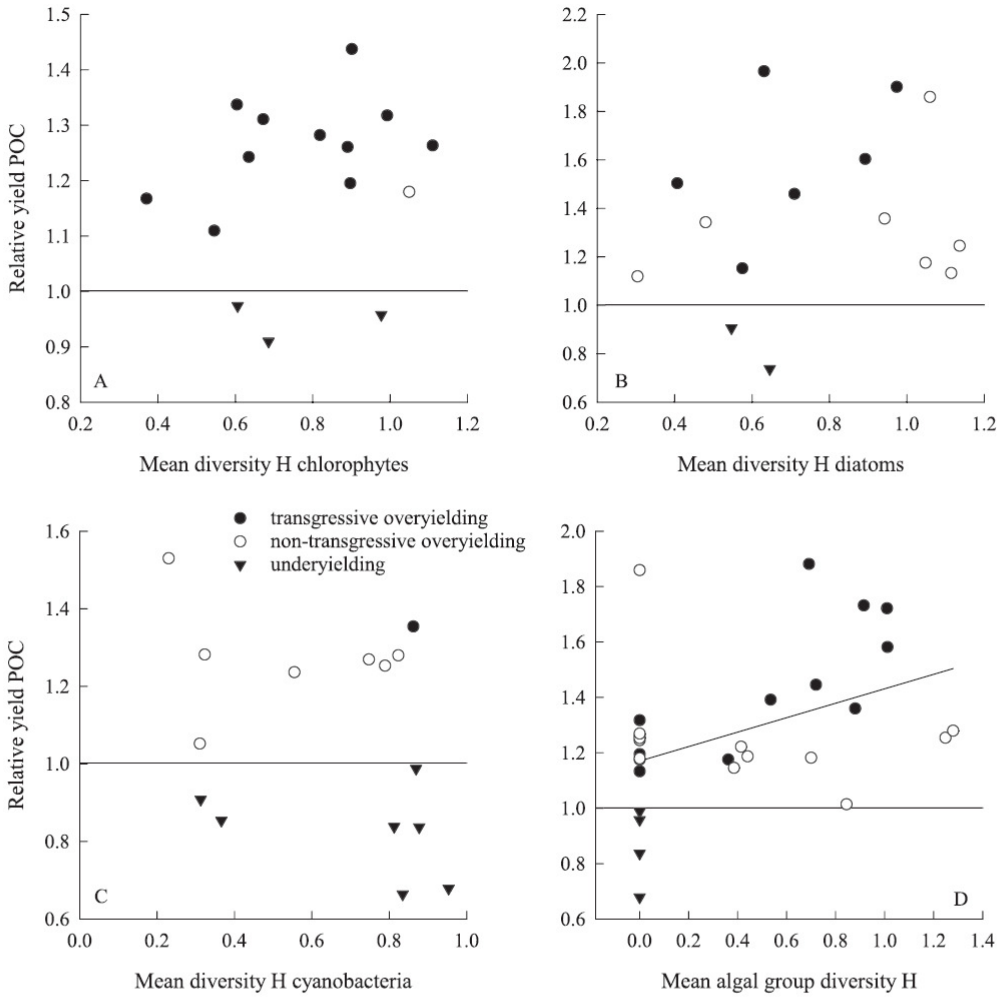

Fig. 2. Relationship between biovolume-based mean species-diversity H and relative yield of POC in (A) chlorophyte communities, (B) diatom communities, and (C) cyanobacterial communities. (D) Displays the relationship between biovolume-based mean algal group diversity H and relative yield of POC (linear regression: relative yield POC = 1.16 + 0.30 × mean algal group diversity H, $r^2 = 0.20$, $p = 0.017$, $n = 30$). The horizontal reference line in all panels at relative yield POC = 1 indicates the transition from underyielding to overyielding.

(± 0.34 SE) mg C L^{-1} per additional algal functional group. Considering mean effect sizes, the communities performed considerably differently. In cyanobacterial treatments, the selection effect was greater than complementarity (paired t-test, $p < 0.001$, $t = -4.57$, df = 14), the latter being negative on average (Fig. 3C,D). In diatom communities, mean selection and mean complementarity effects were equal (paired t-test, $p = 0.21$, $t = -1.31$, df = 14; Fig. 3C,D). In chlorophyte communities, the mean selection effect was not different from zero (one-sample t-test, $p = 0.67$, $t = 0.43$, df = 14), whereas the mean complementarity effect was positive and larger than the selection effect (paired t-test, $p = 0.017$, $t = -2.72$, df = 14; Fig. 3C,D). In communities consisting of more than one algal group, the mean complementarity effect was also significantly higher than the mean selection effect (paired t-test, $p < 0.001$, $t = 5.62$, df = 14), the selection effect being not different from zero (one-sample t-test, $p = 0.41$, $t = -0.86$, df = 14; Fig. 3C,D). Of all communities, the mean selection effect was the highest within the cyanobacterial communities (ANOVA, $F_{3,59} = 8.38$, $p < 0.001$; Bonferroni post hoc test) and the highest mean complementarity effect occurred in the communities consisting of more than one algal group (ANOVA, $F_{3,59} = 23.76$, $p < 0.001$; Bonferroni post hoc test; Fig. 3C,D).

Pigment composition, pigment richness, and specific absorbance yield in vivo—The HPLC analysis followed by an analysis of similarities (ANOSIM) supported our initially stated assumption: there were significant differ-

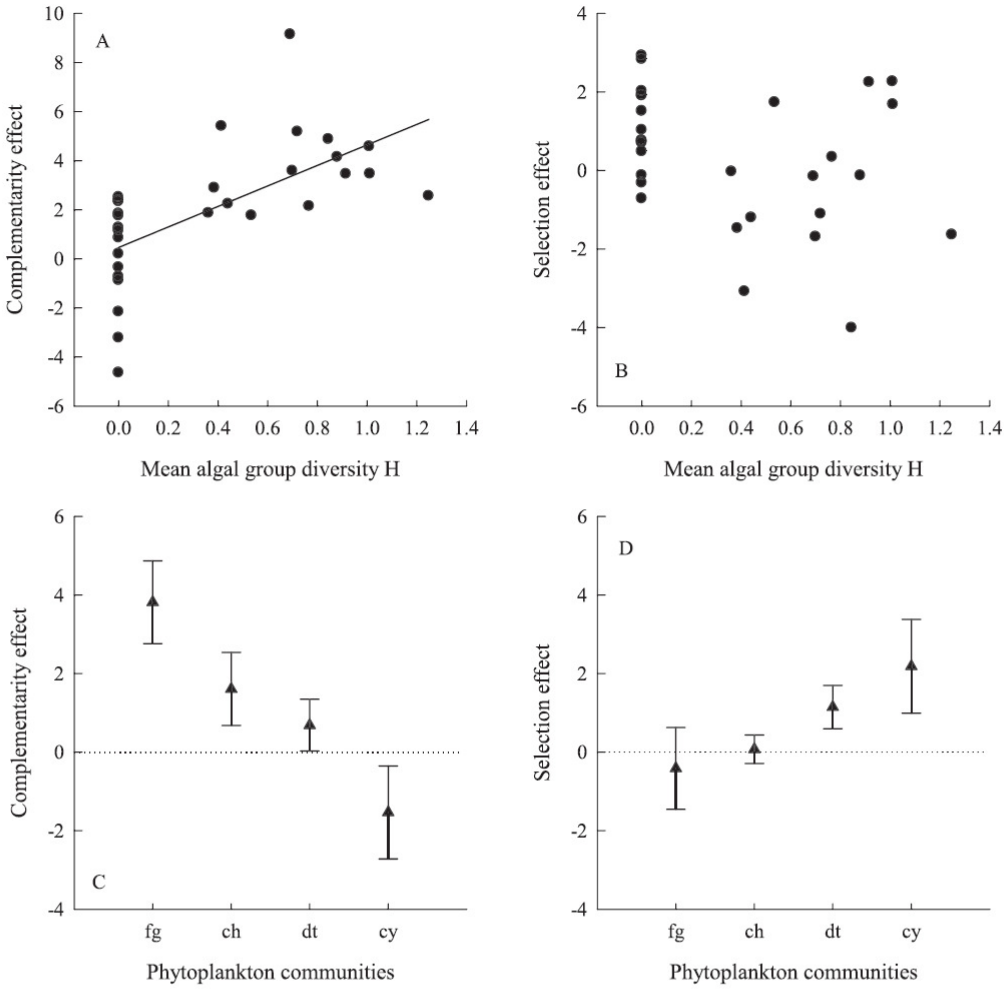

Fig. 3. Relationship between biovolume-based mean algal group diversity H and (A) the complementarity effect (linear regression: complementarity effect = 0.46 + 4.18 × mean algal group diversity H, $r^2 = 0.40$, $p = 0.0002$, $n = 30$), and (B) the selection effect. (C) The mean complementarity effect and (D) mean selection effect in the chlorophyte communities (ch; $n = 15$), diatom communities (dt; $n = 15$), cyanobacterial communities (cy; $n = 15$), and communities with more than one algal group (fg; $n = 15$). Error bars indicate the 95% confidence interval. Dotted horizontal lines are reference lines.

ences in pigment composition among algal (functional) groups ($R = 0.88$, $p < 0.0001$). All communities consisting of species from only one algal group (chlorophytes, diatoms, cyanobacteria, and two chrysophyte monocultures) were found in distinct areas of a nonmetric multidimensional plot, whereas communities consisting of species from different algal groups were found in between (Fig. 4). The initial number of photosynthetic pigments (detected by HPLC) was on average significantly higher in communities consisting of species from more than one algal group than in communities of similar species richness, consisting of either chlorophytes, diatoms, or cyanobacteria (ANOVA, $F_{3,59} = 25.76$, $p < 0.001$; Bonferroni post hoc test; Fig. 5A). Moreover, the diversity (based on relative concentrations) of accessory photosynthetic pigments increased with increasing number of algal groups per community (linear regression, $p = 0.0003$, $r^2 = 0.38$, $n = 30$; Fig. 5A). In vivo absorbance measurements at the beginning of the experimental period revealed an increase in the specific absorbance yield (PAR) with increasing number of algal groups (linear regression, $p = 0.001$, $r^2 = 0.22$; Fig. 5B). Over the range of one to four algal groups per community, raw PAR absorbance per biomass concentration (integrated from 400 nm to 700 nm) ranged between 9.24 and 79.13, and augmented by 6.23 (18.7%) on average per additional algal group. However, we could not find significant effects of species diversity on the absorbance yield within the taxonomic groups (linear regres-

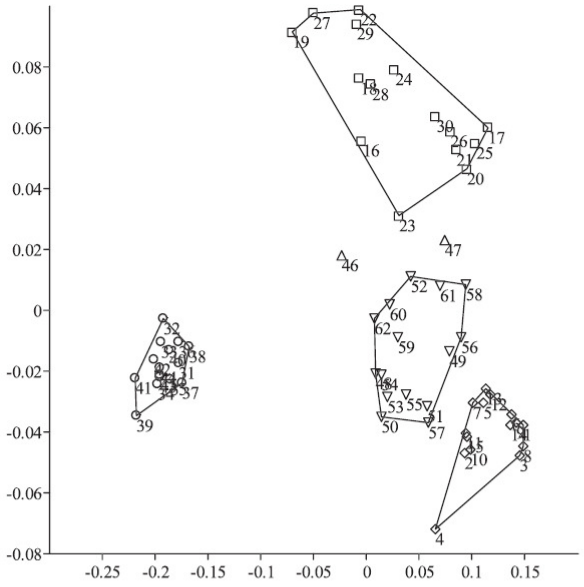

Fig. 4. Nonmetric multidimensional scaling plot representing the pigment composition of the phytoplankton communities. Similarities among communities were calculated using the Bray–Curtis Index based on the concentrations of eight pigments (Fuco, Diad, Allo, Lut, Zea, Chl *b*, Chl *a*, and *β*Car, *see* Pigment analysis). Each numbered point represents one community, numbers and symbols are: chlorophytes (1–15, diamonds), cyanobacteria (16–30, squares), diatoms (31–45, circles), chrysophytes (46–47, triangles upward), and mixed communities with more than one algal group (48–62, triangles downward).

sions: chlorophytes: $p = 0.93$, $r^2 < 0.001$, $n = 25$; diatoms: $p = 0.95$, $r^2 < 0.001$, $n = 22$; cyanobacteria: $p = 0.13$, $r^2 = 0.17$, $n = 22$). Considering the mean specific absorbance yield in vivo in all communities, we did not find significant differences among the groups (ANOVA, $F_{3,59} = 1.70$; $p = 0.18$; Fig. 5C), but a remarkable similarity to the complementarity effect (Figs. 3C, 5C): the effect sizes of both parameters showed an identical descending order, with highest values for communities with more than one algal group, followed by chlorophytes, diatoms, and finally cyanobacteria. A correlation analysis revealed a high positive correlation between the absorbance yield and the complementarity effect of carbon accrual (Pearson product moment correlation $r = 0.999$, $p = 0.0008$, $n = 4$; Fig. 5D).

Discussion

Although significant parts of global primary production (roughly 50%; Field et al. 1998) are performed by unicellular phytoplankton most studies concerning this matter originate from terrestrial environments. In contrast to terrestrial vascular plants, phytoplankton consists of different eukaryotic and prokaryotic groups, representing a large variety of different evolutionary lineages. In light of recent studies showing positive relationships between phytoplankton diversity, resource-use efficiency, and productivity in both field and laboratory experiments (Ptacnik et al. 2008; Striebel et al. 2009), we hypothesized stronger biodiversity effects in communities consisting of several algal groups than in communities of identical species richness but consisting only of single algal groups.

Carbon accrual—The positive correlations between productivity and species diversity that we found in chlorophytes and diatoms are in good agreement with previous studies from planktonic and benthic freshwater algal systems (Powder and Cardinale 2009; Striebel et al. 2009; Vanelslander et al. 2009). However, we show for the first time that biodiversity effects were more pronounced in multifunctional group phytoplankton communities with a high phylogenetic diversity. This effect is consistent with our hypothesis and has so far only been shown for a few terrestrial plant communities (Cadotte et al. 2008). Although niche differentiation processes and resulting complementary resource use are supposed to 'act' similarly in both terrestrial and aquatic environments, this correspondence is still remarkable, considering the fundamental differences in nutrient-uptake mechanisms, biomass allocation, or trophic turnover rates between land plants and unicellular algae (Duffy and Stachowicz 2006). Other (terrestrial) experiments revealed a considerable or even stronger effect of functional group identity than richness (Hooper and Vitousek 1997; Fornara and Tilman 2008; McLaren and Turkington 2010).

Considering the relative yield of POC as a measure of community performance relative to monocultures, we found a similar picture: all algal communities consisting of species from two, three, or four different phylogenetic (functional) groups showed overyielding as compared to their respective monocultures. Moreover transgressive overyielding occurred in more than half of them, a strong indicator for positive interactions such as complementary resource use or facilitation (Hector et al. 2002). Communities consisting of species from only one functional group had on average lower proportions of overyielding, whether transgressive or nontransgressive, with one exception: chlorophyte communities showed the highest amount of transgressive overyielding. Cardinale et al. (2007) calculated a theoretical timespan of 2–5 generations for annual or perennial plants to be necessary for attaining transgressive overyielding. Our experimental period covered ~ 4–10 generations, presuming a generation time of 2–5 d. This would also be consistent with a recent experimental study on benthic diatoms, which reported a similar proportion of transgressive overyielding (54%) on a similar timescale (Vanelslander et al. 2009). Transgressive overyielding can only be explained with some kind of positive interaction and is, therefore, considered as a strong indicator for complementarity and niche differentiation. Because this type of overyielding is found to be of importance in two different aquatic environments (pelagic and benthic) differing in species composition, species interactions, and general ecological conditions, one may assume that this mechanism is of general significance for the performance of multispecies microalgae communities.

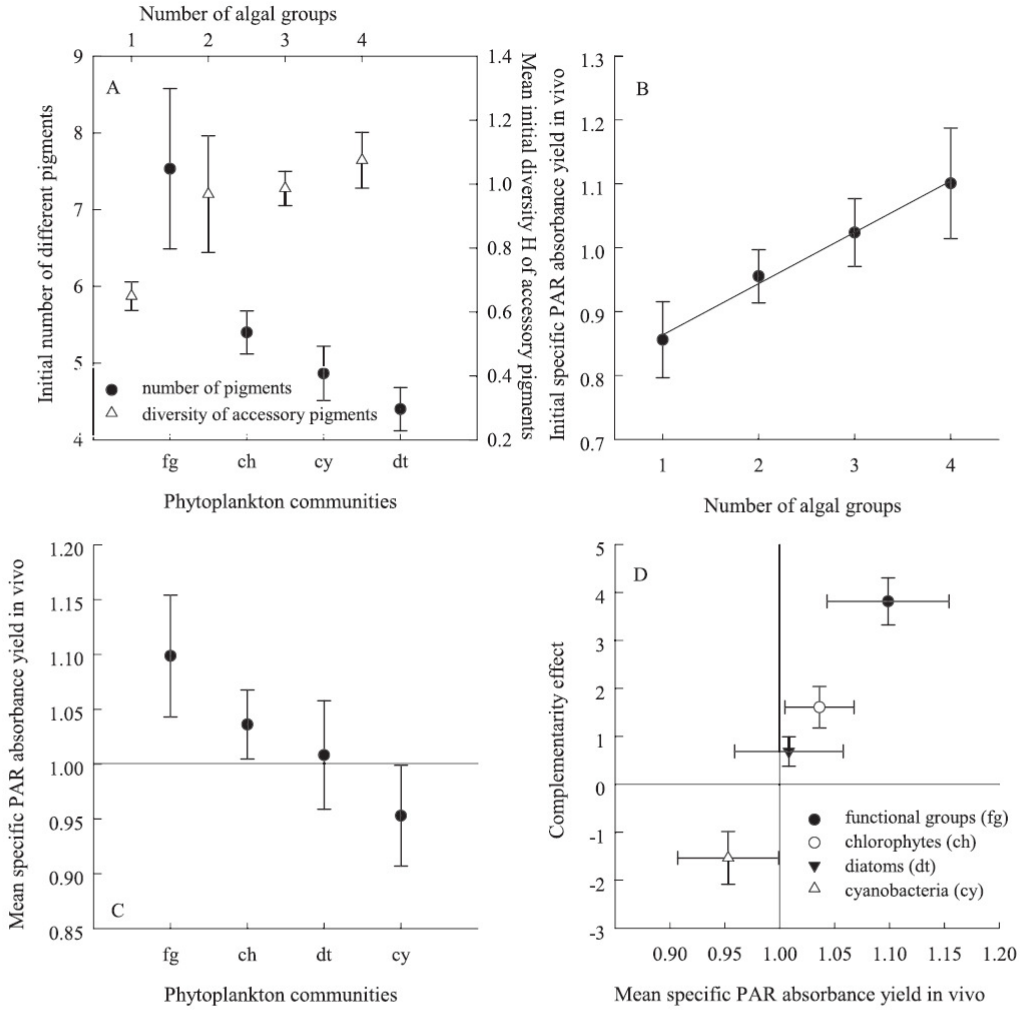

Fig. 5. (A) First plot (filled circles): mean (95% CI) number of pigments in chlorophyte communities (ch; $n = 15$), diatom communities (dt; $n = 15$), cyanobacterial communities (cy; $n = 15$), and communities with more than one algal group (fg; $n = 15$). Second plot (open triangles): relationship between the number of phytoplankton groups per community and the mean diversity of accessory pigments (linear regression: mean initial diversity H of accessory pigments $= 0.53 + 0.15 \times$ number of algal groups, $r^2 = 0.38$, $p = 0.0003$, $n = 30$). (B) Relationship between the number of phytoplankton groups per community and the initial specific PAR absorbance yield in vivo (linear regression: mean initial specific PAR absorbance yield $= 0.78 + 0.08 \times$ number of algal groups, $r^2 = 0.22$, $p = 0.001$, $n = 30$). (C) Mean specific PAR absorbance yield in the chlorophyte communities (ch; $n = 15$), diatom communities (dt; $n = 15$), cyanobacterial communities (cy; $n = 15$), and communities with more than one algal group (fg; $n = 15$). (D) Relationship between the mean specific PAR absorbance yield and the complementarity effect on relative carbon accrual. Error bars indicate the standard error of mean. The reference lines in B ($y = 1$) and C ($x = 1$) indicate the transition from underyielding to overyielding, and from negative to positive complementarity effect (C; $y = 0$).

Pigment diversity and specific absorbance yield in vivo—Our hypothesis of increasing light-use complementarity with increasing algal group diversity in phytoplankton is largely supported by the absorbance data. The biomass-specific absorbance yield showed a strong increase with increasing algal group diversity. Moreover, the observed yield of mixtures of different phylogenetic groups was higher than the yield of mixtures of similar species richness containing only species from single phylogenetic groups (chlorophytes, diatoms, and cyanobacteria). Although the differences in the specific absorbance yields of the single taxonomic groups were not statistically significant, they do still support our hypothesis due to the salient similarity of the absorbance yield effect size pattern with the complementarity effect size pattern in carbon accrual (Figs. 3C; 5B,C). Complementarity in absorbing photons within the

PAR spectrum is, therefore, most likely one crucial factor underlying complementarity in carbon accrual with increasing algal group diversity.

Complementarity and selection effect—One vital question in biodiversity experiments is whether overyielding can be attributed to particular species dominating the community's biomass, or to positive interactions among species (Loreau and Hector 2001). Usually it is both, although the relative strength of the two effects can vary substantially. We had hypothesized that positive interactions mediated by light-use complementarity would increase as phylogenetic (functional) diversity increases. Indeed, there was an increasing importance of complementarity with increasing algal group diversity (Fig. 3). Diatoms and chlorophytes, which had a similar augmentation in relative carbon accrual with increasing species diversity H, did not show a significant positive trend in complementarity, although their overall mean complementarity effects were positive. This supports our hypothesis that physiological differences between phylogenetic groups may give rise to a higher complementary resource use than such physiological differences within a certain phylogenetic group.

The selection effect, which is generally attributed to the presence of highly competitive species dominating the biomass yield in polycultures, exceeded on average the complementarity effect, thereby playing an important role in diatom and cyanobacterial communities. In opposition to these two groups, it did not differ statistically from zero in chlorophytes and in treatments with multiple phylogenetic algal groups (Fig. 3). This pronounced species effect in cyanobacteria and diatoms could largely be attributed to highly productive and competitive species. The three most productive cyanobacterial species in monoculture—*Anabaena cylindrica*, *Pseudoanabaena galeata*, and *Synechococcus* sp.—attained together on average 90.7% of the final biovolume in all communities, where they were present. Similarly, the three most productive diatom species in monoculture—*Navicula pelliculosa*, *Nitzschia palea*, and *Diatoma elongatum*—achieved together on average 80.6% of the final biovolumes. In contrast, in chlorophyte communities and communities consisting of more than one algal group, the three most productive species attained together on average only 69.0% and 44.9% of the final biovolumes, respectively. The only group showing a slight decline of the relative yield of POC as species diversity increases, the cyanobacteria, are known to release chemical substances (allelochemicals) to the environment, which may inhibit the growth of their competitors (Legrand et al. 2003). Although we do not know if this happened in those experimental communities, it corresponds well with the complementarity effect being negative on average. A common hypothesis states that in experimental studies, namely in highly controlled laboratory experiments, monocultures often perform better than mixtures just due to the simplified environment (Duffy 2009; Powder and Cardinale 2009) or the relatively short experimental period (Cardinale et al. 2007; Stachowicz et al. 2008). This would even point toward a possible underestimation of diversity effects such as resource-use complementarity in mesocosm experiments, as compared with real-world ecosystems.

Development of diversity during the experimental time course—Biovolume-based diversity H, whether species H or algal group H, decreased during the experimental period in all communities due to changes in the relative abundances of species (evenness), whereas initial species richness remained constant. However, the changes in H during the experimental periods did not affect the general relationships between diversity H and the response variables in our regression models. A comparison shows similar patterns when either using species richness SR, initial diversity H, final diversity H, or the arithmetic mean of the latter two during the laboratory experiment (Table 3). Choosing the appropriate diversity measure is often rather arbitrary and this might be due to the fact that diversity changes during the experimental period. There can be good reasons for using either the initial (experimental set-up) or final (possibly steady-state) diversity H. Many authors use species richness as a measure of diversity, because it is easy to determine and usually remains constant over a longer period of time (Balvanera et al. 2006). More importantly, biodiversity–ecosystem function experiments are ultimately motivated by the concern for how a loss of species due to human activities will affect ecosystem functioning. However, in this study using Shannon diversity H in terms of biovolume seems to be a better measure than species richness. Because specific biovolumes in phytoplankton communities often vary in the range of one or two orders of magnitude, it is the relative contribution to the total biovolume rather than the total species number that determines its effect (including diversity effects on productivity) on the community level (Hillebrand et al. 2008).

From theoretical considerations, it has been proposed to use continuous classification schemes ('dendrograms') based on some measure of (dis-) similarity instead of categorical measures of functional diversity (functional groups; Petchey and Gaston 2002; Reiss et al. 2009). Cadotte et al. (2008) showed in a meta-analysis on 29 diversity–productivity experiments performed with terrestrial plant communities that a (continuous) measure of phylogenetic diversity, derived from four gene segments, was a better predictor for diversity effects than species or functional group richness. Nevertheless, there was a strong positive correlation between the number of functional groups and the amount of phylogenetic diversity. According to recent taxonomy, all vascular plants group in one single branch of the phylogenetic tree, while the common ancestor of the functional algal groups defined in our experiment dates back much longer, particularly for eukaryotes and cyanobacteria (Falkowski et al. 2004). Therefore, we think that functional dissimilarities, based on phylogenetic differences leading to niche complementarity, should be more pronounced and visible in phytoplankton, even when using a categorical measure to define diversity.

Our results support the conclusion that the loss of a functional group, and thereby a complete particular trait or trait combination, might have more severe consequences

for pelagic communities than the loss of the same number of species originating from different functional groups. Two of the most important threats to aquatic ecosystems, global warming and eutrophication, may not only drastically alter the species composition in pelagic communities, for example by changing nutrient availability or stratification, but also the performance of entire functional algal groups. Climate-related changes in stratification patterns will presumably influence the population dynamics of diatoms because of their need for deep and continuous water-column mixing (Cermeno et al. 2008; Jäger et al. 2008). Because diatoms are one of the most abundant phytoplankton groups in large parts of the marine pelagial (Falkowski et al. 2004), environmental factors that could lead to a considerable decline might impair whole pelagic food webs. In addition to its importance for pelagic food web production, phytoplankton is also affecting biogeochemical fluxes such as the incorporation of CO_2 from the atmosphere into biomass and its export to deep ocean areas (referred to as 'biological pump'). At present, there is no consensus on the mechanisms that control the efficiency of the biological pump, something that varies dramatically, both spatially and temporally (Boyd and Trull 2007). Considering our results, we propose that this efficiency might also be linked to phytoplankton diversity, which would extend its relevance to global biogeochemical processes. Our findings also suggest that effects of changes in functional group diversity can be more important than changes in species diversity. Moreover, effects of species diversity can vary considerably depending on the taxonomic group under examination. Therefore, the doubtless far-reaching consequences for aquatic food-web functioning that may arise from the current loss of biodiversity cannot be predicted from changes in species richness alone. Future studies need to consider useful measures of functional diversity based on the deep phylogenetic branching of phytoplankton groups, with a priori definition of underlying functional traits so as to describe and predict diversity–productivity relationships in pelagic ecosystems.

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MANUSCRIPT I

TROPHIC TRANSFER OF BIODIVERSITY EFFECTS:

FUNCTIONAL EQUIVALENCE OF PREY DIVERSITY AND ENRICHMENT ?

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Abstract

Producer diversity is frequently assumed to be detrimental to herbivores, because less edible taxa are more likely to dominate diverse communities. Many producers are, however, complementary in their resource use, and primary production is often positively related to producer diversity. We performed an experiment with microalgae and a generalist herbivore to explore the hypothesis that such positive effects are transferred up the food chain and are functionally comparable to effects of enrichment with a limiting resource. In both absence and presence of grazers, primary production was positively affected by both light supply and producer diversity. Survival, reproduction and biomass of herbivores were also positively affected by light supply and producer diversity, with both factors contributing equally to grazer performance. We conclude that producer diversity can indeed have similar positive effects on secondary production as enrichment with a limiting resource and discuss conditions under which such positive effects are likely to dominate over negative ones

Introduction

Trophic transfer of primary production is a conceptual cornerstone of ecosystem ecology. Numerous studies have demonstrated that increased primary production usually translates into increased secondary production. Historically, ecologists have focused on enrichment (increased supply with limiting resources) as the source of increased primary production, and a large body of ecological theory has been developed to describe the consequences of enrichment for ecological communities (Oksanen et al. 1981, Holt et al. 1994, Grover 1995). More recently, it has been discovered that primary production is also positively related to producer diversity, a major underlying mechanism being niche complementarity and, consequently, more efficient use of limiting resources by primary producers (van Ruijven and Berendse 2005, Striebel et al. 2009a, Cardinale 2011). Positive effects of diversity on primary production can be on the same order as effects of enrichment (Reich et al. 2001, Fridley 2003). This raises the question: Are resource supply and diversity of primary producers functionally equivalent in that their positive effects on primary production are transferred up the food chain? While studies of biodiversity effects spanning more than one trophic level are receiving increasing attention (Duffy et al. 2007, Srivastava et al. 2009), this hypothesis has, to our knowledge, not yet been clearly formulated and addressed with experiments.

Experimental tests of the hypothesis must fulfill at least three conditions. First, enrichment with a limiting resource and producer diversity must be manipulated independently. Second, primary production must respond positively to each of these factors in isolation to enable a comparison of their relative impacts on secondary production. Finally, only a single species of a generalist herbivore should be present in the system. With several herbivore species it would be difficult to separate effects of producer productivity from effects of herbivore diversity (e.g. synergistic or compensatory responses among different herbivores). While some experimental studies have related herbivore abundance to producer diversity (e.g. Siemann et al. 1998, Koricheva et al. 2000, Gamfeldt et al. 2005), nearly all of them included multiple herbivores and therefore fail to fulfill the last criterion.

Enrichment and trophic transfer of primary production have been particularly well studied in freshwater systems. For example, comparative studies have revealed positive relationships between nutrient enrichment and biomass at all trophic levels, the strengths of these relationships being modulated by food web structure (Hanson and Peters 1984, Persson et al.

1992). More recently, experimental and comparative studies have explored light limitation in lakes. While these studies found positive relationships between light supply and both primary and secondary production (Diehl et al. 2005, Berger et al. 2006, Karlsson et al. 2009), enrichment with light is conceptually different from nutrient enrichment. Specifically, light supply depends not only on incident radiation, but also on physical properties such as water depth and background attenuation (Huisman and Weissing 1994). As a consequence, light and nutrients are often limiting in different parts of the water column (Yoshiyama et al. 2009). Increased carbon fixation at higher light supply therefore tends to increase nutrient use efficiency, which is expressed in an enhanced carbon-to-nutrient ratio of algal biomass (Sterner et al. 1997, Diehl et al. 2005, Berger et al. 2006).

Light differs from mineral resources also in that it is always supplied in a vertical gradient of decreasing intensity and changing spectral quality. Hence, planktonic algae experience large fluctuations in the quantity and quality of light when vertically mixed (Ferris and Christian 1991). The resulting unpredictable shifts in light supply and spectral composition plausibly explain the high diversity of photosynthetic pigments in the phytoplankton (Falkowski et al. 2004). Pigment composition is thus a trait characterizing the spectral niche of an algal taxon (Stomp et al. 2004), and spectrally more diverse phytoplankton communities should harvest light more efficiently. Such patterns have indeed been observed; i.e. more diverse phytoplankton communities show higher pigment diversity, absorb a higher fraction of available light, and fix more carbon (Striebel et al. 2009a, Behl et al. 2011). Interestingly, experiments with natural communities have shown that both light enrichment and increased phytoplankton diversity independently increase nutrient use efficiency, i.e. yield higher carbon-to-nutrient ratios of algal biomass (Dickman et al. 2006, Striebel et al. 2008). These observations support the hypothesis that increased phytoplankton diversity and light enrichment have similar effects on phytoplankton production and we conjecture that these effects should be similarly transferred to herbivores.

Here we describe a laboratory experiment comparing the effects of light enrichment and algal producer diversity on survival, reproduction and biomass of a generalist grazer. We first review a couple of earlier experiments investigating the separate effects of light supply and producer diversity on primary production in absence of grazers. These experiments were conducted with the same algal taxa and under similar conditions as the grazer experiment. We then present the results of the grazer experiment with a focus on comparing the relative contributions of light supply and producer diversity to grazer performance. We found that, in

both absence and presence of grazers, primary production was positively related to both light supply and producer diversity. Survival, reproduction and biomass of herbivores were also all positively related to light supply and producer diversity, with both factors contributing about equally to grazer performance. We conclude that producer diversity can have a similarly strong, positive effect on secondary production as enrichment with a limiting resource.

Materials and Methods

Overview

The main purpose of this study was to test the hypothesis that increased producer diversity can have similar (positive) effects on primary production and herbivore performance as has enrichment with light. To do so, we first re-analyze data from two earlier experiments in which we manipulated light supply and producer diversity separately and in absence of grazers. We then describe the grazer experiment, in which we manipulated light supply and algal species richness in a full factorial design in presence of a generalist grazer, the cladoceran *Daphnia magna*. Because we were solely interested in assessing (and comparing) conjectured *positive* effects of enrichment and producer diversity on grazers, we tried to avoid confounding negative effects of these factors. In particular, we excluded high light intensities (which could lead to unfavorably high C:P ratios, and thus low food quality, of algal biomass) and we excluded algal taxa known to be toxic or inedible. Light supply was therefore constrained to ≤120 µmol photons PAR m^{-2} s^{-1} and the algal species pool consisted exclusively of chlorophytes of similar size.

Experiments without grazers

Striebel et al. (2009b) measured short-term primary production and longer term biomass accrual of 9 species of chlorophytes as a function of light supply. Methodological aspects of this experiment are very similar to the grazer experiment described below and are specified in

detail in the original publication. Important features concerning design, replication, duration, and environmental conditions are also listed in Table 1. Seven of the 9 chlorophyte species are shared with the grazer experiment and three of the light treatments cover a similar range of light supplies (Table 1). For the purpose of this paper we have therefore re-analyzed the effects of light supply on biomass accrual and the C:P ratio of these 7 chlorophytes over the light supply range 10-110 µmol photons PAR m^{-2} s^{-1}.

Behl et al. (2011) measured biomass accrual of 9 species of chlorophytes as a function of species richness. Methodological aspects of this experiment are, again, very similar to the grazer experiment described below and are specified in the original publication, the most important features being listed in Table 1. All 9 chlorophyte species are shared with the grazer experiment. Behl et al. (2011) analyzed effects of chlorophyte diversity on response parameters using Shannon diversity, whereas the grazer experiment was analyzed with species richness as the independent variable (see below). For the purpose of this paper we have therefore re-analyzed the data from Behl et al. (2011) based on species richness (range 1-4 chlorophyte taxa, Table 1).

Grazer experiment

We used 11 different strains of freshwater chlorophytes of similar edibility and size (Table 2). The strains originated from the SAG Culture Collection of Algae (Göttingen) and were precultured for several weeks under constant conditions in a freshwater medium (COMBO; 15.0 μg phosphorus L^{-1}) appropriate for phytoplankton and zooplankton cultivation. We established a species diversity gradient with four diversity levels ranging from mono- to 8-spp. polycultures (1, 2, 4, and 8 different species). Each diversity level (except for the 11 monocultures) was replicated three times with different species compositions (no identical replicates), resulting in a total of 20 communities, randomly comprised of members from the species pool. We established a light intensity gradient with 30, 60, 90, and 120 µmol quanta m^{-2} s^{-1} (measured with a LI-COR LI 191SA Quantum Sensor, Licor, USA in front of the experimental units). This light intensity gradient is within the typical range experienced by phytoplankton in the mixed layer of a temperate lake. The two gradients (light and diversity) were fully cross-classified, yielding a total of 80 treatments.

All treatments were inoculated with an identical total algal biovolume (2.62 x 10^6 µm³

mL^{-1} equaling 0.5 mg particulate organic carbon, POC, L^{-1}), and different species contributed equal biovolumes to communities with two or more species. All inocula were grown under dim light conditions for one day before each treatment received a founder population of eight age-synchronized neonate *Daphnia magna* (max. 12 hours after birth) from our laboratory stock. The communities (500 mL) were exposed to the experimental treatments in 650 mL cell culture flasks over an 11 day period, with a 10 % medium exchange on days 3, 5, and 9. Temperature was constant at 20 ± 0.5 °C with a 16 h light / 8 h dark photoperiod regime. All communities were gently shaken twice a day to prevent algae from sinking and accumulating at the bottom of the culture flask. *Daphnia* populations were monitored qualitatively on a daily basis to follow reproduction and mortality events.

We sampled each algal community on day 1 (before adding the neonates), day 6, and day 11 (after removing all daphnids). Samples were poured through a 80 µm mesh net to retain daphnids, exuviae, and large detrital particles. As a measure of algal biomass, particulate organic carbon (POC) was determined after filtration onto precombusted and acid-washed glass-fiber-filters (Whatman GF/C, Whatman International Ltd.) by elemental analysis (Elemental Analyzer, EA 1110 CHNS, CE Instruments). Particulate phosphorus (PP) was measured after sulfuric acid digestion followed by molybdate reaction. Seston C:P ratios were calculated as the molar ratio of POC:PP. Additionally, we fixed an aliquot of each sample with Lugol's iodine to determine initial (day 1) and final (day 11) phytoplankton composition by inverted microscopy using Utermöhl chambers. A minimum of 100 cells of every species was counted by scanning at least five perpendicular transects or 20 randomly distributed, distinct fields. AnalySIS software (Pro 2.11.006, Soft Imaging Software GmbH) was used to determine biovolumes of cells by measuring 2-dimesional live pictures; biovolumes were calculated from geometric shapes according to Hillebrand et al. (1999) or our own adjustments.

Daphnia body lengths were measured at the onset of the experiment (50 neonates not used in the experiment) and at the end (day 11, all surviving founder individuals and juveniles that hatched during the experiment). Length measurements were obtained electronically employing a microscope combined with a video system ($ALTRA_{20}$ Soft Imaging System) and $cell^{P}$ software (Olympus Soft Imaging Solutions GmbH, Germany). Body length was defined as the distance from the upper edge of the compound eye to the base of the apical spine. Individual dry mass was calculated using the empirical length-mass relationship W = 11.824 x

$L^{2.236}$, where W is dry mass [µg], and L is body length [mm]. On day 4, the day we first detected females with eggs, all founder individuals were scanned for eggs in their brood chambers, and the number of gravid females was determined.

Data processing and Statistics

Effects of light supply and algal species richness on response variables were analyzed with simple (experiments without grazers) or multiple (grazer experiment) linear regression on log transformed data (Table 3). When response variables included zero values data were log(x+n) transformed, where n is the smallest detectable unit. Thus, n = 1 in case of the numbers of gravid and surviving founder *Daphnia* individuals, and n = average biomass of an individual *Daphnia* in case of final *Daphnia* biomass. Algal variables (biomass and C:P ratio) were averaged over days 6 and 11 to better reflect average food conditions for *Daphnia* (separate analyses of days 6 and 11 did, however, reveal qualitatively similar patterns). All statistical analyses were performed with SigmaPlot 11.0 (2008), Systat Software, Inc. Daphnids suffered complete mortality in 14 of the 80 communities. We included these communities in the statistical analyses of *Daphnia* responses but excluded them from the analyses of algal responses. Results of algal statistics were, however, very similar whether those communities were included or excluded.

In the grazer experiment, standardized partial regression coefficients (SPRC) were used as a measure of the relative contributions of light supply and species richness to the response variables. SPRC was calculated as

$$SPRC_x = b_x \times s_x \; / \; s_y$$

where b is the regression coefficient of the independent variable x (light or species richness), and s is the standard error of the independent (x) and dependent (y) variables, as determined in the multiple regression (Table 3). The relative contributions of light supply and species richness to a response variable was calculated as the ratio $SPRC_{SR} / SPRC_{Light}$, where ratios >1 indicate a larger relative contribution of species richness (SR) and ratios <1 indicate a larger relative contribution of light supply.

To further explore whether effects of algal species richness propagated to the herbivore level, we calculated the relative biomass yield of *Daphnia* as the ratio of observed

Daphnia biomass in a given polyculture P_i to the *Daphnia* biomass expected from monocultures of the algal species contributing to polyculture P_i as

$$\text{Relative } \textit{Daphnia} \text{ biomass yield} = \frac{Z_{Pi}}{\sum_{j=1}^{i} Z_{Mj} \times k_j(P_i)}$$

where Z_{Pi} is *Daphnia* biomass in polyculture P_i with i algal species, Z_{Mj} is *Daphnia* biomass in monoculture of algal species j, and $k_j(P_i) = 1/i$ is the proportional contribution of algal species j to total algal biomass in polyculture P_i at the start of the experiment. For statistical analyses relative yield was log transformed. Thus, overyielding occurred when the log transformed ratio was positive, and underyielding when it was negative. The occurrence of zero values (no surviving *Daphnia*) was addressed in two ways: either by excluding zero values from the analysis or by addition of the average biomass of 1 individual *Daphnia* to the values of Z_{Pi} and Z_{Mj} prior to log transformation. Results were similar and we only report the ones where zero values were excluded from the analysis.

Results

Experiments without grazers

In absence of grazers, final algal biomass and the seston C:P ratio were both positively related to light supply over the range 10-110 µmol quanta m^{-2} s^{-1} (Fig. 1a, b; Table 3a, b). Final algal biomass was also positively related to species richness over the investigated gradient from 1 to 4 chlorophyte taxa (Fig. 1c; Table 3c). Species richness had furthermore a positive effect on specific PAR absorbance per unit algal biovolume (Fig. 1d; Table 3d) and per unit seston POC, the latter being non-significant (Table 3e; *see* Behl et al. 2011 for a description of how absorbance was measured).

Grazer experiment

All phytoplankton monocultures and species mixtures established as scheduled, with proportions of component algal species on day 1 deviating in polycultures by only 10 ± 1 % (mean ± s.e.m.) from the scheduled equal biovolumes. By the end of the experiment, algal species richness had not changed in any community, but evenness had decreased notably in all communities. In 14 of the 80 communities, daphnids suffered complete mortality. This happened primarily in low light and low diversity communities. One algal monoculture (*Staurastrum tetracerum*) did not support positive *Daphnia* growth rates at any light level.

Both algal species richness and light intensity had positive effects on algal biomass and the seston C:P ratio averaged over days 6 and 11 (Fig. 1e, f and Table 3f, g), the effect of species richness being somewhat weaker than the effect of light (ratio $SPRC_{SR}/SPRC_{Light}$ 0.53-0.58).

Both algal species richness and light intensity had positive effects on the number of surviving founder individuals (Fig. 2a, Table 3h). Similarly, algal species richness and light intensity had positive effects on the number of egg-carrying individuals on day 4 (Fig. 2b; Table 3i). Note that on day 4 most daphnids did not yet carry eggs in their brood chambers (egg-carrying individuals occurred only in 15% of the populations).

Algal species richness and light intensity had positive effects on the biomasses of both surviving founder individuals and of juvenile daphnids (Fig. 2c, d, Table 3j, k). A positive effect of algal species richness on *Daphnia* biomass was also supported by the calculations of relative biomass yield. The log of this ratio was on average 0.15 (and significantly larger than zero, t-test) for both founders and juveniles (Fig. 3a, b), corresponding to an untransformed relative biomass yield of 1.16 and, thus, on average 16% higher *Daphnia* biomass in polycultures compared to monocultures. In addition, the relative *Daphnia* biomass yield was positively related to algal species richness, the relationship being statistically significant for founders but not for juveniles (Fig. 3a, b; Table 3l, m).

For all *Daphnia* response variables the ratio $SPRC_{SR}/SPRC_{Light}$ was close to 1 (Table 3h-k), indicating that the positive effects of algal species richness and light on *Daphnia* performance were quantitatively very similar.

Impact of algal species identity in polycultures

Notable differences in *Daphnia* biomass were observed in phytoplankton monocultures (*see* Fig. 2c, d). Monocultures of *Scenedesmus obliquus* yielded on average the highest final grazer biomasses of all monocultures (all light levels; Mann-Whitney Rank Sum Test; $U = 16.0$, $P = 0.009$, $n = 44$), and *Scenedesmus* exhibited on average the highest final proportion (49 %) of all algal species in polycultures where it was present. However, no relationship between *Daphnia* biomass and the final proportion of *Scenedesmus* in these polycultures could be detected (linear regression: $r^2 = 0.03$, $P = 0.41$, n = 21, data not shown). There was also no significantly positive relationship between *Daphnia* biomass and the final proportion of any other algal species in polyculture (linear regressions; data not shown). This fits well with the results from the experiments without grazers, where the positive effect of species richness on chlorophyte biomass was exclusively related to complementarity, the mean selection effect being zero (Behl et al. 2011).

Discussion

Functional equivalence of biodiversity and resource enrichment effects

We have investigated the hypothesis that positive effects of producer diversity on primary production are transferred up the food chain, and that these effects may be comparable to effects of enrichment with a production limiting resource. Our point of departure was the recent experimental demonstration that primary production is positively related to the taxonomic diversity of microalgae, and that this relationship is largely a consequence of overyielding [i.e. higher community production than expected based on the yields of the constituent species in monoculture (Striebel et al. 2009a, Behl et al. 2011, Cardinale 2011)]. Overyielding, in turn, is a strong indication of niche complementarity, and at least two complementarity mechanisms have been described for microalgae: spectral complementarity with respect to the capture of photons (Stomp et al. 2004, Striebel et al. 2009a, Behl et al. 2011) and hydraulic complementarity with respect to nutrient uptake in heterogeneous flow environments (Cardinale 2011). Niche complementarity has been documented also among

terrestrial primary producers (e.g. Fridley 2003, van Ruijven & Berendse 2005). From the perspective of a herbivore population, increasing producer diversity can therefore be interpreted as just another form of enrichment: increasing the availability of resources that limit primary production, or increasing the producer community's ability to exploit those resources, have qualitatively similar effects on primary production which, in turn, should be similarly transferred to herbivores.

The combined evidence from our experiments supports this hypothesized functional equivalence of resource availability and resource exploitation capacity: primary production, algal nutrient use efficiency (measured as algal C:P), and survival, reproduction and biomass of *Daphnia* were all positively related to both light supply and producer diversity. Relative grazer yield was higher in poly- than in monocultures, compatible with the hypothesis that the positive effects of algal diversity on *Daphnia* were a consequence of niche complementarity at the producer level. The positive relationship between algal species richness and specific PAR absorbance per algal biomass is furthermore in line with Striebel et al.'s (2009a) observation of spectral complementarity in diverse algal communities. Consequently, more diverse algal communities may have exploited the PAR spectrum more efficiently because of a greater diversity of photosynthetic pigments. Re-analyzing the data for the nine chlorophytes species studied by Behl et al. (2011) we found indeed a positive relationship between species richness and pigment richness (data not shown). This relationship was, however, not statistically significant (r^2 = 0.08, P = 0.18), possibly because only eight different pigments were distinguished (compared to 26 pigments in Striebel et al. 2009a).

The effects of light enrichment and algal diversity on grazers were quantitatively similar over the investigated range of treatment conditions, as indicated by equal magnitudes of their standard partial regression coefficients. On average, the addition of one species to the algal community had roughly the same positive effect on *Daphnia* biomass as had light enrichment by 14 µmol quanta m^{-2} s^{-1}. While these numbers cannot be extrapolated to wider ranging field conditions (positive effects on algal production are, for example, expected to saturate at higher levels of both light supply and species richness), our experiments clearly illustrate that biodiversity effects can be transferred up the food chain just as easily as 'traditional' enrichment effects and may be quantitatively equally important.

Herbivore responses to producer diversity in other studies

Several earlier experimental studies, which documented positive effects of plant diversity on primary production, did also report herbivore responses. These studies found positive (Pfisterer et al. 2003), negative (Koricheva et al. 2000) or no responses (Siemann et al. 1998) of herbivore abundance to plant diversity manipulations. In all of these studies, however, experimental communities included multiple herbivores and higher level consumers and parasitoids. This makes it impossible to distinguish effects of plant productivity from community feedbacks within and above the herbivore level. Moreover, none of the studies did simultaneously investigate effects of resource enrichment. Consequently, these studies cannot address our hypothesis that effects of niche complementarity on primary production can be transferred up the food chain. We are aware of only a single study using a relevant design (Steiner 2001); this study found temporally shifting responses, which will be discussed further down.

Algal nutrient use efficiency and food quality

Similar to experiments with natural lake communities (Dickman et al. 2006, Striebel et al. 2008), seston C:P ratios increased with both increasing light supply and species richness. We have interpreted higher seston C:P ratios as an indication of increased algal nutrient use efficiency that made more energy available to grazers. At very high algal C:P ratios the phosphorus content in algal biomass may, however, become so diluted that *Daphnia* growth is increasingly phosphorus rather than energy limited (Sterner 1993). Under such circumstances, further light enrichment can decrease *Daphnia* performance (Urabe & Sterner 1996). The phosphorus and light supplies in our experiment were deliberately chosen to represent moderate regimes. Nevertheless, 33% of all treatments had seston C:P ratios >250, and a plot of *Daphnia* biomass against seston C:P reveals that the otherwise strong positive correlation between the two variables leveled off around this threshold value (Fig. 3c). Our data thus suggest that the positive effects of both light enrichment and producer diversity on grazers may saturate and even turn negative at high levels of nutrient use efficiency (= high carbon-to-nutrient ratios of producer biomass). A truly negative influence of seston C:P on *Daphnia* performance, which could have obscured the positive effects of light enrichment and algal

diversity, is, however, only indicated for the two treatments with the highest seston C:P ratios exceeding 1000 (Fig. 3c).

Other prey diversity effects on grazers: diet mixing and prey defenses

While our experiments are clearly consistent with the hypothesis that the positive effects of producer diversity on grazer performance were mediated by increased algal production, it is possible that a second form of producer complementarity contributed to this effect, i.e. dietary mixing. The biochemical composition of autotrophs is typically imbalanced with respect to the nutritional needs of their herbivores (Elser et al. 2000, Sperfeld et al. 2012). Consequently, any single plant species will often be deficient in some essential biochemical compounds, and there is growing evidence that herbivores regulate their intake of such compounds by mixing nutritionally complementary plants in their diets (Simpson et al. 2004). Diet mixing has indeed been shown to improve performance in a wide range of herbivores including mammals, fish, and grasshoppers (Pennings et al. 1993, Unsicker et al. 2008, Wang et al. 2010).

Positive effects of diet mixing have also been documented in *Daphnia* and other cladocerans (Boersma & Vijverberg 1995, DeMott 1998), but the evidence is rather mixed (e.g. Narvani & Mazumder 2010). Most cladocerans, including *Daphnia*, are filter feeders with very limited ability to actively select or avoid specific particles. Consequently, *Daphnia* performance is typically reduced when unpalatable or toxic species are present in a food mixture (Gliwicz & Lampert 1990, Lürling 2003). Increased algal diversity could therefore have negative effects on grazers, if unpalatable or toxic taxa are common in the algal species pool. We tried to avoid this issue by only including non-toxic, unicellular chlorophytes in the edible size range in the species pool. With the exception of *Staurastrum*, all algal taxa did indeed support *Daphnia* populations when grown in monoculture (at least at some levels of light enrichment), indicating that poor algal food quality was a minor issue in our experiment. Also, total *Daphnia* biomass accrual in polycultures was independent of the monoculture yields, suggesting that *Daphnia* performance was not driven by the relative abundance of particularly ‘good’ (e.g., *Scenedesmus*) or ‘poor’ (e.g., *Staurastrum*) food-algae.

From the reverse perspective, low food quality did also not seem to convey a grazer-mediated competitive advantage to algae. If anything, the opposite was observed. The species yielding

the highest *Daphnia* biomass in monoculture (*Scenedesmus*) was also most successful in polycultures (averaging 49% of total final algal biovolume), whereas *Staurastrum* did poorly in most polycultures (averaging 2.5% of total final algal biovolume). The latter observation is interesting given the predominant discussion of negative effects of producer diversity on herbivory in the literature (Hillebrand & Cardinale 2004). In particular, it has been argued that more diverse prey communities are more likely to include unpalatable, toxic, or inedible species that would increase in frequency under grazing pressure and ultimately dominate the community (Duffy et al. 2007). This phenomenon has indeed been reported from natural and artificially assembled communities (Steiner 2001, Edwards et al. 2010). However, other experiments show contrasting results in favor of the 'balanced diet hypothesis' (Duffy et al. 2007), which states that consumers benefit from a more diverse prey community, due to broader availability of qualitatively different food resources.

Interactive effects of enrichment and producer diversity

We are aware of only one other study with a somewhat similar experimental design as ours. Steiner (2001) investigated the transfer of primary production to herbivores as a function of producer diversity and nutrient enrichment. Specifically, he created different plankton communities by adding a single grazer species (*Daphnia pulex* or *Ceriodaphnia quadrangula*) to either a monoculture of an edible green alga or a mix of the green alga with a diverse community of pond phytoplankton. The two phytoplankton diversity treatments were cross-classified with two levels of nutrient enrichment. Similar to our experiment, grazer biomass was positively affected by both enrichment and producer diversity during the first 21 days of the experiment. The positive diversity effect on grazers switched, however, sign to a negative one later in the experiment (days 28-42), when grazing resistant algal taxa came to dominate in high diversity treatments. This reversal was, however, only observed in the nutrient enriched treatments, which is consistent with theory. Assuming a resource competition-grazing resistance tradeoff in producers, theory predicts that grazer biomass increases strongly with enrichment when grazing resistant taxa are absent from the community, but only weakly so when grazing resistant taxa are present; grazing resistant taxa, in turn, are predicted to be competitively excluded at low levels of enrichment (Holt et al. 1994, Grover 1995).

Clearly, more experimental studies are needed to clarify the conditions under which increased producer diversity enhances trophic transfer of primary production up the food

chain. A comparison of Steiner's (2001) results with ours tentatively suggests that positive effects of producer diversity on grazers might be transient, if grazing resistant taxa are present in the species pool and if the system is sufficiently enriched. Conversely, if limiting resources are scarce or if grazing resistant taxa are absent, positive effects of producer diversity on grazers should persist also in the long run. In a long-term experiment using a similar pool of edible algal species as the present study, positive effects of producer diversity on *Daphnia* were indeed observed over hundreds of days (S. Behl, unpublished work). It should also be kept in mind that even when positive diversity effects are transient, they may nevertheless be ecologically highly relevant. For example, many plankton communities go through recurrent periods of transient dynamics driven by seasonality and disturbances (Sommer et al. 1986), and in many systems a large fraction of the transfer of primary production to higher trophic levels occurs during transient population peaks (e.g. Platt et al. 2003, Winder & Schindler 2004). We therefore propose that trophic transfer of biodiversity effects has the potential to affect both long-term and seasonal community dynamics and related ecosystem services, and that the concept needs to be included in future biodiversity research.

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Table 1. Comparison of treatment characteristics and environmental conditions in the reported experiments

	Striebel et al. 2009b	Behl et al. 2011	This study
Light treatments [µmol quanta PAR m^{-2} s^{-1}]	10, 20, 110	90	30, 60, 90, 120
Species richness treatments	1	1, 2, 3, 4	1, 2, 4, 8
No. of taxa in species pool	7	9	11
Phosphorus in culture medium [µg P L^{-1}]	10	31	15
Culture volume [mL]	250	400	500
Duration [days]	14	21	11
Average medium exchange rate [% day^{-1}]	10	12.5	3
Total no. of replicates	63	24	80
Initial algal biovolume [μm^3 mL^{-1}]	2.0	5.3	2.6
Temperature [°C]	20	20	20

Table 2. Chlorophyte species used in monoculture and polycultures experiments and their mean biovolumes and cell sizes. Polyculture labels refer to the number of species per community (2, 4, 8) and a letter code (a, b, c) identifying each of the three different communities per diversity treatment.

Code	Chlorophyte species	Max. cell diameter [µm]	Mean cell biovolume [µm³]	In polyculture
Chl	*Chlamydomonas reinhardtii*	10.4	385.6	4b; 8a,c
Mon	*Monoraphidium minutum*	6.7	104.5	4a; 8a,b,c
Sce	*Scenedesmus obliquus*	17.7	294.8	4a,c; 8a,b,c
Sel	*Selenastrum capricornutum*	9.5	113.8	4a,c; 8a,b
Des	*Desmodesmus subspicatus*	8.6	162.2	2c; 4b; 8a,b,c
Gol	*Golenkinia brevispicula*	11.9	907.9	2a; 4b; 8a
Hae	*Haematococcus pluvialis*	16.5	1203.0	2c; 4c; 8b,c
Sta	*Staurastrum tetracerum*	35.0	1641.0	8a,b,c
Tet	*Tetraedron minimum*	8.7	315.3	2b; 4c; 8b,c
Cru	*Crucigenia tetrapedia*	7.1	150.5	2b; 4a; 8a,b
Ped	*Pediastrum simplex* (single cells)	17.1	1125.4	2a; 4b; 8c

Table 3. Simple and multiple linear regression statistics (log $y = a + b \times \log SR + c \times \log Light$) describing the influence of algal species richness (SR) and light intensity (Light) treatments on several independent algal and *Daphnia* response variables (y). Algal and *Daphnia* biomass [µg POC L^{-1}], seston C:P [atomic ratios], Light = PAR intensity [µmol quanta $m^{-2}s^{-1}$], d 6&11 = mean of days 6 and 11, *n* = number of replicates. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant. SPRC = standard partial regression coefficient, s.e.m. = standard error of the mean.

		Overall regression			Coefficients (*b, c*)				Ratio of ($SPRC_{SR}$ / $SPRC_{Light}$)
	y	*n*	r^2	*p*	*a*	Log SR (s.e.m.)	*p*	Log Light (s.e.m.)	*p*	
Striebel et al. 2009b										
a	Log algal biomass	61	0.30		2.64			0.37 (0.07)	***	
b	Log seston molar C:P ratio	61	0.22		1.97			0.42 (0.10)	***	
Behl et al. 2011										
c	Log algal biomass	24	0.53		3.94	0.11 (0.02)	***			
d	Log biovol.-specific absorbance	24	0.29		-6.09	0.51 (0.17)	**			
e	Log POC-specific absorbance	24	0.11		0.89	0.25 (0.15)	n.s.			
This study										
f	Log algal biomass d 6&11	66	0.28	***	1.37	0.26 (0.11)	*	0.81 (0.19)	***	0.53
g	Log seston molar C:P ratio d 6&11	66	0.26	***	0.69	0.29 (0.12)	*	0.83 (0.20)	***	0.58
h	Log No. of surviving founders	80	0.26	***	-0.51	0.37 (0.10)	***	0.58 (0.16)	***	0.98
i	Log No. of gravid founders (day 4)	80	0.23	***	-0.41	0.18 (0.05)	***	0.24 (0.08)	**	1.15
j	Log *Daphnia* biomass (founders)	80	0.32	***	1.34	0.45 (0.10)	***	0.68 (0.16)	***	0.99
k	Log *Daphnia* biomass (juveniles)	80	0.28	***	-0.39	0.86 (0.21)	***	1.24 (0.32)	***	1.06

l	Log founders relative yield	31	0.42	-0.25	0.62 (0.13)	***
m	Log juveniles relative yield	28	0.05	-0.06	0.30 (0.26)	n.s.

Figure legends

Figure 1: Influence of light intensity (Light) [µmol quanta $m^{-2}s^{-1}$] and/or phytoplankton species richness (SR) on (a) final algal biomass [µg POC L^{-1}] and (b) the final molar seston C:P ratio in the study by Striebel et al. (2009b), on (c) final biomass and (d) biovolume-specific PAR absorbance of chlorophytes in the study by Behl et al. (2011), and on (e) mean algal biomass and (f) mean molar seston C:P ratio on days 6 and 11 in the grazer experiment. All axes are $\log_{10}$ transformed. Linear regression equations and statistics are given in Table 3.

Figure 2: Influence of light intensity (Light) [µmol quanta m^{-2} s^{-1}] and phytoplankton species richness (SR) on (a) the number of *Daphnia* founder individuals surviving to the end of the experiment, (b) the number of founder individuals carrying eggs in their brood chambers on day 4, and on the biomasses [µg POC L^{-1}] of (c) founder individuals and (d) juvenile *Daphnia* at the end of the experiment. All axes are $\log_{10}$ transformed. Replicate treatments with identical y-axis values have been slightly offset to make them visible. Multiple linear regression equations and statistics are given in Table 3.

Figure 3: Influence of phytoplankton species richness (SR) on the relative biomass yield of (a) founder individuals and (b) juvenile *Daphnia*. Values >0 indicate overyielding, the means being significantly >0 in both cases (t-test). Linear regression equations and statistics are given in Table 3. (c) Relationship between the seston C:P ratio (mean of days 6 and 11) and final total *Daphnia* biomass [µg POC L^{-1}] (founders plus juveniles). The positive correlation levels off at a seston C:P ratio of c. 250. All axes are $\log_{10}$ transformed.

Figure 1

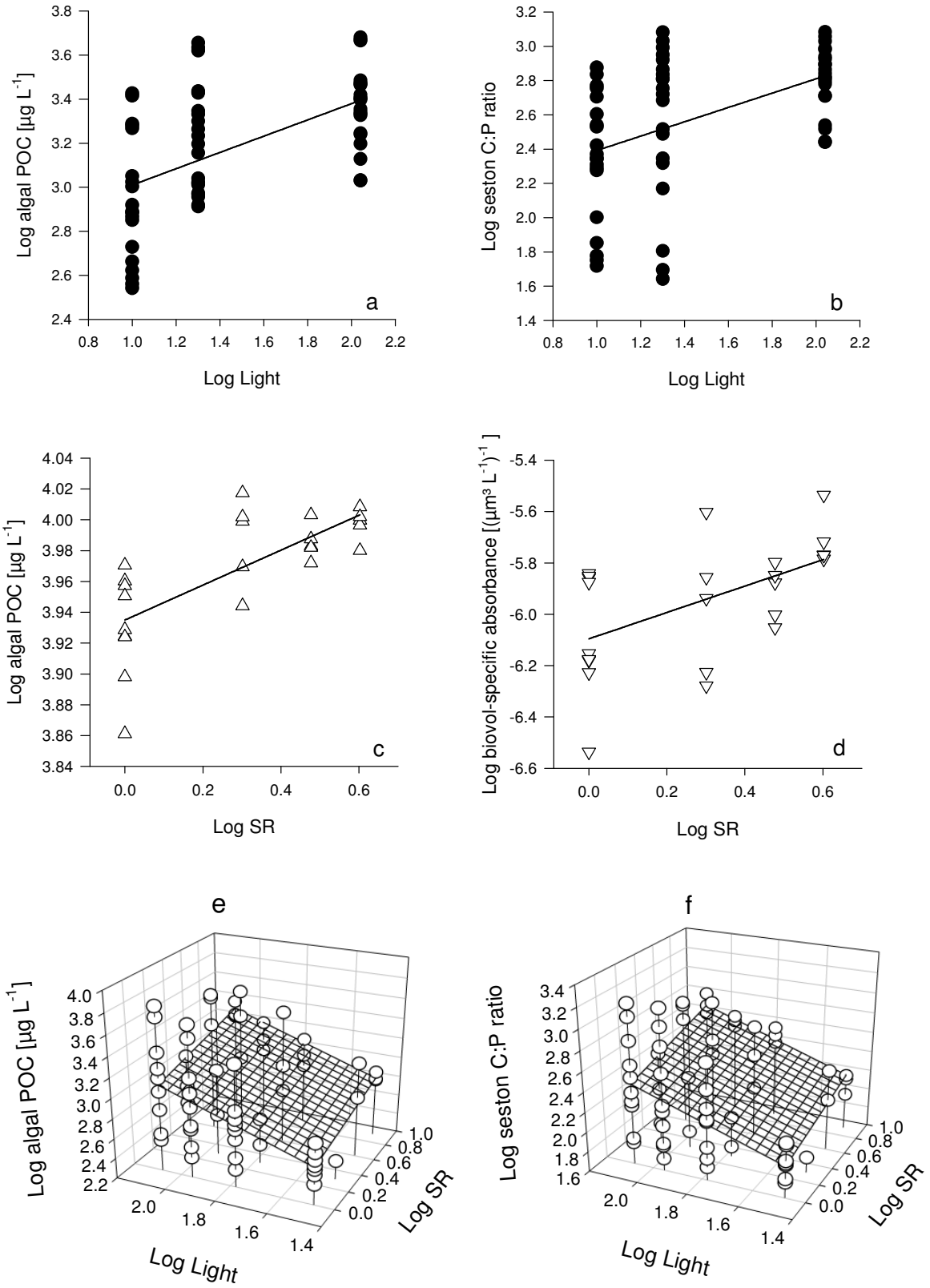

Log algal POC [µg L-1]
Log Light
a
Log seston C:P ratio
b
Log SR
c
Log biovol-specific absorbance [(µm³ L-1)-1]
d
e
f

Figure 2

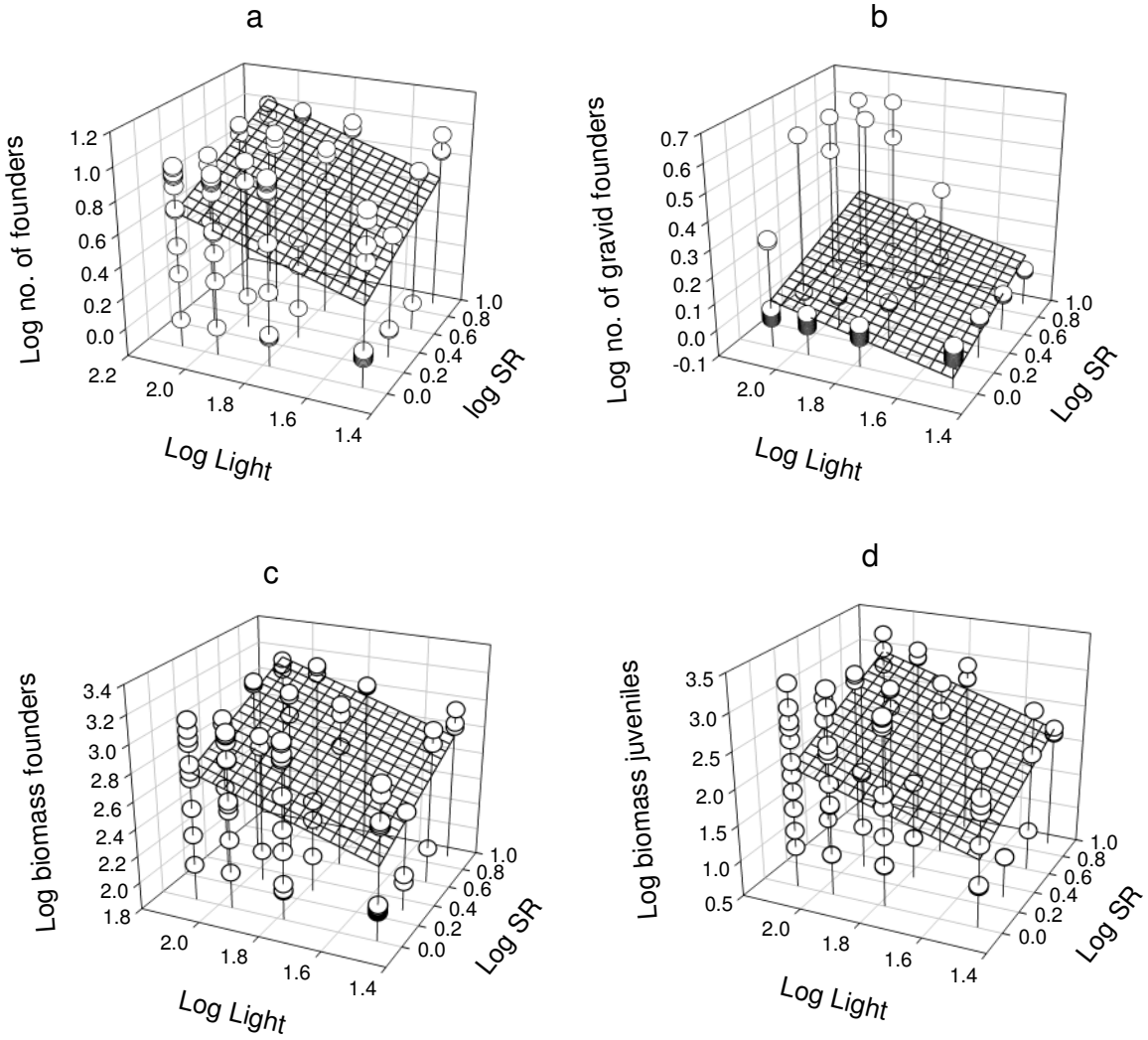
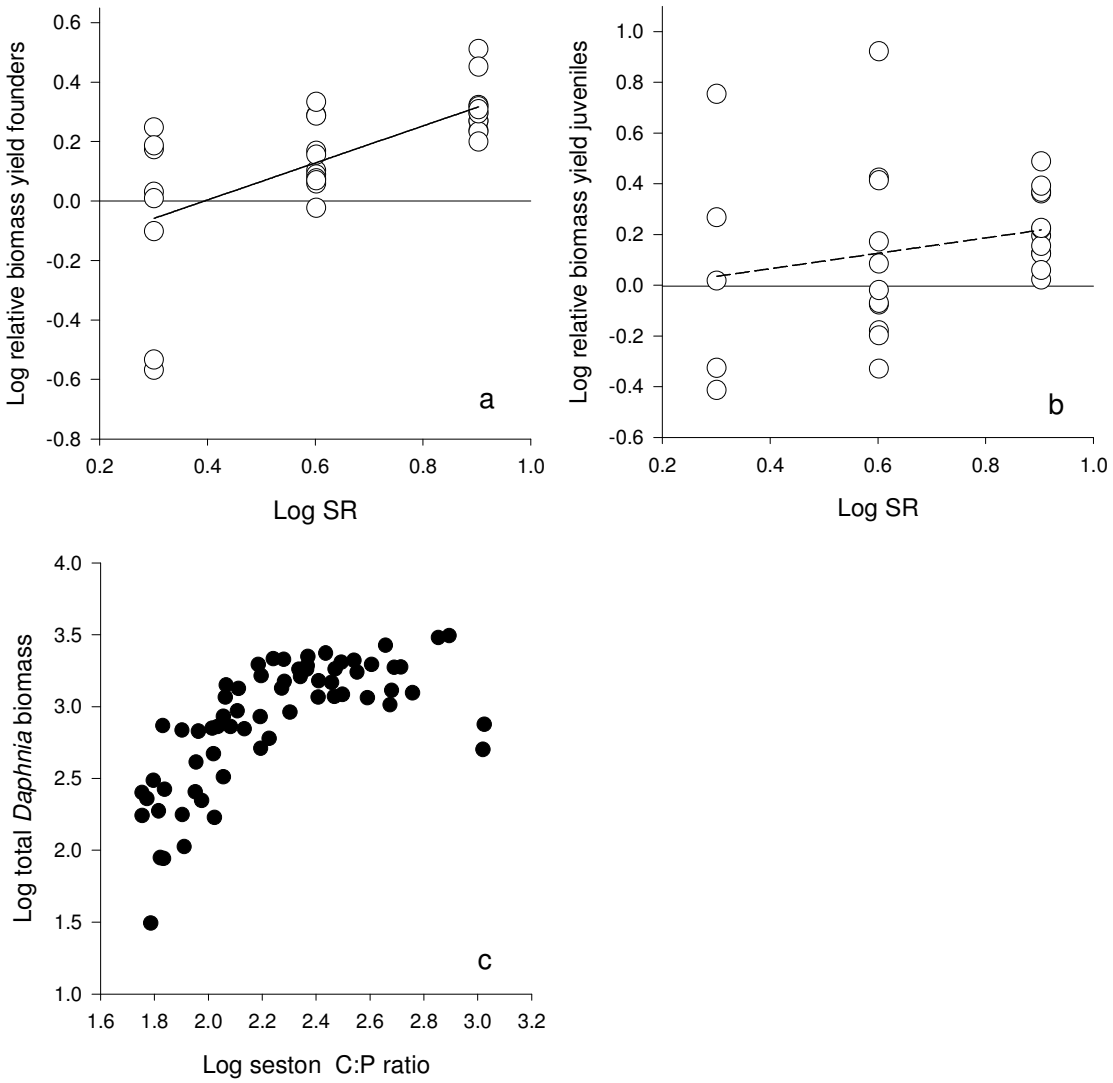

a
Log no. of founders
1.2
1.0
0.8
0.6
0.4
0.2
0.0
2.2
2.0
1.8
1.6
1.4
Log Light
1.0
0.8
0.6
0.4
0.2
0.0
log SR
b
Log no. of gravid founders
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
2.0
1.8
1.6
1.4
Log Light
1.0
0.8
0.6
0.4
0.2
0.0
Log SR
c
Log biomass founders
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
2.0
1.8
1.6
1.4
Log Light
1.0
0.8
0.6
0.4
0.2
0.0
Log SR
d
Log biomass juveniles
3.5
3.0
2.5
2.0
1.5
1.0
0.5
2.0
1.8
1.6
1.4
Log Light
1.0
0.8
0.6
0.4
0.2
0.0
Log SR

Figure 3


Log relative biomass yield founders
Log SR
a
Log relative biomass yield juveniles
Log SR
b
Log total Daphnia biomass
Log seston C:P ratio
c

MANUSCRIPT II

PHYTOPLANKTON DIVERSITY ENHANCES TROPHIC COUPLING IN A LONG-TERM AQUATIC FOOD WEB EXPERIMENT

Stephan Behl and Herwig Stibor

Submitted to *Oikos*

Abstract

Experimental studies revealed positive effects of community diversity on primary productivity. However, the question whether the enhanced productivity at the base of food-webs influences adjacent trophic levels remains unclear. Theoretical considerations expect positive diversity effects on consumers due to a greater variety of prey resources, or negative effects due to the presence of inedible species, becoming dominant under grazing pressures. Another possible source of negative diversity effects has, to our knowledge, not been addressed so far: more diverse primary producer communities potentially use limiting resources more efficiently, and are, therefore, more productive. This effect can be considered functionally similar to a direct enrichment with a limiting resource that constrains primary production. However, enrichment can lead to large consumer population cycles, resulting in a higher stochastic risk of extinction (referred to as 'paradox of enrichment'). To examine the effects of primary producer diversity on consumer populations, laboratory experiments were performed, which involved exposing the freshwater grazer *Daphnia magna* in a gradient of algal species richness (1, 2, 4, or 8 edible chlorophyte species). All treatments received eight neonate founder daphnids and an identical amount of total algal biovolume. The experiments were run in batch cultures, without exchange of growth medium after the start of the experiment. Six parameters related to *Daphnia* population demography, biomass accrual, and stability were followed and determined over a period of up to 263 days. Producer diversity exhibited strong positive effects on the short-term performance of grazers (first reproduction, first population peak), and on grazer long-term performance (mean standing stock, population stability, day of extinction), too. Long-term effects suggest that the importance of species identity in mediating diversity effects may increase over time. Although larger *Daphnia* population peaks were detected in more diverse communities, extinction rates in these treatments were smaller, not higher, as expected from theory.

Introduction

After two decades of intensive research on the role of biodiversity in natural systems, there is considerable scientific consensus on the existence of a general positive relationship between biological diversity (in terms of species, genes or functional traits) and so called 'ecosystem services', a concept which summarises the essential natural resources used (and exploited) to ensure human welfare (Brauman et al. 2007; Cardinale et al. 2011; Mace et al. 2012). Experimental and theoretical studies on the effects of biodiversity provided insights into magnitudes and variability of diversity effects on biomass production, temporal stability, resource depletion, and trophic interactions (Balvanera et al. 2006; Duffy et al. 2007). Earlier studies, which focused primarily on the causes and consequences of diversity *per se* were often restricted to one trophic level (e.g. diversity-productivity relationships in grasslands), and/or short experimental periods that often did not cover more than 1-2 generations (Cardinale et al. 2011). Multi-generation experiments have been conducted rarely, despite their potential to make predictions based on the persistence of diversity effects on longer time scales (Tilman et al. 2006; Fargione et al. 2007). However, in order to understand biodiversity effects in ecosystems, and, in particular, to make decisions for global conservation policies, it is crucial to know if diversity-related effects (e.g. higher productivity or stability) persist on larger scales (in time and space), and in complex food webs as well (Duffy 2009).

In natural food webs, even simple ones, it is difficult to predict how diversity effects emerging at one trophic level, such as increased primary production due to resource partitioning, can affect adjacent or further trophic levels. This may depend on the number and strength of trophic interactions (food web architecture: Duffy et al. 2007; Dickman et al. 2008), including competition among predators (Duffy 2002), the edibility of prey species (Agrawal 1998), feedback mechanisms (nutrient recycling by consumers), or the switch between alternative trophic pathways (Stibor et al. 2004). Importantly, food web architecture and the strength of species interactions may be subject to considerable variation on intermediate time scales, as a result of seasonal variation of environmental factors, including light regimes and temperatures.

Food web architecture and the seasonal succession of pelagic communities in temperate lakes are among the most comprehensively studied systems in ecology (Carpenter et al. 1985; Sommer et al. 1986; Sarnelle 1993). The PEG model, which was developed by Sommer et al. (1986) qualitatively describes a seasonal pelagic succession pattern, stating that

in winter/spring the composition and dynamics of phytoplankton species are largely driven by abiotic factors (light and temperature), whereas competition and grazing (food web processes) shape summer communities (Berger et al. 2010). The transition from abiotic to biotic control of pelagic algal communities coincides with the onset of thermal stratification of the water column in spring, which is followed by a characteristic phytoplankton biomass peak, known as 'spring bloom' (Berger et al. 2007). The subsequent zooplankton (grazer) peak generally results in a strong reduction of algal cells, called the 'clearwater phase', and a community shift towards less edible phytoplankton species. This abrupt decline of edible prey biomass (along with fish predation) often leads to the collapse of the dominant zooplankton populations (Sommer et al. 1986).

Notably, these studies of trophic interactions have traditionally focused on total trophic level biomass, thereby largely neglecting the role of species diversity. However, there is growing evidence that diversity (in terms of species richness and / or evenness) at the primary producer level enhances primary productivity (Cardinale et al. 2011), which is commonly explained by two non-exclusive mechanisms: first by an increased probability that a species-rich community may contain a highly productive species (under the prevailing environmental conditions), or second, by a more efficient (complete) resource depletion, resulting from a higher degree of complementary resource use in a more diverse community (Ptacnik et al. 2008; Power & Cardinale 2009; Striebel et al. 2009; Vanelslander et al. 2011). In both cases, at a given nutrient level, a more diverse community of primary producers would provide a potentially larger amount of biomass, or food (prey), to herbivores. As a trophic consequence, a generally beneficial effect of prey diversity on grazer performance can be expected. However, this simple hypothesis has been challenged in a number of ways.

First, an increasing number of prey species also implies a higher possibility of the presence of non-edible species, which could benefit from grazing and finally dominate the community (Agrawal 1998, Duffy et al. 2002). A second point is that complementary resource utilisation among producers could be functionally interpreted as a specific type of resource enrichment, since both enrichment and diversity can independently lead to higher producer community biomass. Population models predict that resource enrichment can destabilise consumer-prey dynamics by producing large-amplitude oscillations, i.e., alternating phases of very large and very small population sizes. Since smaller population sizes imply a higher (stochastic) risk of becoming extinct, enrichment can have dramatic consequences for consumer populations (*see* Diehl 2007). This counter-intuitive phenomenon

was termed the 'paradox of enrichment' (Rosenzweig 1971) and has been since confirmed in laboratory studies (Diehl 2007), but rarely in nature (Murdoch et al. 1998; McCauley et al. 1999). However, both increasing the proportion of inedible species and increasing the risk of extinction point towards a negative effect of prey diversity on grazer populations.

Besides its role for the accumulation and trophic transfer of biomass, a main focus of biodiversity research has been directed to its consequences for temporal stability of producer communities. It has been suggested for a long time (MacArthur 1955) that 'communities with many interacting species are less prone to large fluctuations (...) than communities with fewer species' (Cottingham et al. 2001). This theory predicts that the variability in total community biomass will decrease with an increase in species richness, due to the statistical averaging of the variations of the individual species ('portfolio effect'). Biologically, this prediction is based on a higher variety of traits that can potentially adapt to environmental fluctuations (McCann 2000; Cottingham et al. 2001) and has been supported by model-based theoretical approaches (Huisman & Weissing 1999; Yachi & Loreau 1999). However, the effects of more diverse and thus potentially more stable producer (prey) communities on grazer populations are still largely unexplored.

In earlier studies, the primary productivity in phytoplankton communities was found to be positively correlated to trait diversity in the spectral absorption of light (Striebel et al. 2009; Behl et al. 2011), leading to a higher biomass accumulation in more diverse algal assemblages. Here, a long-term laboratory experiment (up to 263 days) is reported, where *Daphnia magna* neonates were grown in a gradient of different-diverse chlorophyte communities (batch cultures), in order to examine the long-term impact of prey species richness on the biomass, demography and stability of *Daphnia* populations.

Materials and Methods

Food web experimental design

A set of 11 freshwater chlorophyte strains was used (Table 1; SAG Culture Collection of Algae, Göttingen) that had been pre-cultured for several weeks under the same conditions in a phosphorus-reduced (15.0µg P/L) freshwater medium (COMBO), which was appropriate for

phytoplankton and zooplankton cultivation. A species-richness gradient was established with four levels consisting of monocultures and polycultures, containing one, two, four, or eight different species. Each community was replicated twice and each diversity level (except monocultures) was replicated five times with different species compositions, resulting in a total of 52 communities that were randomly comprised of members from the species pool. Initially, identical total algal biovolumes were set in all treatments (5.24 x 10^6 μm^3 mL^{-1}, equalling 1.0mg particulate organic carbon, POC L^{-1}), and different species contributed equal biovolumes to communities containing two or more species.

Algae were grown under equal dim light conditions for one day, before each treatment received a founder population of four age-synchronised neonate *Daphnia magna* (max. 12 hours after birth) from a laboratory stock. Temperature in the climate chamber was maintained at a constant 20 ± 0.5°C with a 16 h light/8 h dark photoperiod regime. The communities (500ml) were exposed to 90µmol quanta m^{-2} s^{-1} (photosynthetically active radiation, PAR: 400-700nm) in 650ml cell culture flask batch cultures. The growth medium was not changed during the experimental period (batch culture). Each treatment was conducted until the complete extinction of the *Daphnia* population. The treatments were gently shaken once a day to prevent algae from sinking and accumulating at the bottom of the culture flasks.

Measurements and calculations of D. magna *parameters*

The development of *Daphnia* populations was monitored quantitatively on a daily basis, or on a twice-daily basis after day 20, determining the total number of individuals and the reproduction and mortality events. To prevent daphnids from accidental injuries, and in order to avoid cross contamination of algal communities, the *Daphnia* biomasses were not measured during the experiment. Instead, the biomass was estimated from a population (>300 individuals) of the same *Daphnia magna* culture strain grown under identical environmental conditions and food algae mixtures. The measured dry weights of these daphnids were converted into particulate organic carbon (POC) applying a conversion factor of 0.50 (Wetzel 2001). *Daphnia* demography was characterised by the following six parameters:

(1) *Day of first reproduction* [day]: the day when the first individuals of the F1 generation hatched in a population.
(2) *Day of first population peak* [day]: the day when the total number of daphnids in a population reached the first maximum.
(3) *Size of first population peak* [individuals]: the number of daphnids that was reached at the first population peak.
(4) *Mean* Daphnia *standing stock* [individuals]: the number of daphnids in a population averaged over the experimental period.
(5) *Day of population extinction* [day]: the day when the last daphnid of a population died.
(6) *Population stability index* [day^{-1}]: calculated as the inverse of the coefficient of variation of the daily standing stock

The relative performance of polycultures was calculated as the difference between observed *Daphnia* performances in polyculture (replicate means), and the performance expected from the weighted component monocultures (replicate means). 'Performance' served as a surrogate for each of the six measured parameters with variable units. 'Over-performance' was found to occur when the difference was positive, and 'under-performance' when it was negative.

Measurements and calculations of phytoplankton parameters

On day 1, before adding the neonates, and on the respective day when all daphnids of a treatment had died, each community was sampled to analyse the carbon and phosphorus content of phytoplankton biomass. Samples were poured through a net (80µm mesh size) to retain daphnids, exuviae, and large detrital particles. POC, as a measure of algal biomass, was determined subsequent to filtration onto pre-combusted and acid-washed glass-fibre-filters (Whatman GF/C, Whatman International Ltd.) by Elemental Analysis (Elemental Analyser, EA 1110 CHNS, CE Instruments). Algal biomass particulate phosphorus (PP) was measured after sulphuric acid digestion followed by a molybdate reaction.
Additionally, an aliquot of each sample was fixed with Lugol's iodine to verify the accuracy of the initial phytoplankton composition (day 1), and the final composition. Phytoplankton diversity was determined by inverted microscopy using Utermöhl chambers. A minimum of 100 cells of each species was counted by scanning at least 20 randomly distributed, distinct fields. AnalySIS software (Pro 2.11.006, Soft Imaging Software GmbH, Germany) was used

to determine the biovolumes of cells by measuring two-dimensional live pictures. Subsequently, biovolume calculations were defined by assessing geometric shapes. Algal diversity was calculated as Shannon Diversity Index H, using the measured biovolumes of algal cells (Begon et al. 2006).

The total phytoplankton biomass in each community ('phytoplankton standing stock') was regularly assessed during the experimental period by means of the light attenuation coefficient k_d (Kirk 2011) for PAR light (400-700nm):

$$k_d = (\mathrm{Ln}(I_{in}) - \mathrm{Ln}(I_{out})) / z$$

k_d = light attenuation coefficient [m^{-1}]
I_{in} = incident light (90µmol quanta m^{-2} s^{-1})
I_{out} = transmitted light [µmol quanta m^{-2} s^{-1}]
z = light path length (0.12 m)

From k_d, the phytoplankton biomass was calculated, using a phytoplankton POC–k_d relationship, which was obtained from simultaneous measurements of both parameters for all communities on the first and the last day of the experiments (linear regression:
POC [mg L^{-1}]= $-11.09 + 3.10 \times k_d$, $r^2 = 0.66$; $p < 0.0001$; $n = 104$)

Results

Establishment of experimental communities and conditions

All phytoplankton communities established as scheduled. Proportions (biovolumes) of component algal species in polycultures were checked immediately after the initial set-up, revealing that proportions differed by 10 ± 1% (mean ± s.e.m.) from the scheduled equal proportions. Neonate daphnids established as well, and reproduced subsequently in all algal communities, except in one monoculture replicate of *Monoraphidium minutum* and *Carteria*

sp., respectively. Initial and final seston C:P ratios did not differ significantly between the communities of the four species richness levels (Initial: ANOVA on ranks, $H_{3,25} = 2.51$, $P = 0.47$; Final: ANOVA on ranks, $H_{3,25} = 2.94$, $P = 0.40$), indicating that phosphorous pools, crucial for *Daphnia* growth, were similar among treatments.

Persistence of phytoplankton species richness and diversity gradients

By the end of the individually different experimental periods, the number of algal species had not changed in any monoculture or two-species polyculture, but had decreased in communities consisting of four or eight algal species. However, there was still a significant gradient of species richness present (linear regression: $r^2 = 0.94$, $P < 0.0001$; Fig. 1a). With regards to the biovolume-based Shannon diversity index, H, all communities except the monocultures showed a decrease in phytoplankton diversity over time. However, final diversity levels remained separated by a strong gradient (linear regression: $r^2 = 0.68$, $P < 0.0001$; Fig. 1b).

General time course of grazer population dynamics

Despite considerable quantitative variations between treatments, most *Daphnia* populations showed a qualitatively similar time-course: some days after the addition of four founder neonates, daphnids reproduced parthenogenetically, resulting in a first population peak. Following this peak, populations collapsed and either died out, or built up further peaks, which were decreased in size (Supplementary material Appendix 1 Fig. A1-A5). Replicates were usually quite similar to each other regarding the timing and the number of individuals at the first population peak, but diverged remarkably in their days of extinction (*see* Supplementary material Appendix 1 Fig A1-A5). Considering each *Daphnia* population, the six measured parameters varied as follows (min/mean/max): Day of first reproduction (6/8.4/31); Day of first population peak (8/14.5/54); Size of first population peak (9/72.7/126); Mean *Daphnia* standing stock (3.3/20.6/43.8); Day of population extinction (8/64.7/263); Population stability index (11.9/63.4/220.6).

Absolute grazer performance: parameters of reproduction, abundance, and population stability

Daphnids feeding on highly diverse phytoplankton communities reproduced significantly earlier (linear regression: $r^2 = 0.16$, $P = 0.045$; Fig. 2a), and the first population peak took place earlier on average when compared to daphnids in less diverse algal communities (linear regression: $r^2 = 0.19$, $P = 0.026$; Fig. 2b). Regarding the population size, a higher number of individuals were found at the population peak (linear regression: $r^2 = 0.28$, $P = 0.006$; Fig. 2c), as well as larger *Daphnia* mean standing stocks (linear regression: $r^2 = 0.19$, $P = 0.028$; Fig. 2d) with increasing initial algal species richness. Finally, *Daphnia* populations became extinct later when grazing on species-rich algal assemblages (linear regression: $r^2 = 0.16$, $P = 0.041$; Fig. 2e), and the population stability (1/coefficient of variation of daily standing stock) was slightly, but not significantly, higher (linear regression: $r^2 = 0.08$, $P = 0.17$; Fig. 2f).

Relative grazer performance: polycultures vs. monocultures

Relating the absolute performance of *Daphnia* populations in diverse algal communities (polycultures) to their performances in the component monocultures allows the discovery of diversity effects, which can be explained by the presence of particularly beneficial prey species (and not by diversity *per se*). *Daphnia* population parameters no. 1-4 were significantly different from 0, with under-performance occurring for parameters 1 and 2 (one sample t-tests: day of 1st reproduction: $t = -4.39$, $P < 0.001$, n = 15; day of 1st population peak: $t = -5.42$, $P < 0.001$, n = 15; Fig. 3) and over-performance occurring for parameters 3 and 4 (one sample t-tests: size of 1st peak: $t = 5.70$, $P < 0.001$, n = 15; *Daphnia* mean standing stock: $t = 5.38$; $P < 0.001$, n = 15; Fig. 3). Regarding the day of extinction and the population stability (parameters 5 and 6), the relative performance of *Daphnia* populations in polycultures was not statistically different from 0 (one sample t-tests: (day of extinction: $t = 2.08$, $P = 0.057$, n = 15; population stability: $t = 1.19$, $P = 0.25$, n = 15; Fig. 3).

Trophic coupling: producer and consumer mean standing stocks

Estimates of mean *Daphnia* and mean phytoplankton standing stocks (in terms of biomass POC) revealed a significant increase in mean grazer biomasses with increasing initial

phytoplankton species richness (linear regression: r^2 = 0.19; P = 0.028; Fig. 4), but no association was found between the initial phytoplankton species richness and mean algal standing stock (linear regression: r^2 = 0.11; P = 0.11; Fig. 4).

Discussion

Disentangling the manifold interactions among species in a food web has long been a central point of interest in community ecology (MacArthur 1955, Carpenter et al. 1985, Persson et al. 1992,). Today, scientists try to integrate various aspects of biodiversity into these investigations of producer-consumer interactions, making the issue even more complex. While there have been numerous theoretical studies modelling producer-consumer interactions in diverse communities (Thébault & Loreau 2003; Tirok & Gaedke 2010), experimental data from diverse producer-consumer systems, especially long-term (multi-generation) data, is scarce.

Short-term grazer population responses

The measured *Daphnia* parameters 1-3 (day of 1st reproduction, day of 1st population peak, and size of 1st population peak) could be addressed as 'short-term parameters', describing the immediate reaction of grazer populations faced with different-diverse prey environments. Obviously, parameters 1 and 2 are somewhat coupled, since the timing of the first reproduction determines to a certain degree (but not entirely) the timing of the first population peak. Nevertheless, the combination of earlier reproduction / earlier population peaks and the strikingly higher numbers of daphnids at those peaks indicate a strong positive effect of phytoplankton (prey) species richness on grazer population performance (Fig. 2 a-c). These results confirm earlier experiments conducted using a similar experimental set up, where the final *Daphnia* population biomass (measured after 11 days, which matches quite well the timing of the average peak in the present experiment) was significantly higher in species-rich algal communities (S. Behl, unpublished data). Strong negative effects of algal diversity on

Daphnia populations were not expected, since the experimental communities did not include harmful or grazing-resistant species on purpose.

However, apart from resistant species, a negative diversity effect could also result from an increased 'dilution' of a particularly favourable prey species with increasing species richness in diverse communities. In that case, the favourable alga in a monoculture would enhance the *Daphnia* performance (more than any polyculture), a phenomenon which was not observed in these experiments (Fig. 2 a-c). Instead, the performance of *Daphnia* populations feeding on diverse algal communities could not be predicted from the component species in diverse algal communities, as indicated by the relative performances that differed from zero (over- or under-performance; note that under-performance does not imply 'worse', but in this case 'earlier'; Fig. 3). Despite a clear pattern for all three short-term-parameters, an inherent draw-back of the experimental design is that the data cannot reveal underlying reasons for the positive prey diversity-grazer performance relationships.

Principally, two options that influence grazer performance (in the absence of predators and competitors) exist: food quantity and food quality, (or a combination of both). The nutritional quality of prey items has long been recognised being of vital importance for generalist suspension feeders such as *Daphnia* sp. in particular, because they often indiscriminately ingest all seston particles with a given size or shape (Vanni & Lampert 1992). Apart from toxicity and inappropriate shapes, prey quality in aquatic communities is mainly defined by the presence and concentration of a handful of molecules, including vitamins, fatty acids, and phosphorus (Becker & Boersma 2005, Müller-Navarra 2008). The latter is often normalised to biomass carbon (expressed as carbon-to-phosphorus (C:P) ratio) and has consistently been shown to determine the nutritional quality of phytoplankton (e.g., Urabe & Sterner 1996, Andersen et al. 2007). In this experiment, the algal C:P ratios did not differ significantly between the species richness levels, meaning that stoichiometric effects on zooplankton growth were potentially independent of algal diversity.

The phytoplankton fatty acid profiles were not measured in this experiment. While there is evidence regarding the meaningful differences in fatty acid composition (and hence nutritional quality) between algal groups (such as chlorophytes, cyanobacteria, diatoms, and cryptophytes; Ahlgren et al. 1990; Brett & Müller-Navarra 1997), there are, to our knowledge, no studies reporting and systematically testing the food web effects of such differences between species within algal groups. Existing studies that show the synergistic

effects of algal mixtures on grazers were largely restricted to mixtures of only two prey species and did not reveal underlying reasons (Vanni & Lampert 1992; Boersma & Vijverberg 1995). Interestingly, some of these studies noted that quality-related effects were most important for juvenile stages and under low food concentrations (< 1mg C L^{-1}: Vanni & Lampert 1992; Andersen et al. 2007). Hence, due to the exclusive use of species from one algal group (chlorophytes) in the diversity gradient, and due to the lack of differences in phytoplankton algal C:P ratios, as well as a comparably high initial food supply (average of 1.15mg C L^{-1}), it can be argued that food quality might have contributed to the observed positive diversity effects on the short-term parameters of *Daphnia* performance, but was definitely not the major cause.

Besides nutritional quality, resource quantity is of elementary importance for herbivore grazers (Carpenter et al. 1985). In contrast to nutritional quality, food quantity has already been linked to species richness or diversity in a number of theoretical and experimental studies (reviewed by Cardinale et al. 2011), showing that more diverse primary producer communities exhibit higher productivity and biomass production (Power & Cardinale 2009; Striebel et al. 2009; Behl et al. 2011; Vanelslander et al. 2011). This 'overyielding', which denotes a higher biomass production than is predicted from monocultures, is commonly attributed to complementary resource use or facilitation among species in diverse communities, rather than to the dominance of highly productive species (Fargione et al. 2007; Cardinale et al. 2011).

In a previous study assessing diversity-productivity relationships in phytoplankton communities (using the same algal strains under similar environmental conditions and resource supplies, but in the absence of grazers), an average increase of chlorophyte community biomass of 0.50mg C L^{-1} (5.9 %) per additional algal species was found after 21 days (Behl et al. 2011). This increase was correlated with complementary light use based on diverse photosynthetic pigment composition. Assuming this biomass increase is also a realistic estimate for the current experiment, it would indicate that during the time from starting the experiment to the end of the first population peak (which is approximately 21 days) the mean algal biomass in 8-species-communities could potentially have reached up to 4.0mg C L^{-1} more than in the monocultures. Clearly, extrapolating such concrete numbers must be considered carefully, but this potentially higher amount of available prey biomass

may still be sufficient to explain the 2.6 times higher number of daphnids (equalling 0.6mg C L^{-1}) in 8-species treatments at the population peak (as compared to monocultures).

Long-term grazer population responses

Besides demographic parameters describing short-term responses of *Daphnia* populations (parameters 1-3), three further parameters were assessed (mean *Daphnia* standing stock, day of population extinction, and population stability index), which include population dynamics beyond the first pronounced population peak, and which allow conclusions regarding the fate of diversity effects on longer time scales to be reached.

In comparison with the short-term effects, the link between initial phytoplankton diversity and the long-term parameters, in particular population extinction and stability, was not that pronounced. The absolute grazer performance increased with increasing algal species richness in both cases (Fig. 2 e, f), indicating a delayed extinction and a gradually higher temporal stability of *Daphnia* populations feeding on higher-diverse algal communities. However, regarding the stability index, the relative performance (based on comparisons with the performances in monocultures) did not statistically differ from zero (Fig. 3). In this case, the better performance of grazers in polycultures can be sufficiently explained by the composition of phytoplankton communities, i.e. by algal species identity. However, it must be noted that the observed lack of statistical evidence for relative over-performance does not exclude the option that complementary resource use or facilitation among algal species has contributed to the positive diversity effects (Hector et al. 2002).

It is also important to note that the initial algal species composition did not remain constant, instead, both species numbers and equal distributions of biomass (evenness) generally decreased as a function of time due to resource competition among prey species (Tilman 1977; Huisman et al. 1999). This continuous change in species composition is inherent to all long-term experiments, where the initial design is not permanently adjusted by the experimenter. Therefore, calculations of relative *Daphnia* performances can be somewhat misleading, especially when the established species compositions deviate substantially from the composition that was initially set. To overcome this dilemma, one could use an index of mean Shannon diversity, determined at several instants of time during the experiment (Behl et

al. 2011). However, a disadvantage of doing so is that mean diversity can no longer be treated as an independent variable, since diversity is modified by producer-grazer interactions.

Jiang et al. (2009) argued that diversity-productivity relationships in natural ('mature') communities often differ from the clear positive link that is commonly found in designed experiments. They attributed this discrepancy to the fact that 'synthetic communities' are often designed for an abnormally high evenness (i.e. unrealistic rank-abundance patterns) and a reduced role of competitive exclusion, due to short experimental periods. Both would keep communities 'immature', thereby producing positive diversity effects that may not occur in natural (mature) communities (Jiang et al. 2009). In the present study, the experimental design (long-term batch cultures) allowed phytoplankton species to compete up to 263 days (corresponding to 50-100 generations, based on an estimated generation time of 2-5 d). This long-term incubation resulted in a continuous decline of species numbers and evenness and 'mature communities' (Fig. 1). Nevertheless, the initially set prey diversity gradients remained intact, though on a consistently lower level, making it likely that long-term effects on *Daphnia* populations also resulted from diversity-related enhanced productivity. Moreover, less-steep diversity gradients are consistent with less pronounced diversity effects on longer time scales, since differences in trait variability should then be smaller between low and highly diverse primary producer communities. In addition, the relative importance of the remaining prey species identity (i.e. the individual properties) may also increase with time.

Mean standing stocks and the paradox of enrichment: Implications for food webs

Increasing phytoplankton diversity resulted in an overall increase of mean grazer standing stocks and simultaneously in constant mean phytoplankton standing stock biomasses (Fig. 4). Surprisingly, this pattern corresponds to the patterns seen in the classical food web theory of trophic cascades (Oksanen 1981), where 'An increase in potential productivity […] at the bottom of the food chain will [...] always translate into an increase at the top trophic level, whereas the biomass of primary producers will increase only in odd-linked food chains' (Persson et al. 1992). The only difference between these classical patterns and the present study, remarkably, is that the 'increase in potential productivity' was not due to higher nutrient supply rates, but due to higher phytoplankton diversity. Obviously, directly increasing the availability of a resource through enrichment, or increasing the ability of the community to exploit a given resource level through a greater variety of different traits (i.e.

diversity), can result in a similar net increase in primary productivity. This 'functional equivalence of diversity and resource enrichment' extends the common concept that more diverse communities (with more different traits) would be able to exploit a certain amount of resources more efficiently, leading to a higher total community productivity (Ptacnik et al. 2008; Cardinale 2011).

Notably, the functional equivalence of producer diversity and resource enrichment would also have direct implications for consumer-prey dynamics, with regards to the 'paradox of enrichment' (Rosenzweig 1971, Murdoch et al. 1998): A grazer population feeding on a more diverse, and thus potentially biomass enriched, prey community should exhibit larger population cycle amplitudes, leading to a greater risk of extinction. Indeed, larger amplitudes of *Daphnia* populations in species-rich algal communities were found, manifest in the size of the first population peak. However, these populations did not show a greater risk of extinction, instead, they tended to be more stable and long-living. Regarding natural plankton communities, Murdoch et al. (1998) attributed the absence of paradox behaviour to the presence of inedible algae, acting as a 'nutrient sponge', among other hypotheses. Grazing should favour the growth of inedible species, thereby reducing the availability of nutrients to the edible algae-grazer system and preventing enrichment-driven large amplitude cycles.

However, the absence of inedible prey species in these experiments allowed for two conclusions regarding the lack of paradox behaviour: either enrichment via a higher efficiency of resource use in diverse communities was not sufficiently strong, or prey diversity can buffer the 'paradox of enrichment'. Slightly different responses of individual algal species to grazing and nutrient availability, seen as time lags, and species oscillations resulting from the competition process itself (Huisman & Weissing 1999), could be more pronounced in species-rich communities, thereby preventing herbivore populations from potential rapid extinction after the population peak.

In summary, the results of this study show that both positive short-term and positive long-term effects of prey diversity on herbivore populations can be observed in a simple predator-prey system. Further studies must now investigate how strong these effects are in real-world ecosystems, which are, in contrast to simplistic laboratory experimental set-ups, characterised by multiple trophic interactions and fluctuating environmental conditions.

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Table 1. Chlorophyte species used in monoculture and polycultures experiment and their mean biovolumes and cell sizes.

No.	Chlorophyte species	Mean cell size [µm] (max. diameter)	Mean cell biovolume [µm³]
1-1	*Chlamydomonas reinhardtii*	10.4	385.6
1-2	*Monoraphidium minutum*	6.7	104.5
1-4	*Selenastrum capricornutum*	9.5	113.8
1-5	*Desmondesmus subspicatus*	8.6	162.2
1-6	*Carteria* sp.	20.6	1176.5
1-7	*Phacotus lenticularis*	7.0	139.7
1-8	*Golenkinia brevispicula*	11.9	907.9
1-11	*Haematococcus pluvialis*	16.5	1203.0
1-21	*Planktosphaeria gelatinosa*	11.4	665.9
1-10	*Tetraedron minimum*	8.7	315.3
1-13	*Pediastrum simplex* (single cells)	17.1	1125.4

Figure legends

Figure 1: (a) Final number of algal species (open circles) and (b) final algal Shanon diversity index H (closed circles) in the experimental communities. Initial values (grey triangles) were predefined and serve for comparison. Linear regression statistics are: $SR_{end} = 0.26 + 0.81 \times SR_{start}$; $r^2 = 0.94$, $P < 0.0001$; n = 26; $H_{end} = 0.04 + 0.41 \times H_{start}$; $r^2 = 0.68$, $P < 0.0001$, n = 26). Data points of final species richness (SR end) and final diversity (H end) are replicate means ± s.e.m.

Figure 2: Relationship between the initial number of algal species (SR) in a community and six parameters characterizing *Daphnia* population performance. Linear regression statistics are: (a) Ln day of first reproduction = 2.33 - 0.056 × SR; $r^2 = 0.16$, $P = 0.045$, n = 26; (b) Ln day of first population peak = 2.89 - 0.069 × SR; $r^2 = 0.19$, $P = 0.026$, n = 26; (c) Ln size of first population peak = 3.43 + 0.15 × SR; $r^2 = 0.28$, $P = 0.006$, n = 26; (d) Ln mean *Daphnia* standing stock (individuals) = 2.54 + 0.10 × SR; $r^2 = 0.19$, $P = 0.028$, n = 26; (e) Ln day of population extinction = 3.36 + 0.12 × SR; $r^2 = 0.16$, $P = 0.041$, n = 26; (f) Ln population stability = 3.66 + 0.07 × SR; $r^2 = 0.08$, $P = 0.17$, n = 26. Data points are replicate means ± s.e.m.

Figure 3: Performance of *Daphnia* populations grazing on phytoplankton polycultures (two, four, or eight species), compared to their expected performance raised from measurements of the populations grazing on the respective component monocultures. The reference line (y=0) indicates that *Daphnia* performance in polycultures matched exactly the expectations from the monocultures. Note that 'performance' has different units (days, individuals, day^{-1}), which are given with the measured parameters in brackets. Data points are means ± 95% confidence intervals.

Figure 4: Relationship between the initial number of algal species and the mean *Daphnia* standing stock [µg POC L^{-1}], and the mean phytoplankton standing stock [mg POC L^{-1}]. Data points are replicate means ± s.e.m. Regression statistics are: *Daphnia*: Ln *Daphnia* mean standing stock = 6.41 + 0.10 × number of algal species, $r^2 = 0.19$, $P = 0.028$, n = 26; *Phytoplankton*: Ln phytoplankton mean standing stock = 1.39 + 0.042 × number of algal

species, $r^2 = 0.11$, $P = 0.11$, n = 26. *Daphnia* POC was calculated from daphnid numbers using length-weight relationships and phytoplankton POC was calculated based on PAR light attenuation (*see* Methods).

Figure legends for Supplementary material Appendix Figures A1-A5

Temporal dynamics of total *Daphnia* populations (founders and offspring) in algal monoculture (Fig. A1, A2) and polyculture treatments (Fig. A3-A5). Monoculture codes x-y and x-y' are identical replicates with x indicating the initial number of algal species and y indicating the algal identity (as given in Table 1).

Figure 1

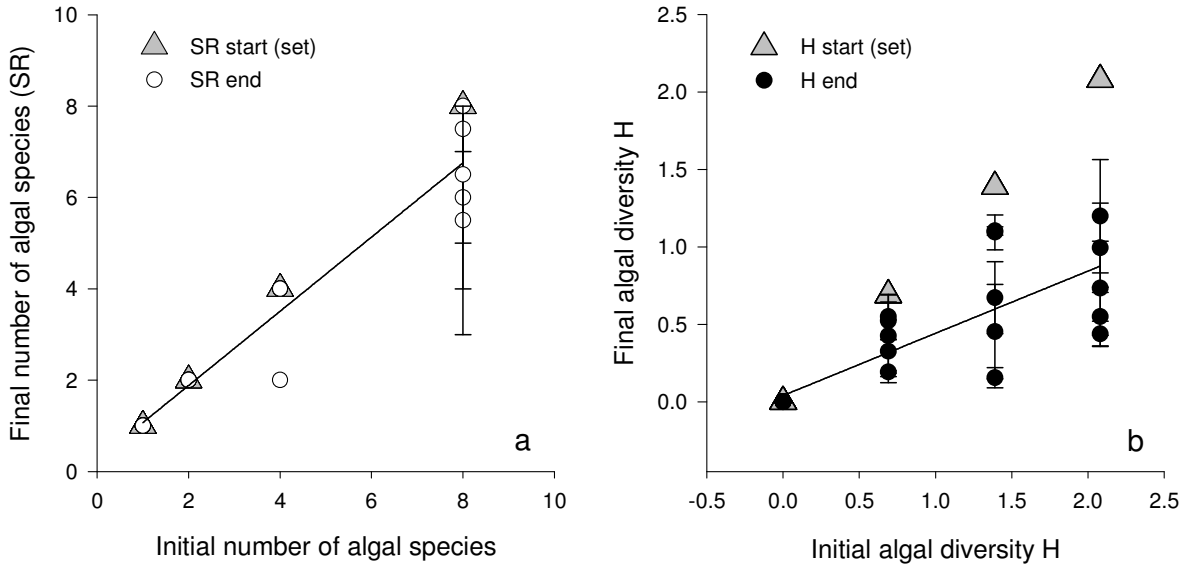

SR start (set)
SR end
Final number of algal species (SR)
Initial number of algal species
a
H start (set)
H end
Final algal diversity H
Initial algal diversity H
b

Figure 2

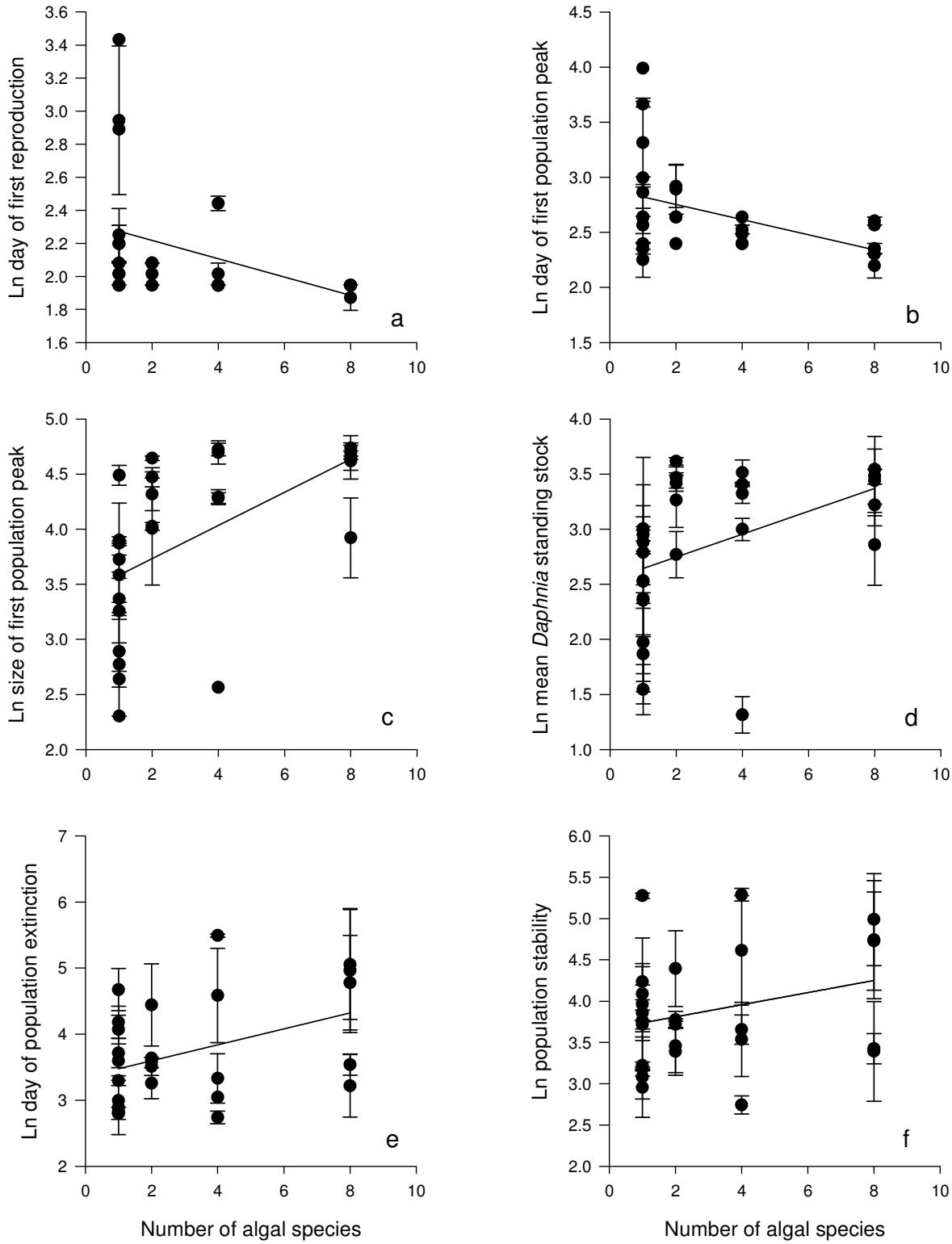

Ln day of first reproduction
a
Ln day of first population peak
b
Ln size of first population peak
c
Ln mean *Daphnia* standing stock
d
Ln day of population extinction
e
Ln population stability
f
Number of algal species
Number of algal species

Figure 3

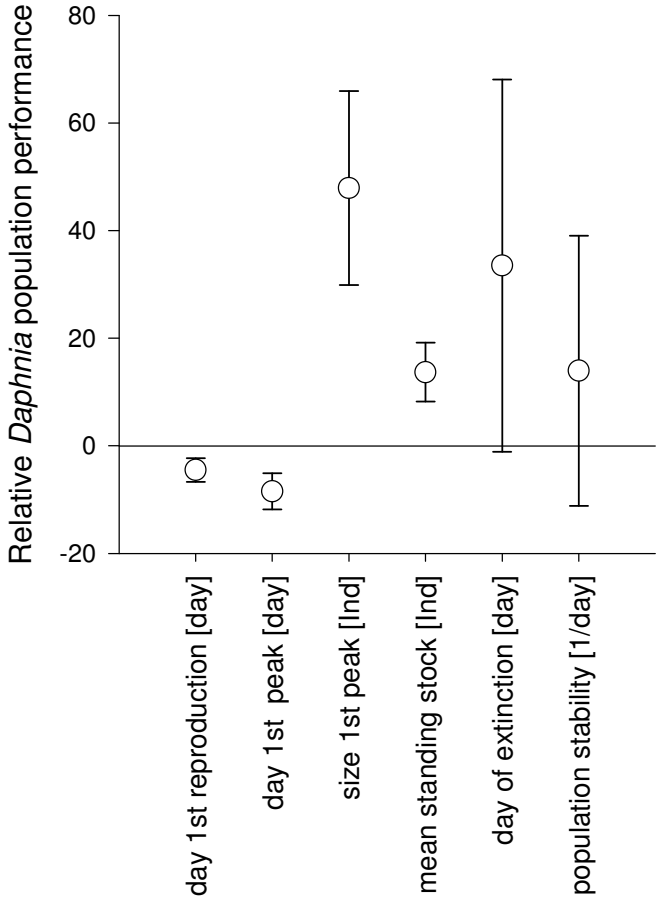

Relative *Daphnia* population performance
80
60
40
20
0
-20
day 1st reproduction [day]
day 1st peak [day]
size 1st peak [Ind]
mean standing stock [Ind]
day of extinction [day]
population stability [1/day]

Figure 4

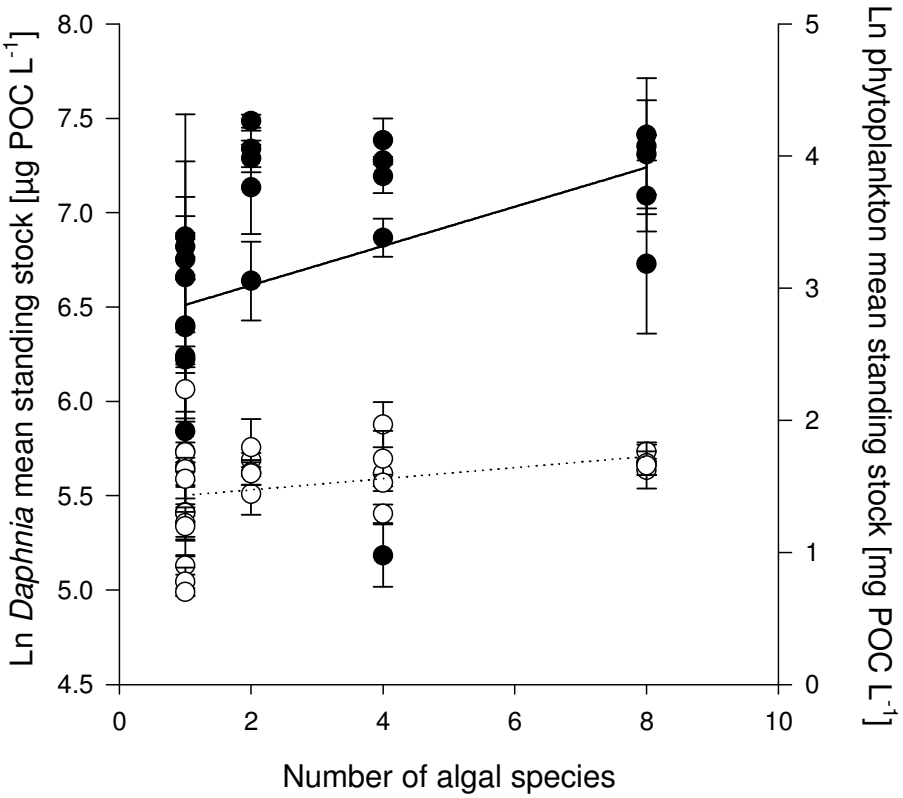

Ln *Daphnia* mean standing stock [µg POC L^{-1}]
Ln phytoplankton mean standing stock [mg POC L^{-1}]
Number of algal species
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
5
4
3
2
1
0
0
2
4
6
8
10

Figure A1: Monocultures 1

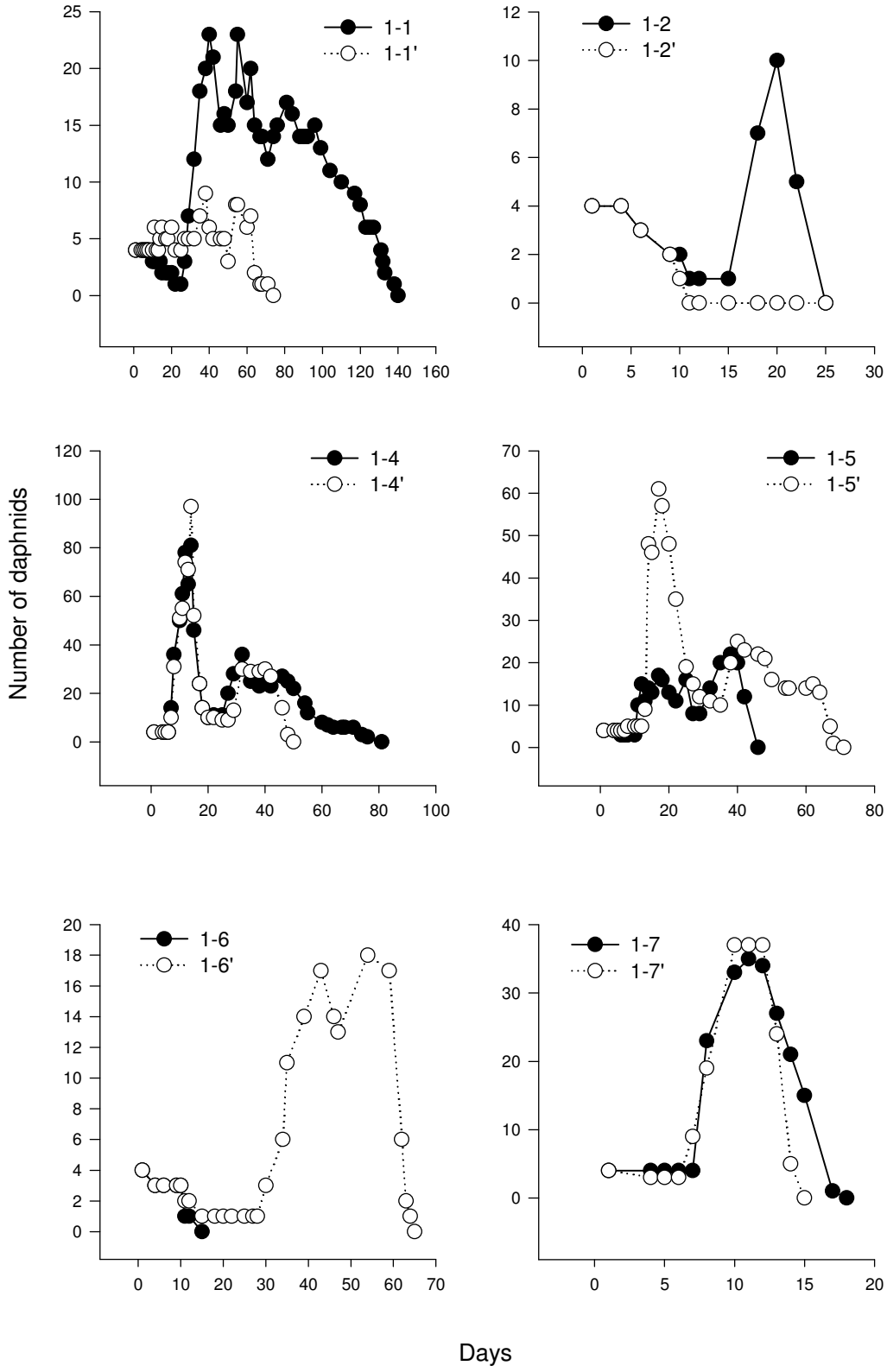


Figure A2: Monocultures 2

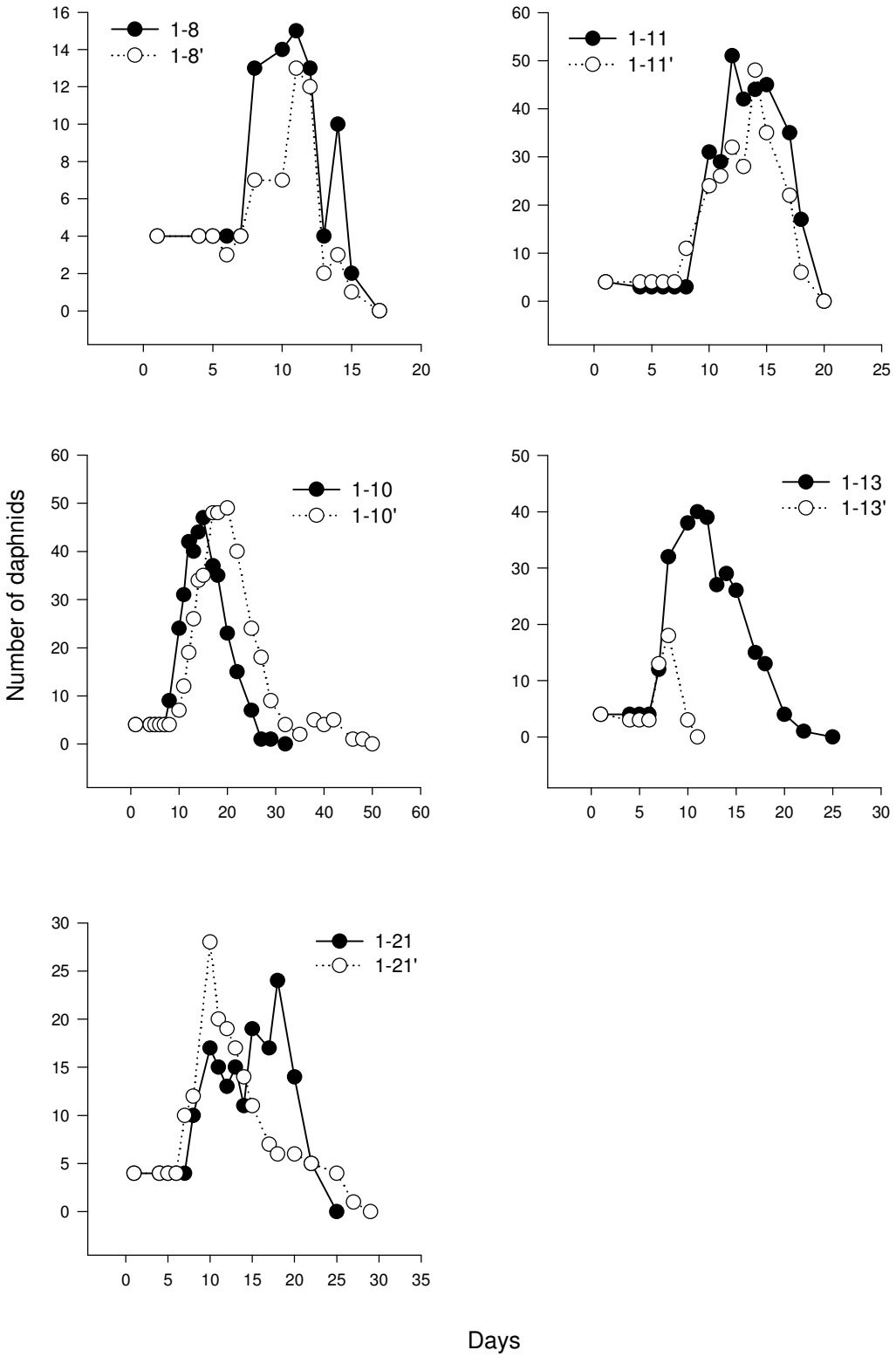


Figure A3: Two-species polycultures

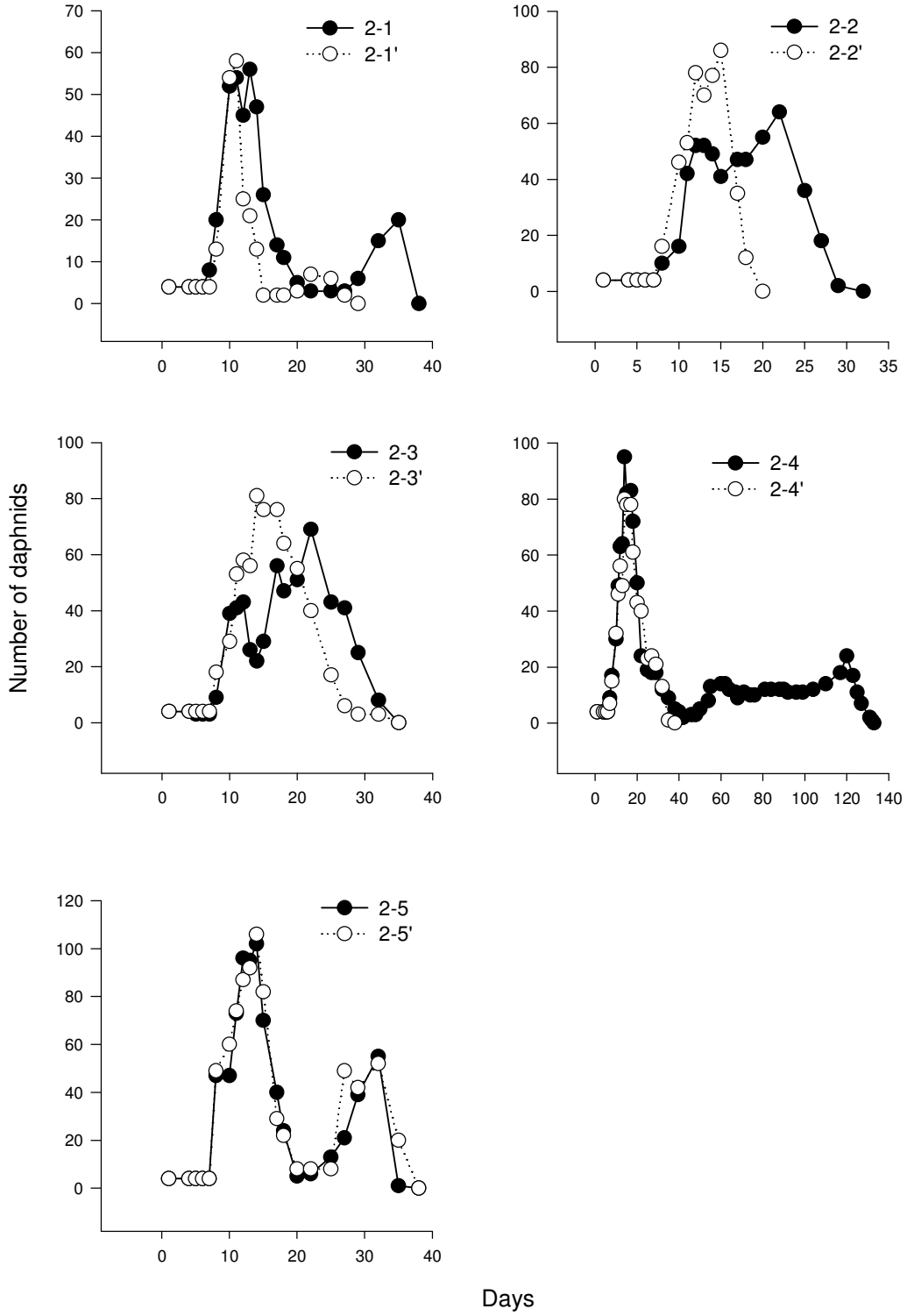


Figure A4: Four-species polycultures

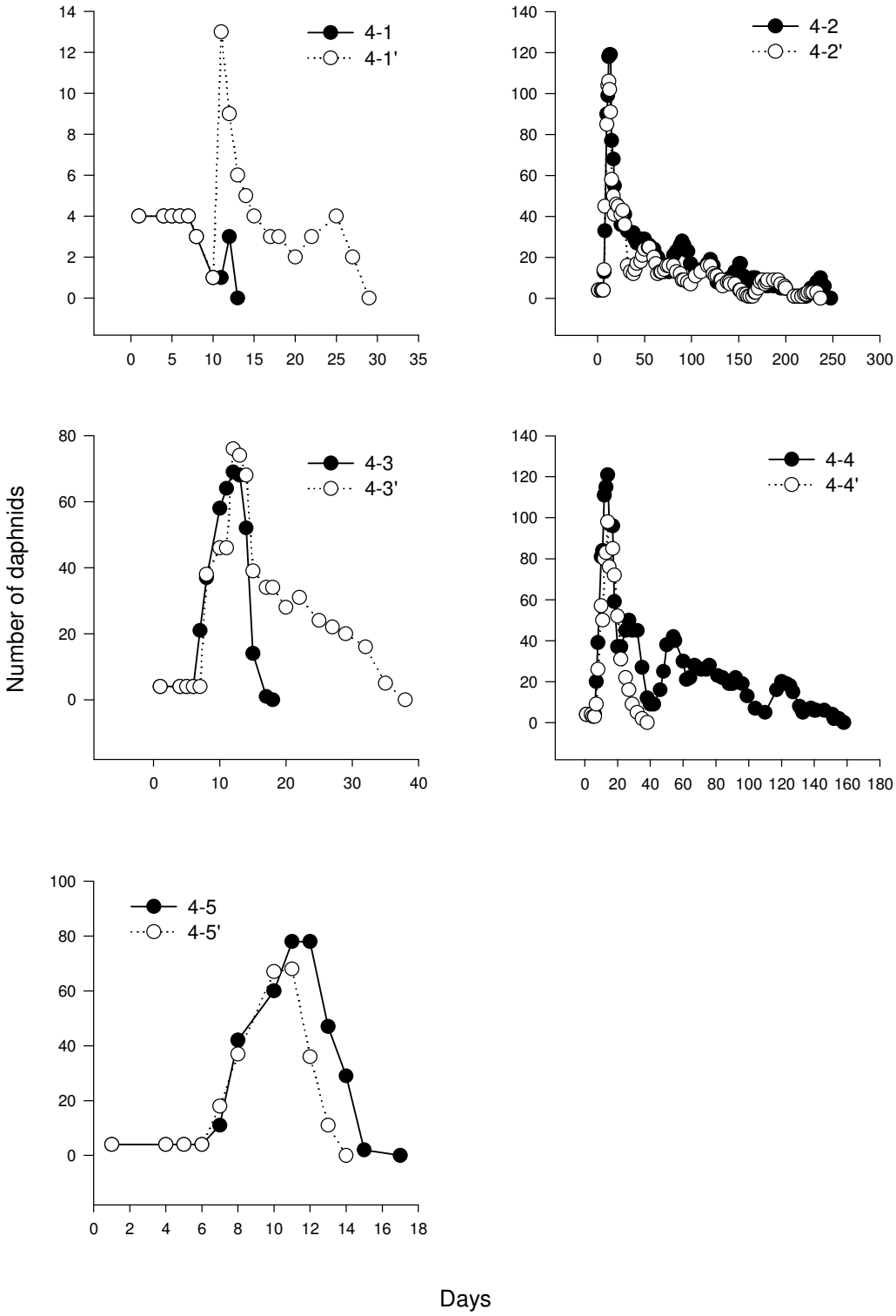
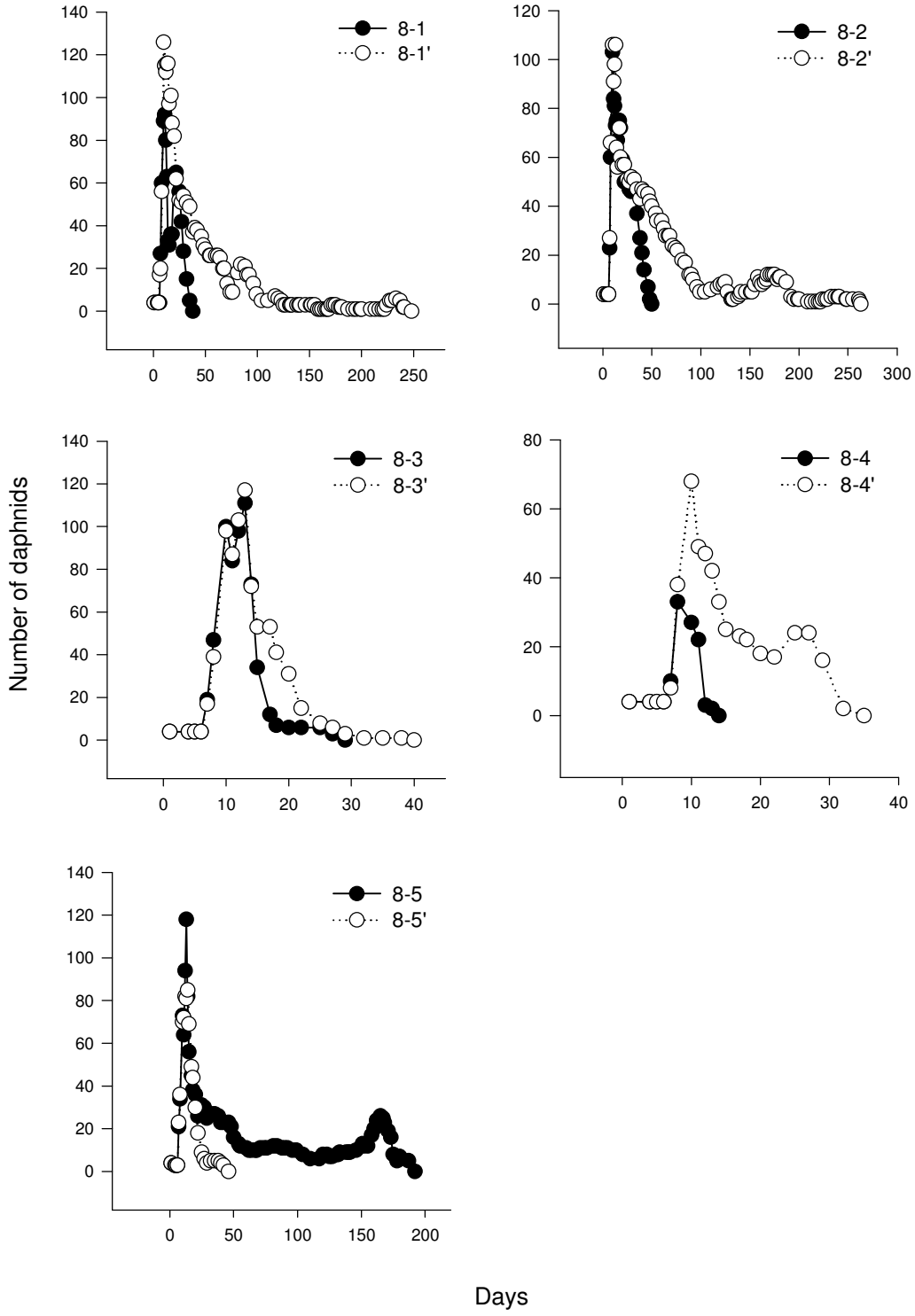


Figure A5: Eight-species polycultures



MANUSCRIPT III

DIVERSITY AND THE PERFORMANCE OF MARINE PHYTOPLANKTON COMMUNITIES

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Submitted to *Nature*

Abstract

A variety of human activities are accelerating species loss[1], resulting in reduced ecosystem services and diminished 'safe operating space' for people[2]. Cumulative evidence suggests that species diversity can influence vital ecosystem properties, such as nutrient dynamics, autotroph primary production, and the yield of economically important species[3-5]. However, there is little information relevant to the impact of taxonomic diversity on the performance of autotroph communities in the marine pelagial, which is the earth's largest ecosystem based on primary production. Because marine phytoplankton account for about half of global primary production, support all economically important fisheries, and are a major driver of biogeochemical cycles, diversity-productivity relationships for this functional group are scientifically and economically important[6]. Results of this investigation demonstrate that marine phytoplankton diversity is linked to phytoplankton community performance at scales ranging from small laboratory studies to oceanic ecosystems. Growth was positively correlated with diversity in laboratory and field manipulations, and along diversity gradients occurring naturally in Atlantic, Pacific and Mediterranean phytoplankton communities. The positive correlation is associated with diversity-dependent use of light across the photosynthetically active radiation (PAR) spectrum. Our results indicate that diversity at the unicellular base of marine food webs is the foundation of successful marine conservation.

Marine pelagic environments are characterized by less habitat complexity and greater connectivity than many other ecosystems. Spatial differences in species diversity and composition of vagile marine pelagic microbial communities, therefore, are expected to be commensurately low[7]. Nevertheless, there are pronounced spatial differences in marine phytoplankton diversity. These diversity patterns are driven mainly by the physical and chemical properties of the water column such as thermal stratification, as well as the availability of light and growth limiting nutrients[8,9]. Niche differences in the utilization of key resources may explain the coexistence of species[10] and the more efficient exploitation of available resources by diverse species assamblages[11].

A hitherto largely neglected aspect of phytoplankton resource partitioning is the manner in which different spectral components of photosynthetic active radiation (PAR) are exploited[12-14]. Compared to terrestrial plants, a large proportion of phytoplankton biomass in the oceans is light-limited for photosynthesis[15-16]. Floating phytoplankton communities experience continuous shifts in light supply with regard to both total irradiance (by water depth) and the spectral distribution of irradiance (by selective spectral absorption related to seawater itself and its dissolved and particulate components). Therefore, competition for light is less predictable in water than on land, where total irradiance is typically the only consideration. Niche-specialization related to both light quality and quantity may, therefore, have been more important in the evolution of aquatic primary producers than of land plants. Consistent with this idea, algae use a greater variety of photosynthetic pigments for light harvesting than do terrestrial primary producers. In addition to chlorophyll *a*, all phytoplankton species possess further accessory photosynthetic pigments in taxon-specific combinations and quantities, characterized by specific absorption patterns[17,18]. Thus, pigment richness is an important component of phytoplankton functional diversity that may result in more efficient light harvesting and carbon accrual by species-rich communities possessing higher concentrations of accessory pigments[14,19,20].

We investigated the functional performance of marine phytoplankton along gradients of diversity in 1) 1.2×10^{-1} L laboratory microcosms, 2) 3.5×10^{2} L mesocosm systems, 3) 10^{6}-10^{9} L landlocked marine lakes, and 4) open ocean (pelagic) zones.

We established 65 laboratory communities with random mixtures of species along a gradient from one to nine species drawn from a pool of 17 algal strains originating from the North Atlantic (English Channel). Artificially assembled communities using random combinations

of species are essential for the determination of causal relationships between diversity and ecosystem functioning, as they allow full control over community species composition. These experiments with laboratory communities showed that biomass-specific primary production increased with diversity (Fig. 1a). More diverse communities demonstrated elevated resource use efficiencies for growth, as indicated by higher specific primary production given identical resource supplies. The increase of specific net primary production (sPP) with genus richness (GR) was best described by the linear regression: $\text{Ln (sPP)} = 0.61 + 0.48 \times \text{Ln (GR)}$.

In addition to experiments with assembled communities, removal experiments have been employed to study the ecological impacts of local, nonrandom extinctions and changes in the natural species abundance[21]. Such experiments provide data on diversity – ecosystem functions in communities formed by natural assembly processes and shared evolutionary history. However, removal of individual species is not possible when working with suspended pelagic communities of unicellular organisms. As an alternative, we investigated the consequences of phytoplankton species loss by comparing productivity of North Atlantic phytoplankton communities where species richness was manipulated by dilution. Specific primary production of experimentally manipulated natural phytoplankton community subsets decreased with decreasing diversity. Species loss resulted in a significant reduction of specific primary production under identical resource supply regimes. The increase of specific net primary production (sPP) with genus richness (GR) was best described by the linear regression: $\text{Ln (sPP)} = -0.82 + 0.79 \times \text{Ln (GR)}$ (Fig. 1b).

To analyse the link between diversity and gross growth rates of phytoplankton along a spatial diversity gradient of connected marine habitats, we measured diversity and the growth efficiency of phytoplankton communities sampled in landlocked marine lakes and lagoon sites located in the archipelago of Palau, Micronesia. These locations allowed for the comparison of closely related phytoplankton communities assembled during the past 5000 - 10000 years that differ in diversity but exist in close geographic proximity under similar climatic conditions.

Analyses of diversity and growth of these Pacific phytoplankton communities revealed a positive diversity – productivity relationship. Phytoplankton gross growth rates (GGR) estimated using data from the dilution experiments[22] and normalized for nutrient availability (total phosphorus, TP) increased with phytoplankton genus richness ($\text{Ln } (GGR_{TP}) = - 6.36 +$

1.02 × Ln (GR); Fig. 2a). Total phosphorus is generally considered an appropriate surrogate for general nutrient supply. Nutrient limitation assays indicated that P was the limiting nutrient at most of the sampling sites (Fig. 2a). However, the positive relationship between diversity and growth was still present even when gross growth rates were not normalized for TP (Ln GRR = -1.429 + 0.45 × Ln(GR); Supplementary Figure 1). Additionally, in each phytoplankton sample we measured the fluorescence yield of photosystem II, F_0, excited by blue (450 nm) and white light[22]. We found a positive link between algal genus richness and the ratio of F_0 in blue and white light, indicating that PAR was more evenly utilized in more diverse communities (LUE_{PAR} = -0.0065 + 0.32 × Ln(GR); Fig. 2b). This relationship suggests a positive link between diversity and light use efficiency (LUE).

Further investigation of the relationship between phytoplankton diversity and specific production included long term data obtained from open ocean areas. We analysed the link between functional diversity (pigment richness) and specific primary production in available data from sampling stations in the Atlantic (BATS), the Pacific (HOT), and the Mediterranean Sea (DYFAMED). All these long term sampling stations are characterized by nutrient-poor, oligotrophic waters, representing the majority of marine pelagic ecosystems. Light-normalized specific net primary production (LsPP) was positively correlated with pigment richness (PR) in phytoplankton from the Atlantic (Ln (LsPP) = -6.06 + 0.44 × PR), the Pacific (Ln (LsPP) = -4.05 + 0.45 × PR) and the Mediterranean Sea (Ln (LsPP) = -5.37 + 0.19 × PR) which clearly indicates higher performance within the more functionally diverse communities, where elevated pigment richness results in more efficient conversion of light energy to growth (Fig. 3).

To compare the relationships between genus richness and specific primary production between all the previously described data sets, we converted the available data on pigment richness from the sampling stations HOT, BATS and DYFAMED to mean genus richness (GR_M) using measured relationships between pigment data and genus richness (Supplementary Fig. 2). Regression analyses between genus richness and light-normalized specific primary production of all investigated communities resulted in positive slopes ranging from ~0.3 to 0.8. There was no clear link between the regression slopes and geographical identity or scale. Regression slopes were, however, negatively related to the

mean genus richness (Slopes = 0.83 -0.15 × Ln (GR_M); Fig. 4). Our data point towards a general, global relationship between phytoplankton functional diversity and performance. Figure 4 indicates a positive but decelerating link between genus richness and phytoplankton growth. Such a decelerating relationship would be expected where there is increasing niche overlap, and thus increasing redundancies of the functions of different species[24]. The importance of niches in the world's largest and evolutionarily oldest photosynthetic primary producer community suggest functional segregations are responsible not just for diversity[10], but also the consequences of species diversity for ecological communities.

However, care must be taken to avoid confounding diversity – productivity relationships with resource mediated productivity effects. While marine phytoplankton biomass production is constrained by resource availability, the efficiency with which available resources are used is clearly a function of phytoplankton diversity.

Diversity effects on phytoplankton growth are not only linked to marine production where the yield of harvestable marine species is an identifiable consequence. Diversity – productivity relationships in marine phytoplankton also impact global ecosystem services. Atmospheric composition, global biogeochemical cycles or the biological transport of atmospheric CO_2 into deep ocean reservoirs by phytoplankton sedimentation, the so called biological carbon pump, are all based on diversity-related marine photosynthetic carbon fixation[6,25,26].

Various human activities influence the diversity of phytoplankton organisms by acting on chemical and physical properties of pelagic environments. Coastal development and the production and use of agricultural fertilizers result in the enrichment of otherwise growth limiting nutrients and subsequent formation of anoxic 'dead' zones. Fossil fuel combustion is raising atmospheric CO_2 concentration, which directly affects water chemistry (pH) and indirectly influences water column stratification by increasing sea surface temperatures. These environmental changes are all known to have strong impacts on species composition and diversity of pelagic microbial communities[26-28]. New concepts for biodiversity conservation must therefore also include the microbes that fundamentally drive ecosystem services[29]. Such concepts must be based on a detailed understanding of the role of microbial diversity in ecosystem services. In addition to meta-analyses describing diversity-productivity relationships, process-oriented knowledge about the cardinal ecophysiological mechanisms underlying these relationships is urgently needed.

Methods Summary

Sixty-five laboratory communities were prepared, each containing one, three, five, seven or nine species selected from a pool of 17 algal strains. Thirteen replicates per species richness treatment were established with randomly designed new species combinations. Each community had a volume of 120 ml. Algal communities were cultured at 18°C with an illumination of 60 µmol photons m^{-2} s^{-1}. Primary productivity was measured by monitoring oxygen production with oxygen optodes in light and dark bottles, incubated for 4 h. Phytoplankton biomass carbon was estimated from phytoplankton biovolume using established volume-to-carbon relationships.

For experiments with natural phytoplankton communities, indoor mesocosms (350 L) were filled with 1 µm filtered seawater from the Bay of Brest. Mesocosms were inoculated with 0.001, 0.01, 0.1, 1, 10 and 100 mL of 250 µm filtered seawater. Phytoplankton carbon content and net primary production was analysed after 4 wks of incubation as described above. Taxonomic composition was determined by microscopic examination. To analyse for diversity – growth relationships along a spatial diversity gradient, we sampled 13 marine lakes located in the islands of Palau and four sampling sites in the lagoon of the Palau archipelago, Micronesia. Integrated water samples were analysed for total phosphorus and phytoplankton taxonomy. Phytoplankton gross growth rates were estimated by standard dilution methods. F_0 was measured with an AquaPen fluorometer (PSI, Drásov, Czech Republic) equipped with a blue and a white LED light source.

Available phytoplankton primary production measurements, pigment and light data from sampling stations in the Mediterranean, the Atlantic and the Pacific were used to estimate light-normalized net specific primary production in relation to pigment richness. Pigment richness was used to quantify phytoplankton functional diversity for all time series analyses. All statistical analyses were performed with Sigma Plot 11.0; when necessary data were ln-transformed to ensure normal distribution (Kolmogorov Smirnov test) and equal variances (Levene`s test).

Methods

A) Experiments

Laboratory microcosm experiments with laboratory algal strains

Experiments with artificial phytoplankton communities established with randomly assigned combinations of one, three, five, seven and nine species were conducted. Each diversity treatment was replicated 13 times with new species combinations assembled from a pool of 17 North Atlantic phytoplankton strains. Experiments were run in 120 ml of algal growth medium at 18°C and illumination of 60 µmol quanta $m^{-2}s^{-1}$. Diversity treatments were adjusted to the same initial biovolume, measured by a Beckmann Z1 cell counter.

Indoor mesocosm systems with natural algal communities

Six indoor mesocosm systems of 350 L each were established in an environmental chamber (18°C, 60 µmol quanta $m^{-2}s^{-1}$), filled with 1 µm pre-filtered seawater from the Bay of Brest. Mesocosms were inoculated with 0.001, 0.01, 0.1, 1, 10 and 100 mL of seawater, sampled from the Bay of Brest just prior to initiation of the experiment (June 2009). Seawater inoculum was filtered through 250 µm gauze to remove meso-zooplankton. The six dilution levels of seston resulted in different phytoplankton communities under identical environmental conditions after 4 wks of inoculation. Phytoplankton taxa richness of each mesocosm was determined by microscopic examination. The experiment was replicated a second time with 0.001, 0.01, 0.1, 1, and 10 ml of seawater inoculum as described above, immediately after termination of the first experiment.

Primary productivity measurements

The same analyses were conducted for both experiments (laboratory algal communities and diluted natural algal communities). Oxygen production and respiration rates (for the calculation of primary production) were measured using oxygen optodes mounted into 5 ml glass bottles standing on sensor dish readers (SDR, PreSens). Oxygen was measured once per minute for 4 h in light- and dark-incubated bottles. Carbon incorporation was calculated from

oxygen production by assuming a respiratory quotient of 1. The study was replicated using new sub-samples from micro- and mesocosms; the mean of the replicates was used for statistical analyses. Algal specific carbon contents were estimated from established biovolume-to-carbon relationships.

Field experiments in marine lakes Palau

Samples were collected from pelagic marine communities in the Palau archipelago, Micronesia, including landlocked marine lakes and ocean sites. Integrated water samples were collected with a 2 m long tube sampler from depths of 0 (surface) to 10 m or from 0 to the bottom in lakes less than 10 m in depth. Samples were filtered through 250 µm gauze to remove meso-zooplankton and stored in a dark, cooling box until further treatment in the laboratory. In the laboratory 500 mL of each water sample were used to perform standard dilution experiments to estimate gross growth rates and micro-grazing (10 replicates per lake). Nutrient limitation assays were performed according to published protocols[30]. All phytoplankton treatments for dilution experiments and nutrient limitation essays were incubated in a large, shaded outdoor incubator exposed to natural light illumination and photoperiod. Water temperature in the incubator was similar to lake water temperature (29-32°C). Maximum incubator light intensity at the surface at noon (1200) was identical to lake surface light levels at the same time (~ 1100 µmol quanta m^{-2} s^{-1}). Growth responses of algal communities were measured using fluorometric Chl *a* analyses. The fluorescence transients of photosystem II (OJIP) were measured with an AquaPen fluorometer (PSI) equipped with a blue (450 nm) and a white LED light source. F_0 was defined as the fluorescence intensity 50 µs after onset of illumination. Phytoplankton samples from all sampling sites were fixed with 1% Lugol's iodine and counted in sedimentation chambers with an inverted microscope at the highest possible taxonomic resolution; identification of diatoms was aided by scanning electron microscopy (SEM).

B) Time series on phytoplankton dynamics

Station DYFAMED is located in the central zone of the Ligurian Sea, NW-Mediterranean Sea (43°25'N, 07°52'E). Since 1991, monthly pigment profiles from the surface to 200 m depth were collected, along with data on particulate and dissolved nutrient concentrations and

primary production rates[31]. Station BATS is located in the North Atlantic Gyre (31°40'N, 64°10'W) 82 km southeast of the island of Bermuda. Monthly profiles of hydrological and biological properties, including pigment data and primary production rates, have been collected since 1988[32]. Station HOT is located in the North Pacific Gyre (22° 45'N, 158° 00'W), 100 km north of the Hawaiian archipelago. As at the BATS station, monthly profiles of pigments and particulate organic carbon (POC) stocks, along with primary production rates have been measured since the late 1980s[33]. In all sites, primary production rates were measured using the ^{14}C method. Pigments and POC were measured using standard HPLC methods and an elemental analyser.

C) Data processing

Light normalized specific primary production

Primary production rates (PP) at depth *z* were normalised to ambient light (W m^{-2}) and POC concentration (mmol C m^{-3}), to obtain a light-normalized specific primary production rate. Light at depth *z* on day *i*, $PAR_{(z, i)}$, was estimated from surface PAR (W m^{-2}) and chlorophyll *a* concentration (Chl-a, µg L^{-1}), with:

$$PAR_{(z,i)} = PAR_{(z-\Delta z,i)} \exp\left(-k_{(\bar{z},i)}\Delta z\right)$$

where $k_{(\bar{z},i)}$ is the mean extinction coefficient between depth z and depth z-Δz. At each depth z; k(z,i) was calculated using[34]:

$$k_{(z,i)} = 0.04 + 0.0088 \times Chl-a_{(z,i)} + 0.054 \times Chl-a_{(z,i)}^{2/3}$$

A climatology (from 1991 to 2001) of mean daily surface PAR ((z=0),i) was built using predicted downward solar radiation from the European Centre for Meteorological Weather Forecast. At each depth z, the light use efficiency 'LUE' (unit: mg C m^{-3} d^{-1} (W m^{-2})$^{-1}$ (mmol C m^{-3})$^{-1}$) was calculated as follows:

$$LUE(z,i) = PP(z,i) / PAR(i,z) / POC(i,z)$$

LUE(z,i) was computed from the surface (z=0) down to the bottom of the euphotic zone, which is defined as the depth at which PAR(i,z) = 0.01 × PAR(i,z=0).

Pigment richness

Pigment richness (the number of pigments present per sample) was computed from measured pigment concentrations. We used a threshold of 20 ng pigment per kg of organic particulate carbon, as this consistently produced the highest coefficient of determination (r^2). Even at lower thresholds, however, the positive relationship between pigment richness and resource use efficiency remains significant. Genus richness was estimated from pigment richness using the relationship identified between pigment and genus richness in marine lakes:

$$\text{Genus richness} = \exp\left(\frac{(\text{pigment richness} - b)}{a}\right),$$

with $b \pm$ s.e. = 10.46 ± 2.90,

and $a \pm$ s.e. = 1.97 ± 1.04.

For each pigment richness data point, a mean taxon richness was computed from 30 estimates of taxon richness, with a and b being randomly sampled within their lower and upper limits, i.e., b = [7.56-13.36] and a = [0.93-3.01] (Supplementary Fig. 2).

Figure legends

Figure 1: Diversity – phytoplankton performance relationships in diversity manipulated communities growing under controlled environmental conditions. a) Specific primary production (sPP) of 65 assembled laboratory communities as a function of genus richness (GR). Ln (sPP) = 0.61 + 0.48 × Ln (GR), r^2 = 0.17; p = 0.0006; n = 65. b) Specific primary production of 11 diversity-diluted phytoplankton communities originating from the Bay of Brest as a function of genus richness (GR). Ln (sPP) = -0.82 + 0.79 × Ln (GR); r^2 = 0.58; p = 0.0061; n = 11. Dotted lines indicate the 95% confidence interval.

Figure 2: Diversity – phytoplankton performance relationships along a spatial gradient of diversity. a) Gross growth rates (GGR_{TP}) normalized for total phosphorus of 17 marine lake and ocean phytoplankton communities from the archipelago of Palau as a function of genus richness (GR). Ln (GGR_{TP}) = - 6.36 + 1.02 × Ln (GR); r^2= 0.41; p = 0.006. b) PAR spectrum light use efficiency (LUE; Fo_{White}/Fo_{Blue}) as a function of genus richness (GR). LUE_{PAR} = -0.065 + 0.32 × Ln (GR); r^2 = 0.49; p = 0.002. Circles: P limited communities, triangles: NP colimited communities, squares: no N or P limitation. Open symbols: marine lakes, filled symbols: ocean sites. Dotted lines indicate the 95% confidence interval.

Figure 3: Diversity – phytoplankton performance relationships at long term sampling stations: Light normalized specific primary production (LsPP) as a function of pigment richness (PR) for: Atlantic phytoplankton communities (black circles, station BATS):
Ln (LsPP) = -6.06 + 0.44 × PR; r^2 = 0.38; p < 0.001; n = 502. Pacific phytoplankton communities (open circles, station HOT): Ln (LsPP) = -4.05 + 0.45 × PR; r^2 = 0.42; p < 0.001; n = 306. Mediterranean phytoplankton communities (grey circles, station DYFAMED): Ln (LsPP) = -5.37 + 0.19 × PR; r^2 = 0.21; p < 0.001; n = 80. Dotted lines indicate the 95% confidence interval.

Figure 4: Slopes of genus richness – specific phytoplankton production relationships versus mean genus richness (GR_M) of investigated phytoplankton communities. Slopes = 0.83 - 0.15 × Ln (GR_M); r^2 = 0.70; p = 0.037. Data points are means ± s.e.m.

Supplementary Figure 1: Diversity – phytoplankton performance relationships along a spatial gradient of diversity. Gross growth rates (GGR) of 17 marine lake and ocean phytoplankton communities from the archipelago of Palau as a function of genus richness (GR): Ln GRR = -1.42 + 0.32 × Ln(GR); r^2 = 0.29; p = 0.02. Circles: P limited communities; triangles: N and P co-limited communities; squares: no N or P limitation. Open symbols: marine lakes, filled symbols: ocean sites.

Supplementary Figure 2: Diversity – phytoplankton performance relationships at long term sampling stations: Light normalized specific primary production (LsPP) as a function of genus richness (GR) for: Atlantic phytoplankton communities (black circles, station BATS): Ln (LsPP) = -4.79 + 0.61 × Ln(GR); r^2 = 0.17; p < 0.001; n = 502. Pacific phytoplankton communities (open circles, station HOT): Ln (LsPP) = -2.51 + 0.67 × Ln(GR); r^2 = 0.32; p < 0.001; n = 305. Mediterranean phytoplankton communities (grey circles, station DYFAMED): Ln (LsPP) = -4.91 + 0.44 × Ln(GR); r^2 = 0.20; p < 0.001; n = 80.

Figure 1

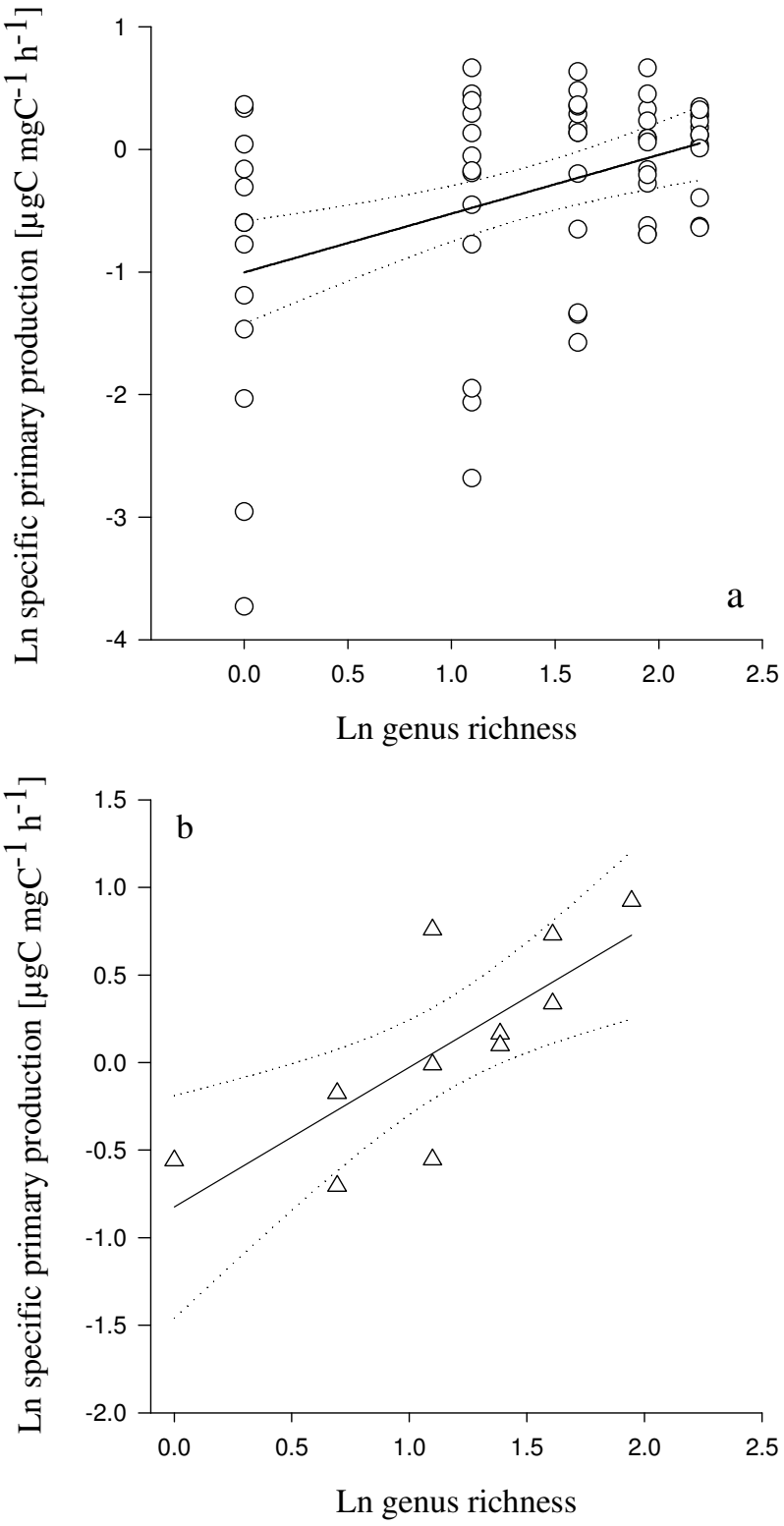

Ln specific primary production [µgC mgC-1 h-1]
1
0
-1
-2
-3
-4
a
0.0
0.5
1.0
1.5
2.0
2.5
Ln genus richness
Ln specific primary production [µgC mgC-1 h-1]
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
b
0.0
0.5
1.0
1.5
2.0
2.5
Ln genus richness

Figure 2

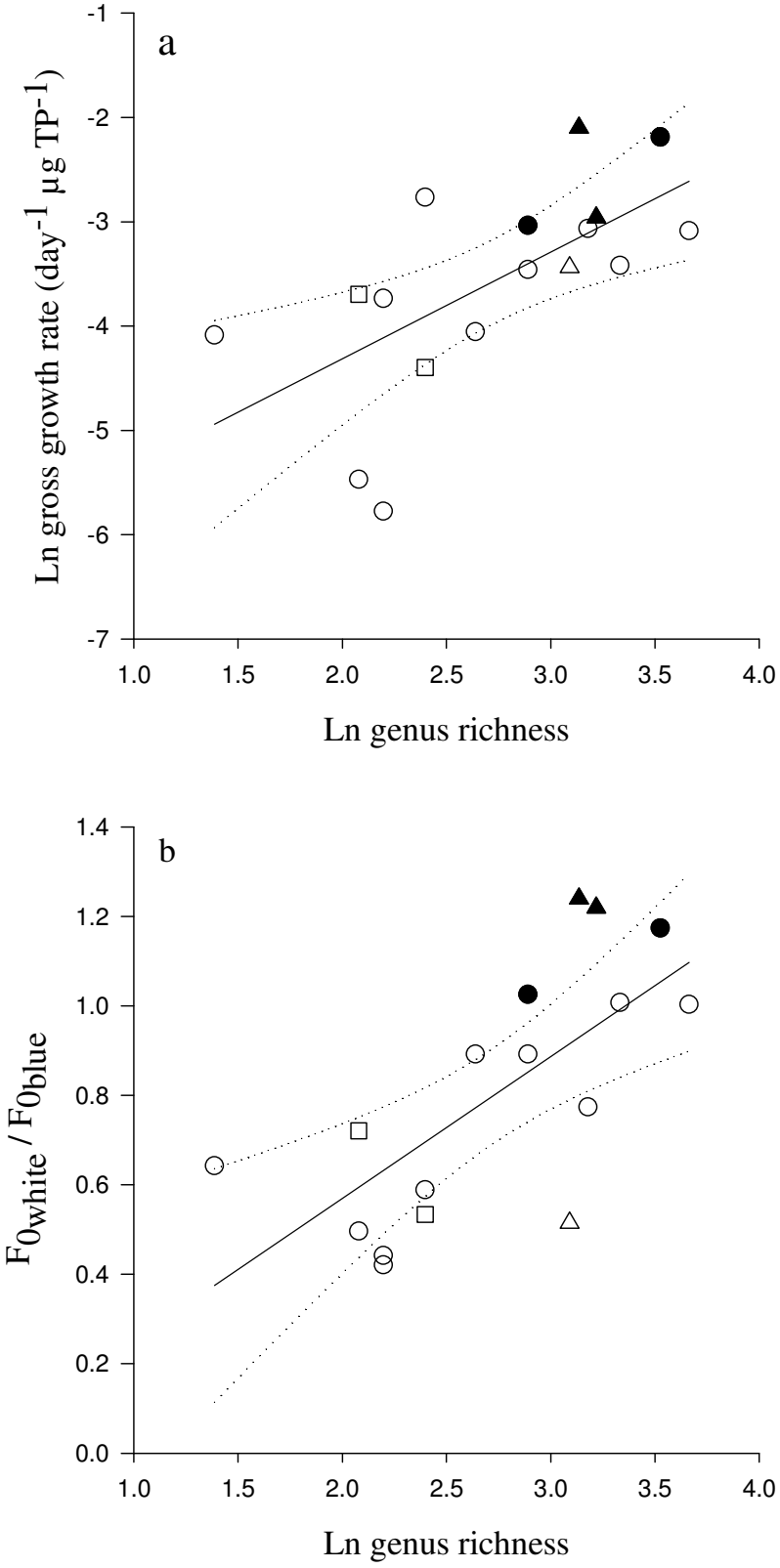

a
Ln gross growth rate (day-1 µg TP-1)
-1
-2
-3
-4
-5
-6
-7
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Ln genus richness
b
F0white / F0blue
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Ln genus richness

Figure 3

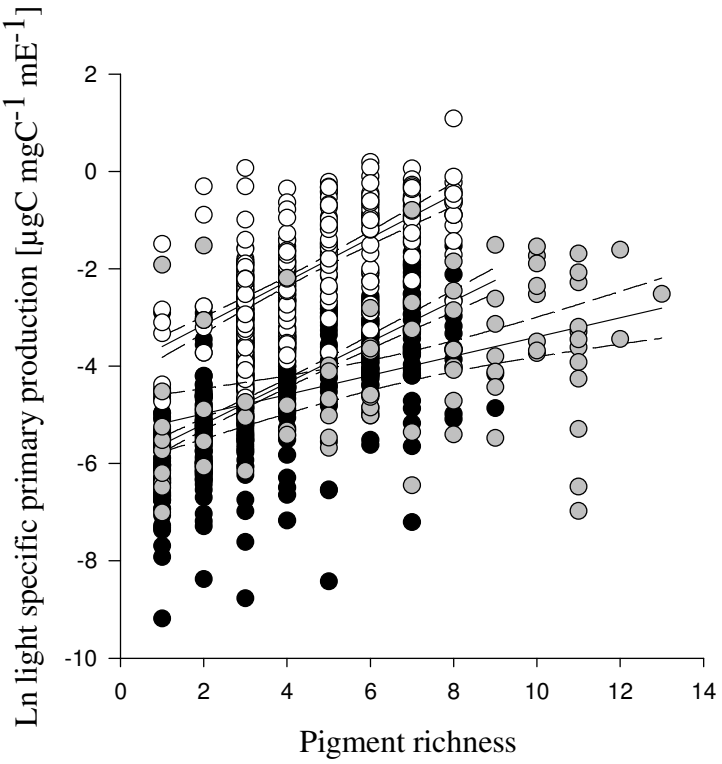
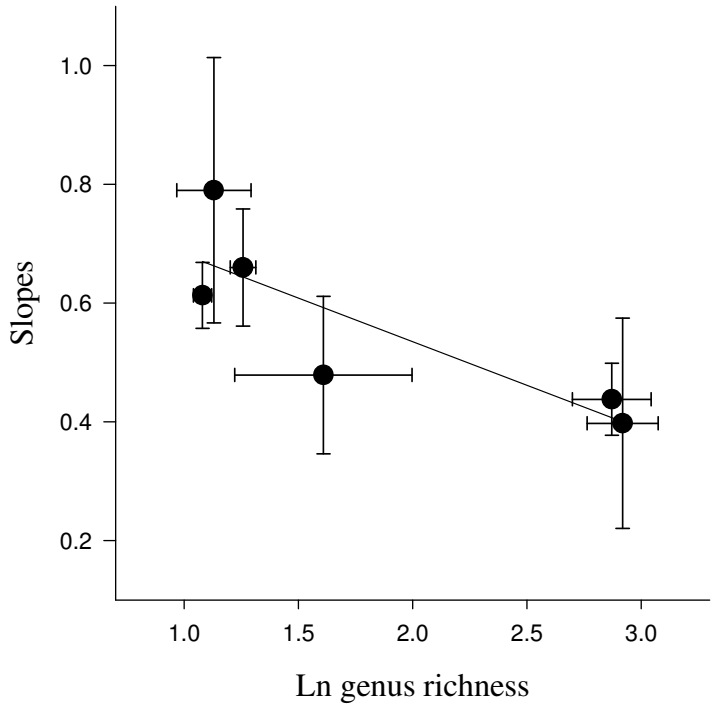
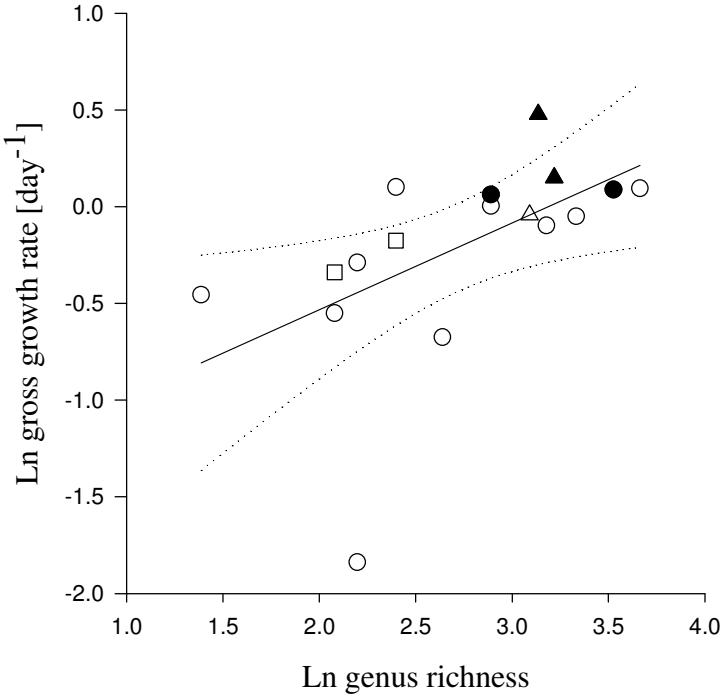


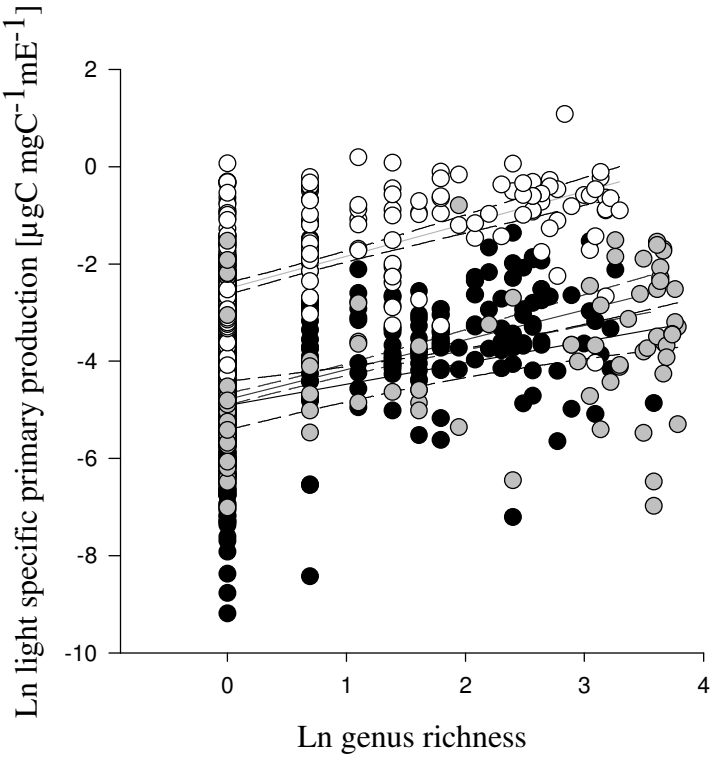
Figure 4



Supplementary Figure 1



Supplementary Figure 2



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4. GENERAL DISCUSSION OF RESULTS

In my thesis, I raised and tested a suite of hypotheses about the relationship between species diversity and ecosystem functioning. These hypotheses covered a broad spectrum of ecological questions, ranging from the ecophysiological mechanisms underlying diversity effects in phytoplankton communities and their implications for pelagic food webs, to their general validity and importance in aquatic environments. I addressed these issues experimentally in laboratory and field (mesocosm) experiments, by use of freshwater and marine phytoplankton and zooplankton communities.

Since the early 1990s, when the ongoing and accelerating loss of habitats and species started to gain broad public attention, the quantity of scientific publications on this issue has been growing exponentially (Balvanera et al. 2006). First, observational and comparative data, gathered mainly from grasslands and agriculturally used plant communities, revealed correlations between species richness and productivity (Trenbath 1974, Willey 1990). This relation in turn pointed towards the worrying conclusion that a loss of species richness might reduce productivity and thus generally impair food web processes. One of the largest data sets concerning aquatic communities (>2000 phytoplankton samples from Scandinavian and Finnish lakes and >500 samples from the Baltic Sea) was recently assembled and analysed by Ptacnik and co-workers (Ptacnik et al. 2008). They found higher resource use efficiency (i.e., primary producer biomass per unit of limiting nutrient) in more diverse phytoplankton communities, which was consistent with the positive diversity-productivity patterns observed in terrestrial environments.

However, to understand the fundamental role that biodiversity plays in mediating ecosystem processes, and to predict the consequences of a rapid diversity decline, descriptive patterns alone (here: positive correlations) are insufficient (Levin 1992, Tilman 2000, Ptacnik et al. 2008). Instead, such patterns need to be addressed experimentally, in order to unveil the mechanisms that underlie and evoke them. But, despite this obvious claim, there is still a wide gap between the great abundance of studies dealing with diversity effects and the scarcity of studies proposing and testing the underlying mechanisms. Most biodiversity – ecosystem functioning (BEF) studies, which assigned diversity effects to the presence of certain functional groups / traits (e.g., N_2-fixers, root morphology), in reality hardly measured the

stated mechanism (Cardinale et al. 2011). One main achievement of this work is that I was able to identify and test a trait-based, physiological mechanism that drives diversity effects in phytoplankton communities, and to find experimental evidence for its relevance (Publications I, II, and Manuscript III). We showed that differences in photosynthetic pigment composition among phytoplankton species provide the possibility for niche differentiation along the photosynthetically active radiation (PAR) spectrum. This differentiation in turn enables species in a community to use light complementarily (i.e., absorb light in distinct wavelength bands), which means that diverse communities may exploit the light supply more completely than species-poor ones. Following Hutchinson's niche definition (Hutchinson 1957, Colwell & Rangel 2009), this also implies that wavelength-specific absorption, mediated through individual pigment composition, must be considered a niche axis of phototrophs, which corresponds to light quality in the physical niche space.

The fact that light is a key resource for (terrestrial and aquatic) phototrophic organisms has been the subject of a long history of scientific investigation. Also, the great variety of pigments and their absorption characteristics have long been known. However, the focus of ecological questions dealing with light has traditionally been placed on light quantity, not quality (Vojtech et al. 2008, Dubinsky & Schofield 2010). Light quality has predominantly been considered from a physiological point of view, since it was known that certain algae and higher plants are capable of adapting their relative pigment composition as a reaction to the prevailing light spectrum in their environment ('chromatic adaptation'; Engelmann & Gaidukov 1902, Falkowski & LaRoche 1991).

It was only in recent years that the ecological role of light quality in the context of niche differentiation and competition among aquatic primary producers gained increased attention. Stomp et al. (2004, 2007) reported on laboratory experiments with natural communities, where niche differentiation in light use among red and green cyanobacteria promoted coexistence. Bidigare et al. (1992) showed that not only the spectral light quality changes with water depth, but so also does the efficiency of light absorption by different pigments (the 'spectrally weighted absorption coefficient'): while the absorption efficiency of Chl *a* decreases with water depth, accessory pigments (such as Chl *b*, *c*, and carotenoids) exhibit an overall increase in absorption efficiency (Falkowski et al. 2004b).

While these examples illustrate the potentially significant role of pigment-dependent spectral absorption in aquatic communities, our experiments were to our knowledge the first to consider this in the context of diversity–productivity relationships (Publications I, II, and

Manuscript III). First, comparative field data from 46 pre-alpine lakes (Publication I) and three open ocean sampling stations (Ligurian Sea, North Atlantic, and North Pacific; Manuscript III) confirmed the pattern described by Ptacnik et al. (2008), who found a positive correlation between algal species richness and resource use efficiency (based on phosphorus as limiting resource). Additionally, we extended these findings in that we related phytoplankton taxon richness to community pigment richness (i.e., the number of photosynthetically active pigments present), and calculated for each oceanic sample site a light-normalized specific primary production rate based on *in situ* irradiance and ^{14}C uptake measurements ('light use efficiency'). Although the described patterns are very consistent among sites that vary considerably in environmental conditions (Scandinavian soft water lakes and brackish Baltic Sea water in Ptacnik's study; pre-alpine hard water lakes and warm, oligotrophic open ocean sites in our studies [Publication I, and Manuscript III]), such observational data from natural communities have an essential drawback: phytoplankton is part of a multi-trophic food web. This means that varying algal standing stock biomass between sites can be either a result of different productivity and resource use efficiency, but can also simply be the result of different grazing pressure.

To circumvent this problem, we performed a suite of laboratory experiments, using pre-defined combinations of freshwater and marine algal species, and excluded grazers. We were able to show that more diverse algal communities exhibit a higher number of pigments, a higher specific absorbance, and a higher short-term (four hours oxygen production) and long-term (two / four weeks biomass accrual) productivity (Publications I, and Manuscript III).

Although species diversity (the number and evenness of species) has successfully proven to be a good predictor of certain process rates in (mostly primary producer) communities (Cardinale et al. 2011), many ecologists do not feel entirely comfortable with this species-based approach (e.g., Loreau et al. 2001, McGill 2006, Cadotte et al. 2008, Dzialowski & Smith 2008, Hillebrand & Matthiessen 2009, Chao et al 2010). By contrast, they advocate a trait-based approach, where 'species' equals a multi-trait-complex, meaning that a community is treated as a frequency distribution of functional trait values. This perspective seems to be much more promising for fixing the mechanisms that underlie diversity effects, and it offers a further substantial advance: from the functional trait distribution of a community it should be

possible to better make predictions about the fate of a community process (such as productivity or temporal stability) if a certain species / functional trait disappears.

However, there are also several problems associated with this concept. First of all, in an experiment, functional traits must be identified *a priori.* Therefore one must have a very clear idea of the process of interest (e.g., primary production), of the functional traits that may be involved in that process (e.g. nutrient uptake abilities), and how these traits are distributed among the species / individuals in the community. Unfortunately, for most ecosystem processes, little is known about the identity and the distribution of functional traits within and between communities (Lavorel & Garnier 2002, McGill 2006).

Most experiments and theoretical studies that defined functional traits focused either on root morphology, growth period, or atmospheric N_2 uptake via symbiotic bacteria (e.g., Hooper & Vitousek 1997, Tilman et al. 1997, Fornara & Tilman 2008), or, relating to light, on shade tolerance and canopy structure (Fridley 2003, Vojtech et al. 2008, Morin et al. 2011). By contrast, our study presented in Publication II was the first to assign functional groups (FG) based on photosynthetic pigments (as functional traits), and thus based on light use in different wavelength bands of the PAR light spectrum. We defined functional groups (diatoms, chlorophytes, chrysophytes, and cyanobacteria) *a priori*, based on different pigment compositions, which provide functional traits responsible for energy uptake (light absorption) and thus play a fundamental role in biomass accrual (the target process of interest). The results confirm the chain of arguments presented above (higher pigment diversity–complementary light use–higher light use efficiency–higher productivity; *see* Introduction), though in a much more systematic experimental design: combining algal species from the same functional group versus species from different functional groups, is to minimize (species from the same FG) or maximize (species from different FGs) the overlap in pigment composition and absorbance characteristics, and thus maximizes / minimizes the potential effects of niche differentiation and complementarity along the light spectrum.

In BEF experiments, positive effects on productivity are commonly dedicated to resource use complementarity and / or facilitation among species / functional groups. Unfortunately, complementary resource use itself is often quite difficult to measure *in situ*. Therefore, Loreau & Hector (2001) introduced a method that assigns observed (measured) diversity effects to the performance of individual species ('selection effect'), or to interactions among species

('complementarity effect'). The method has become a standard tool for analysing BEF experiments, although, there are two major points of criticism.

First, it is a *post hoc* method, without predictive character which, furthermore, cannot be performed in natural environments with natural communities (due to the lack of species monocultures). Second, the method itself does not prove the presence of any underlying mechanism, nor is the 'complementarity effect' a mechanism. Rather, 'mechanisms can result from complementarity, and these mechanisms can have effects on ecosystem level processes, such as primary productivity' (Petchey 2003). The main benefit of this method is that it allows for (mathematical) partitioning of the net biodiversity effect into one part arising from the dominant species and a second part arising from positive species interactions: the latter may be explained by complementary resource use or facilitation among species.

We applied the method to laboratory experiments with assembled phytoplankton communities and were able to show that the complementarity effect (based on biomass accrual) increased with increasing diversity, while the selection effect was zero, on average (Publication I). More importantly, we showed that the complementarity effect was highest (and the selection effect lowest) in communities consisting of two or more functional groups, and a very high correlation between a community's complementarity effect and its specific light absorbance *in vivo* could be detected (Publication II). These results can be considered strong evidence for the proposed hypothesis of spectral light partitioning in algal communities and its relevance for primary productivity. Moreover, they bridge the gap between pattern (positive diversity – productivity relationship) and underlying mechanism (complementary use of light), something that has hardly been accomplished in many BEF experiments (Cardinale et al. 2006, 2011).

While the interface between primary producers and resources seems to be a logical starting point for BEF experiments, a next step would be to integrate higher trophic levels. It was argued that the relevance of diversity-related questions to real ecosystems (and to ecosystem services exploited by humans) might even increase with increasing trophic position, due to a 'bias in extinction by higher trophic level' (Duffy 2002). The rationale is that population size, total biomass, and species richness generally decrease with increasing trophic position, whereas demographic stochasticity and pressure by human harvesting increases. A smaller number of species, however, suggests a lower redundancy of functional traits present in a community. Therefore the loss of species from higher trophic levels could have relatively

stronger implications for food web structure and trophic cascades (e.g., weakening of top-down control; Terborgh et al. 2001) than the loss of species from lower trophic levels.

Diversity effects in higher trophic levels can principally be addressed in several ways. First of all, similar to experiments known from the primary producer level, one can ask how consumer diversity affects resource (i.e., prey) capture. Experiments dealing with this question have reported on effects similar to algae or plant communities: more diverse grazer communities exploited their resources (prey species) more efficiently through complementarity in diet range (Naeem & Li 1997, Norberg 2000, Sommer et al. 2001), thereby often yielding higher biomass standing stocks (Balvanera et al. 2006, Cardinale et al. 2006). However, as opposed to primary producer communities, this overyielding regularly resulted from single productive species rather than from positive species interactions (Cardinale et al. 2006, Duffy et al. 2007). These partially inconsistent results may arise from the generally more complex interactions of animals with their resources: plants compete for relatively simple abiotic resources, while animals prey upon and compete for living and evolving organisms that are additionally competitors among each other. These differences may influence the intensity and nature of competition among consumer species, and also diversity effects on resource (prey) use (Duffy 2002).

A further way of examining diversity effects in higher trophic levels is to ask how prey diversity affects predator performance. Theoretical expectations point towards a negative influence of primary producer diversity on herbivores, due to a higher chance of the presence of species that are toxic or resistant to consumption. Under grazing pressure, such inedible species are likely to face reduced competition for light and nutrients, finally leading to primary producer communities dominated by inedible prey species. This hypothesis has gained notable support by experimental and theoretical work in aquatic food webs (Leibold 1996, Agrawal 1998, Steiner 2001).

Compared to these studies, we used a new conceptual approach: we investigated if and how increased productivity in diverse phytoplankton communities (which was known from preceding experiments, presented in Publications I and II) would influence demography and growth of non-diverse herbivorous zooplankton populations. In order solely to assess the potential magnitude of positive effects of producer diversity on grazers, we tried to avoid confounding effects by using only edible prey and a single grazer species. In two series of laboratory experiments, we showed that prey diversity positively affects grazer population performance in terms of increased grazer biomass production, survival rates, and reproductive

success (Manuscripts I, II). Most notably, we found consistent results in short-term (11 days), and multi-generation (up to 263 days) experiments. While the positive effects seemed to be predominantly a result of higher primary productivity (prey quantity), we cannot completely exclude effects of increased 'prey quality'. Higher prey quality refers to a higher probability of containing essential macromolecules (such as fatty acids or vitamins), or limiting nutrients (such as phosphorus) in more diverse prey communities (e.g., Andersen et al. 2007, Müller-Navarra 2008). However, equal biomass phosphorus contents in algal communities, and estimations of established transfer efficiencies, make it seem reasonable to assign diversity effects to prey quantity (through increased primary productivity), rather than to prey quality.

In a recent meta-analysis, Cardinale and co-workers summarized the progress that has been achieved in biodiversity-ecosystem function research during the last two decades, finally addressing important open questions (Cardinale et al. 2011). One of these questions that is so far almost unexplored is how strong and important are diversity effects, not *per se* but in relation to other environmental forces. This does not necessarily imply harmful, anthropogenic perturbations, such as climate change or habitat destruction, but also natural (e.g., seasonal) variability in environmental conditions such as resource availability. There exist relatively little direct experimental evidence about the strength of diversity effect relative to abiotic factors (Duffy 2009). Dzialowski & Smith (2008) investigated diversity effects in grazer–algae systems under two different nutrient regimes, and found grazer diversity effects on algal biomass only in nutrient-enriched treatments. Wojdak (2005) reported on an aquatic food web experiment, where diversity effects of consumers (snails) on several ecosystem processes were comparable in size, or even stronger than those of substantial nutrient enrichment.

As opposed to the studies described above, which focused on grazer diversity, we tested the relative importance of algal species diversity versus light intensity, a major abiotic driver of pelagic food web dynamics. Both factors were crossed in meaningful gradients in a full factorial design, to assess their relative impact on consumer (*Daphnia magna*) performance (Manuscript I). Results were quite surprising, since they revealed that both factors quantitatively contributed the same positive effects on *Daphnia* growth, survival and reproduction. Although the experimental period was rather short (including roughly two generations of grazers), these results already point towards an interesting aspect that has not, to our knowledge, yet been formulated in BEF experiments: resource supply (here: light

enrichment) and diversity of primary producers may be functionally equivalent in the sense that their positive effects on primary production can evoke quantitatively similar positive effects on higher trophic levels.

A common feature to many BEF experiments is that they include relatively few species and that positive effects on investigated processes (such as productivity) start saturating at relatively low diversity levels (Schwartz et al. 2000). This has led to the assumption that ecosystem processes can be maintained by a relatively small number of species, and that BEF experiments would generally overestimate true effect sizes in real-world ecosystems, because they test (and extrapolate) diversity effects at the lower edge of species numbers in natural communities (Duffy 2009). Indeed, most natural communities are governed by strong rank abundance patterns with a few dominating and many subordinate species (Schwartz et al. 2000, Jiang et al. 2009). However, this does not necessarily mean that rare species do not significantly contribute to ecosystem processes. By contrast, Duffy (2009) pointed out that the above described early saturation of processes in BEF experiments is most probably an artefact of either simplified experimental conditions (small, homogenous plots, short experimental duration), or of the fact that most experiments have focused only on a single response variable. However, different ecosystem response variables are probably dominated by different species (including rare species), so maintaining multiple functions may require even more species than expected from BEF experiments.

As a whole, my experiments contribute to the ongoing debate about the validity and relevance of BEF experiments to understanding biodiversity – ecosystem functioning relationships in real-world communities. A particular strength of this work is that we addressed a set of simple hypotheses about diversity – ecosystem functioning relationships, an underlying ecophysiological mechanism, and food web consequences repeatedly in several distinct systems (freshwater and marine environments, lake mesocosms and laboratory microcosms, natural and synthetic communities). Although the experimental designs varied considerably in scale (time and space) and in the methods used to determine effects and mechanisms, results were strikingly consistent, suggesting that these results are robust and are also relevant to natural plankton dynamics.

From a global perspective, it is particularly important that the diversity effects on productivity were shown to be similar in freshwater and marine communities, indicating their significance to the productivity and food web dynamics of the world's largest ecosystem, the

marine pelagial. Apart from providing the energetic base of most aquatic food webs, phytoplankton plays a pivotal role in mediating biogeochemical fluxes such as the carbon export to deep ocean areas (referred to as ‘biological pump’; Boyd & Trull 2007). Therefore our experiments suggest that an initially unnoticed loss of species or functional traits from the nearly invisible realm of phototroph plankton organisms will ultimately have strong and visible effects on global scale ecosystems.

5. OUTLOOK

Beyond the infinite number of particular, context-dependent questions associated with the causes and consequences of biodiversity, there exist a handful of general and prevailing topics which touch nearly all experimental and theoretical work in the field of BEF research. Addressing these topics in a more concise framework will yield a deeper understanding of diversity and its implications for ecosystems. Stimulated by recent publications and insights from my own work, I present the following three topics, which I consider to be of high relevance for substantial progress in future biodiversity research.

5.1 One consistent diversity measure and concept

Despite the growing importance and impact of studies dealing with diversity-related topics, there is still a somewhat surprisingly low accordance about the most appropriate measure to use. According to a review by Balvanera et al. (2006), *species richness* (393 counts) is the most common diversity measure used in experiments and theoretical studies, followed by *functional group richness* (23), *diversity indices* (19), and *evenness* (11). This means that not only has the vast majority of studies been based on species richness, but also entails that the accumulated knowledge in the field comprises a strong bias towards species richness.

Clearly, species (or taxon) richness, i.e., the number of present taxa, is the most intuitive measure when considering the ultimate motivation of biodiversity – ecosystem functioning research, the ongoing global species loss. However, the ecological impact of a taxon on its environment (and thus to a certain extent also its economical value) is more likely to be reflected by the presence and 'activity' of taxon-specific traits than by a taxon's presence *per se*. Hence, much more than hitherto, BEF research should focus on target processes of interest and the (experimental) identification of functional traits that underlie and evoke them. Of course, from a conservation biology point of view, it can be argued that a trait cannot be preserved without preserving the species / taxon to which the trait belongs. Likewise, a loss of species / taxa means removing them entirely from the system, not only a particular single trait. However, these arguments rely on species identity (keystone species or individuals as 'multi-trait-complexes'), rather than on species richness.

From a purely functional point of view, species / taxa matter only insofar as their traits and interactions evoke and contribute to maintain certain ecosystem processes. A trait-based approach has three major advantages over the species-based concept: first, it logically ties diversity to niche theory; second, it recognises functional traits as primary mechanistic drivers of ecosystem processes; and third, it can therefore be considered a measure with a truly predictive characteristic. For these reasons, future studies should relate ecosystem processes to reasonable measures of functional trait diversity, rather than to species richness.

5.2 Integrating realistic species combinations, interactions, and loss scenarios

Today, most evidence and insights regarding biodiversity – ecosystem functioning relationships have been acquired by use of artificially assembled experimental communities. Species are usually randomly drawn from pools of well-defined laboratory strains, and equal proportions of each drawn species are combined to create different diverse communities. In some experimental designs, initially created community compositions (e.g., number of species or equal biomass proportions) are even maintained by the experimenter during the experimental period. In species loss experiments, loss is also usually random, i.e., each species has the same chance of being lost.

While these procedures predominantly arose out of analytical and statistical considerations (mainly in order to differentiate identity from diversity effects), and are entirely valid for that purpose, they have also invoked considerable criticism (e.g., Jiang et al. 2009): experimental communities are synthetic, meaning that randomly assembled species combinations do not probably coexist in natural communities, and do not have shared ontogenetic and evolutionary histories. Moreover, equal proportions and random extinction events are highly unrealistic in nature, where communities are usually dominated by only a few species and where extinction and species assembly and turnover are selective events (caused by abiotic factors, competition, predation, or anthropogenic impact), rather than stochastic.

To overcome these shortcomings, future BEF experiments should re-focus on natural communities and create experimental diversity gradients, e.g., by strong dilution of such natural communities. By doing so, one can preferentially simulate a loss of rare species, which is more likely to occur in nature, than random loss. Moreover, while artificially assembled communities allow for the assessment of maximum and / or minimum diversity

effects, communities derived from natural communities by some kind of experimental forcing are more suitable for assessing more realistic magnitudes of diversity effects, as occur in nature.

5.3 Establishing adequate scales in BEF experiments

The bulk of BEF experiments has been conducted in highly simplistic settings, including controlled, constant abiotic factors (temperature, irradiance, nutrients, food supply), reduced biological interactions (few species and trophic levels, homogeneous spatial distribution of individuals and populations), small, artificial habitats (culture vessels, pre-treated field plots), and short experimental duration (often one generation or even less).

Using simplified and highly controlled study systems is by no means inadequate: by contrast, it is an appropriate tool for investigating and distinguishing between effects of various potential influence variables. Similarly, it is an appropriate tool to elucidate particular mechanisms that underlie diversity effects. However, the question arises as to whether the observed patterns and results obtained from such simple systems are generally adequate to make predictions for the real-world communities and ecosystem functioning threatened by species loss.

Several recent studies (reviewed in Cardinale et al. 2011) indicate that on average the strengths of diversity effects even increase with increasing experimental duration, and tend to increase with spatial scale (both can be dedicated to a higher degree of environmental heterogeneity, covarying with space or time). However, besides time and space, trophic complexity is probably the most puzzling, but also the most important, scale to address, for two reasons: first, any diversity effect results from species interactions (competition, predation, niche differentiation, etc.), and second, (nearly) all natural communities are part of complex food webs.

Unfortunately, it is not clear what to expect when up-scaling simple one- or two-trophic-level-systems to systems consisting of multiple trophic levels, where each trophic level contains various species (and even more functional traits). Diversity-borne effects that emerge at one level or subsystem could be either cancelled out or reinforced at another level (or subsystem). Therefore, future BEF experiments should focus on larger food webs, and more complex species interactions, than hitherto. Conducting whole food web experimental manipulations (under *in situ* environmental conditions) using natural communities is probably

the most promising approach to making reliable predictions about the fate of ecosystem functioning under reduced diversity.

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7. PERSONAL NOTES

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Civilian service

09. 2000 - 07. 2001	Stiftung Pfennigparade, München

Academic education

10. 2001 - 12. 2006	Studies in biology at Ludwig-Maximilians-Universität München Main subject: Ecology Minor subjects: Zoology, Systematic Botany, Anthropology & Human Genetics
08. 2006	Diploma thesis: 'Einfluss der Artendiversität auf die Licht- und Nährstoffnutzung des Phytoplanktons'
Since 09. 2007	PhD studies at Ludwig-Maximilians-Universität Munich, Department Biology II, Aquatic Ecology Advisor: Prof. Dr. Herwig Stibor Funded by a personal scholarship from Studienstiftung des deutschen Volkes (09. 2007- 09. 2011).

7.2 PUBLICATIONS AND MANUSCRIPTS

Striebel M., **S. Behl**, S. Diehl, and H. Stibor. 2009. Spectral niche complementarity and carbon dynamics in pelagic ecosystems. *The American Naturalist* 174:141-147.

Striebel M., **S. Behl**, and H. Stibor. 2009. The coupling of biodiversity and productivity in phytoplankton communities: consequences for biomass stoichiometry. *Ecology* 90:2025-2031.

Behl S., A. Donval, and H. Stibor. 2011. The relative importance of species diversity and functional group diversity on carbon uptake in phytoplankton communities. *Limnology and Oceanography* 56:683-694.

Behl S., S. Diehl, V. de Schryver, and H. Stibor. 2012. Trophic transfer of biodiversity effects: functional equivalence of prey diversity and enrichment? *Ecology and Evolution, submitted manuscript.*

Behl S., and H. Stibor. 2012. Phytoplankton diversity enhances trophic coupling in a long term aquatic food web experiment. *Oikos, submitted manuscript*.

Stibor H., **S. Behl**, P. Pondaven, B. Beker, and M. N. Dawson. 2012. Diversity and the performance of marine phytoplankton communities. *Nature, submitted manuscript*.

7.3 PRESENTATIONS

Behl S., M. Striebel, L. Schlüter, and H. Stibor. Diversitätsbestimmung von Phytoplanktongemeinschaften (vor)alpiner Seen mittels Mikroskopie, Pigmentanalyse (HPLC) und CHEMTAX. (Poster). Deutsche Gesellschaft für Limnologie (DGL), Jahrestagung 2006, Dresden.

Behl S., M. Striebel, and H. Stibor. Linking biodiversity, productivity, and stoichiometry: a field experiment. (Poster). Biodiversity Research - Safeguarding the Future 2008, Bonn.

Behl S. and H. Stibor. Diversitätseffekte in Phytoplanktongemeinschaften. (Talk). Deutsche Gesellschaft für Limnologie (DGL), Jahrestagung 2008, Konstanz.

Behl S. and H. Stibor. Functional diversity in phytoplankton communities. (Talk). American Society of Limnology and Oceanography (ASLO), Aquatic sciences meeting 2009, Nice, France.

Behl S. and H. Stibor. Particular species or functional trait: how does diversity influence biomass accrual in phytoplankton communities? (Poster). Munich Interact 2009, München.

Behl S., V. de Schryver, and H. Stibor. Trophic effects of phytoplankton diversity on freshwater pelagic communities: laboratory experiments. (Talk). American Society of Limnology and Oceanography. Aquatic sciences meeting 2011, San Juan, Puerto Rico.

Diehl S., M. Striebel, **S. Behl**, M. Stockenreiter, and H. Stibor. Spectral niche complementarity and the diversity-productivity relationship in phytoplankton. (Invited talk). Ecological Society of America, Annual meeting 2011, Austin, USA.

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9. DECLARATION

Diese Promotion wurde im Sinne §12 der Promotionsordnung von Prof. Dr. Herwig Stibor betreut. Ich erkläre hiermit, dass die Dissertation keiner anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

9.1 Eidesstattliche Versicherung

Ich versichere hiermit an Eides Statt, dass die vorgelegte Dissertation von mir selbständig, ohne unerlaubte Hilfe angefertigt wurde.

_____ _____

Ort, Datum Unterschrift

9.2 Beitrag der Koautoren und eigener Beitrag

Publikation I

Ich war an Konzeption, Durchführung und Auswertung sämtlicher Labor- und Freilandexperimente maßgeblich beteiligt. Insbesondere führte ich die taxonomische und quantitative Bestimmung der Phytoplanktonproben durch. Weiterhin war ich wesentlich bei der Fertigstellung des Manuskripts, sowie bei der Bearbeitung der Gutachterkommentare und der Änderungsvorschläge beteiligt. Maren Striebel war maßgeblich an der Konzeption, Durchführung und Auswertung der Labor- und Freilandexperimente beteiligt und federführend bei der Verfassung des Manuskriptes und der Bearbeitung der Gutachterkommentare. Herwig Stibor war an Konzeption, Auswertung und dem Verfassen des Manuskriptes beteiligt. Sebastian Diehl half bei der Auswertung der Daten und Überarbeitung des Manuskriptes.

Publikation II

Ich war maßgeblich für die Konzeption, Durchführung und Auswertung der Versuche und das Schreiben des Manuskripts, sowie die Bearbeitung der Reviews verantwortlich. Herwig Stibor war an der Konzeption der Versuche beteiligt und half beim Verfassen des Manuskripts. Anne Donval führte die Pigmentanalysen (HPLC) durch und gab wertvolle Hinweise zu Analytik und Auswertung der Pigmentmuster.

Manuskript I

Ich war maßgeblich für Konzeption, Durchführung und Auswertung der Versuche und das Verfassen des Manuskripts, sowie die Bearbeitung der Gutachten verantwortlich. Herwig Stibor war an der Konzeption der Versuche beteiligt und half bei der Auswertung der Daten und dem Verfassen des Manuskripts. Sebastian Diehl war an der Auswertung der Daten und dem Verfassen des Manuskriptes beteiligt. Vera de Schryver war an Konzeption, Durchführung und Auswertung des Experiments im Rahmen ihrer Diplomarbeit beteiligt.

Manuskript II

Ich war maßgeblich für die Konzeption, Durchführung und Auswertung der Versuche und das Verfassen des Manuskripts verantwortlich. Herwig Stibor war an der Konzeption und Auswertung des Experiments und bei der Fertigstellung des Manuskripts beteiligt.

Manuskript III

Herwig Stibor, Philippe Pondaven und ich waren gleichermaßen an Konzeption, Durchführung und Auswertung der Experimente in Palau, sowie am Verfassen des Manuskripts beteiligt. P. Pondaven analysierte die Zeitreihendaten und H. Stibor führte die Laborversuche (Brest) durch. Beatriz Beker zählte und bestimmte die Phytoplanktonproben aus Palau. Michael N. Dawson gab wertvolle Hilfestellung vor Ort (Palau) und trug zur Fertigstellung des Manuskriptes bei.

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