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The Nutrient-Load Hypothesis: Patterns of Resource Limitation and Community Structure Driven by Competition for Nutrients and Light

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ABSTRACT: Resource competition theory predicts that the outcome of competition for two nutrients depends on the ratio at which these nutrients are supplied. Yet there is considerable debate whether nutrient ratios or absolute nutrient loads determine the species composition of phytoplankton and plant communities. Here we extend the classical resource competition model for two nutrients by including light as additional resource. Our results suggest the nutrient-load hypothesis, which predicts that nutrient ratios determine the species composition in oligotrophic environments, whereas nutrient loads are decisive in eutrophic environments. The underlying mechanism is that nutrient enrichment shifts the species interactions from competition for nutrients to competition for light, which favors the dominance of superior light competitors overshadowing all other species. Intermediate nutrient loads can generate high biodiversity through a fine-grained patchwork of two-species and three-species coexistence equilibria. Depending on the species traits, however, competition for nutrients and light may also produce multiple alternative stable states, suppressing the predictability of the species composition. The nutrient-load hypothesis offers a solution for several discrepancies between classical resource competition theory and field observations, explains why eutrophication often leads to diversity loss, and provides a simple conceptual framework for patterns of biodiversity and community structure observed in nature.

Keywords: biodiversity, resource competition, eutrophication, nitrogen, phosphorus, light limitation.

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Introduction

Since its appearance in the *American Naturalist*, Tilman's (1980, 1985) resource-ratio hypothesis has become one of the leading conceptual theories on how competition for nutrients and light shapes the species composition of aquatic and terrestrial communities. The resource-ratio hypothesis predicts that the outcome of competition is determined by the ratios at which growth-limiting resources are supplied. This prediction is well founded in mathematical theory (León and Tumpson 1975; Taylor and Williams 1975; Tilman 1980, 1982) and has been extensively tested in highly controlled competition experiments with bacteria (Smith 1993), phytoplankton (Tilman 1977; Sommer 1985; van Donk and Kilham 1990), zooplankton (Rothhaupt 1988; Ciros-Pérez et al. 2001), and terrestrial plants (Dybzinski and Tilman 2007). The resource-ratio hypothesis received additional support from field studies in aquatic and terrestrial ecosystems (Inouye et al. 1987; Sommer 1989, 1993) and provided a major advance in the development of ecology as a theoretical and experimental science (Grover 1997; Miller et al. 2005).

Yet there is still considerable debate on whether and to what extent nutrient ratios or absolute nutrient loads determine the species composition of natural communities. Numerous studies have shown that eutrophication often leads to diversity loss and the dominance of only a few species in terrestrial vegetations (Grime 1973; Stevens et al. 2004; Harpole and Tilman 2007; Hautier et al. 2009). This indicates that absolute nutrient levels may have major effects on plant species composition. In freshwater and marine ecosystems, the question about absolute versus relative nutrient levels is of major importance for the prediction of harmful algal blooms. For instance, several cross-system comparisons have revealed a strong relationship between the dominance of potentially harmful cy-

anobacteria in phytoplankton communities and ratios of total nitrogen (TN) to total phosphorus (TP) (Smith 1983; Smith and Bennett 1999; Havens et al. 2003; Nõges et al. 2008; Vrede et al. 2009). However, just as much evidence has been provided that absolute concentrations of TN or TP are even better predictors for cyanobacterial dominance (Trimbee and Prepas 1987; Canfield et al. 1989; Jensen et al. 1994; Reynolds 1998; Downing et al. 2001; McCarthy et al. 2009). As Smith (2003, p. 130) noted, "*this extremely important fundamental question remains unresolved, and is a key topic for future eutrophication research.*"

One plausible solution for this unresolved debate is that nutrient enrichment changes the species interactions from competition for nutrients to competition for light (Donald 1958; Tilman 1985; Aerts et al. 1990; Olff et al. 1993; Passarge et al. 2006). High nutrient levels can support high plant and phytoplankton biomass, which casts shade deeper down in the vegetation or water column. Hence, competition for light often plays a prominent role in eutrophic ecosystems (Huisman et al. 2004; Hautier et al. 2009). It is not immediately obvious, however, how shading will affect the species composition. Competition for light is conceptually more complex than competition for nutrients, because of the unidirectional nature of the light flux and the resulting vertical gradient in light availability (Weiner 1990; Rees and Bergelson 1997; Perry et al. 2003).

In a series of papers, Huisman and Weissing (1994, 1995) developed a theory on competition for light that explicitly incorporated the unidirectional nature of the light gradient. They showed that competition for light in well-mixed waters can be investigated by a similar mechanistic approach as in Tilman's competition theory. The model predictions were supported by laboratory competition experiments with phytoplankton species (Huisman et al. 1999; Passarge et al. 2006; Agawin et al. 2007; Van de Waal et al. 2011), and have been applied in several field studies (Diehl et al. 2002; Ptacnik et al. 2003; Huisman et al. 2004; Berger et al. 2006; Jöhnk et al. 2008). Subsequent work investigated other aspects of competition for light in phytoplankton communities, including incomplete mixing (Huisman et al. 2004, 2006; Jäger et al. 2008; Yoshiyama et al. 2009; Ryabov et al. 2010), fluctuating light conditions (Litchman and Klausmeier 2001; Litchman et al. 2004), photoinhibition (Gerla et al. 2011), and the underwater light spectrum (Stomp et al. 2004, 2007; Striebel et al. 2009). The results also motivated several follow-up studies on competition for light in terrestrial plant communities (Dybzinski and Tilman 2007; Vojtech et al. 2007; Hautier et al. 2009). However, the role of nutrient ratios versus absolute nutrients levels was not investigated further.

In this article, we investigate how competition for light modifies nutrient-ratio effects on community structure. For this purpose, we extend Tilman's (1980, 1982) graph-

ical-mechanistic approach on competition for two nutrients by incorporating competition for light (Huisman and Weissing 1994, 1995). We keep our model as simple as possible to focus on the essentials of competition for nutrients and light. For instance, the model assumes complete mixing, with a spatially homogeneous distribution of nutrients and species. This assumption is particularly relevant for phytoplankton communities in well-mixed waters. However, many of our findings may also be of interest for competition studies in other ecosystems such as terrestrial plant communities.

Competition Model

We use essentially the same model structure as in earlier work (Tilman 1982; Huisman and Weissing 1994, 1995), but now extended to competition for two nutrients and light. The model considers a vertical water column, illuminated from above, in which nutrients and several phytoplankton species are homogeneously mixed.

Light enters the water column from above, and light intensity decreases exponentially with depth due to light absorption by water and various other components (e.g., dissolved organic matter, suspended clay particles). Light is also absorbed by the phytoplankton community itself. More specifically, let $I(z)$ denote the light intensity at depth z, where z ranges from 0 at the water surface to the maximum depth z_M at the bottom of the water column. According to Lambert-Beer's law,

$$I(z) = I_{in}e^{-(K_{BG}+\Sigma_{j=1}^{n}k_jN_j)z}, \qquad (1)$$

where I_{in} is the incident light intensity at the water surface, K_{BG} is the background turbidity due to light absorption by water and other nonphytoplankton components, k_j is the specific light attenuation coefficient of phytoplankton species j, N_j is the population density of phytoplankton species j, and n is the number of phytoplankton species. We define I_{out} as the light intensity at the bottom of the water column (i.e., $I_{out} = I(z_M)$). Note that the vertical light gradient is dynamic in time. A growing phytoplankton population will absorb more light and thereby reduces light availability in the water column.

The specific growth rates of the phytoplankton species depend on ambient nutrient and light availability. More precisely, we assume that the local specific growth rate of a species at a given depth in the water column, $\mu_j(z)$, is determined by the most limiting resource at that depth, as in Von Liebig's (1840) "law of the minimum":

$$\mu_j(z) = \mu_{max,j}\min[f_{1j}(R_1), f_{2j}(R_2), g_j(I(z))], \qquad (2)$$

where $\mu_{max,j}$ is the maximum specific growth rate of species j, min is the minimum operator, and the functions $f_{1j}(R_1)$, $f_{2j}(R_2)$, and $g_j(I(z))$ describe growth limitation by nutrient

1, nutrient 2, and light, respectively. The exact shape of the functions $f_{1j}(R_1)$, $f_{2j}(R_2)$, and $g_j(I(z))$ may depend on the species and environmental conditions. Here, we describe the resource-limited growth rate of species j as an increasing saturating function of the local nutrient and light availability using Monod's (1950) equation. That is, for nutrient-limited growth,

$$f_{ij}(R_i) = \frac{R_i}{M_{ij} + R_i}, \tag{3}$$

and for light-limited growth

$$g_j(I(z)) = \frac{I(z)}{H_j + I(z)}, \tag{4}$$

where M_{ij} is the half-saturation constant for nutrient i of species j, and H_j is its half-saturation constant for light.

The depth-averaged specific growth rate of a species, $\bar{\mu}_j$, is then obtained by integrating the local specific growth rates of all individuals of this species over the entire depth of the water column:

$$
\begin{aligned}
\bar{\mu}_j &= \frac{1}{z_M} \int_0^{z_M} \mu_j(z)dz \\
&= \frac{1}{z_M} \int_0^{z_M} \mu_{\max,j} \min[f_{1j}(R_1), f_{2j}(R_2), g_j(I(z))]dz.
\end{aligned}
\tag{5}
$$

The net rate of change of a species depends on the balance of its growth and loss rate. Hence, the population dynamics of n phytoplankton species is described by

$$\frac{dN_j}{dt} = (\bar{\mu}_j - l_j)N_j, \tag{6}$$

where $j = 1, \ldots, n$ and l_j is the specific loss rate of species j due to cell death, grazing, viruses, and so on.

Nutrients enter the water column from surface runoff, river inflow, or the sediment below and are taken up by the phytoplankton species. Accordingly, changes in the ambient concentrations of the two nutrients, R_1 and R_2, are described as

$$\frac{dR_i}{dt} = \frac{F}{z_M}(R_{in,i} - R_i) - \sum_{j=1}^{n} c_{ij}\bar{\mu}_j N_j, \tag{7}$$

where $i = 1, 2$. The first term on the right-hand side describes the influx and efflux of nutrients into and from the water column. Here, $R_{in,i}$ is the concentration of nutrient i in the influx and will henceforth be called the nutrient load, and F is the flow rate of the influx and efflux. The nutrient flux is mixed over the entire depth of the water column, which is accounted for by the depth

z_M. The second term describes nutrient consumption by the phytoplankton community, where c_{ij} is the content of nutrient i in species j.

Parameter values were chosen to be within a realistic range for freshwater and marine phytoplankton species (Huisman et al. 1999; Passarge et al. 2006; Agawin et al. 2007). The model variables and parameters are summarized in table 1.

Results

In the following sections, we first investigate the growth of a single species on two nutrients and light. As a next step, we extend the model to analyze competition for nutrients and light between different sets of species. Throughout our analysis, we consider an incident light intensity high enough to support population growth at low population densities.

Dynamics of a Single Species

Figure 1 illustrates depth profiles of the local specific growth rate of a phytoplankton species. Because both nutrients are homogeneously mixed, the nutrient-limited growth rates $f_{ij}(R_i)$ are constant over depth. In contrast, light availability decreases with depth, and hence the light-limited growth rate $g_j(I(z))$ decreases with depth as well.

It is useful to define the light intensity $I_{co,j}$ and depth $z_{co,j}$ at which the local specific growth rate switches from nutrient-limited to light-limited growth (fig. 1B). This light intensity is implicitly given by $g_j(I_{co,j}) = \min[f_{1j}(R_1), f_{2j}(R_2)]$. In view of equations (3) and (4), this yields

$$I_{co,j} = H_j \min\left(\frac{R_1}{M_{1j}}, \frac{R_2}{M_{2j}}\right). \tag{8}$$

Inserting $I_{co,j} = I(z_{co,j})$ and $I_{out} = I(z_M)$ into equation (1), the depth $z_{co,j}$ at which the local specific growth rate switches from nutrient-limited to light-limited growth is given by

$$z_{co,j} = z_M\left[\frac{\ln(I_{in}) - \ln(I_{co,j})}{\ln(I_{in}) - \ln(I_{out})}\right]. \tag{9}$$

Figure 2 displays which resource limits the depth-averaged growth rate of a species as function of both nutrient loads. The different regions in this graph can be interpreted in terms of the three depth profiles of figure 1:

Nutrient limitation. At low nutrient loads, sufficient light reaches the bottom of the water column (i.e., $I_{out} > I_{co,j}$). In this case, the specific growth rate is either limited by

Table 1: Symbols with their interpretation and dimension

Symbol	Interpretation	Dimension	Value
Independent variables:			
t	Time	day	
z	Depth	m	
Dependent variables:			
N_j	Population density of species j	million cells mL^{-1}	
R_i	Environmental concentration of nutrient i	μmol L^{-1}	
$I(z)$	Light intensity at depth z	μmol photons m^{-2} s^{-1}	
I_{out}	Light intensity at bottom of water column	μmol photons m^{-2} s^{-1}	
Species parameters and functions:			
$\bar{\mu}_j$	Depth-averaged specific growth rate of species j	day^{-1}	
$f_{ij}(R_i)$	Specific growth rate of species j when limited by nutrient i	day^{-1}	
$g_j(I)$	Specific growth rate of species j when limited by light	day^{-1}	
$\mu_{\text{max},j}$	Maximum specific growth rate of species j	day^{-1}	.8−1
l_j	Specific loss rate of species j	day^{-1}	.25
M_{ij}	Half-saturation constant of species j for nutrient i	μmol L^{-1}	.001−5
H_j	Half-saturation constant of species j for light	μmol photons m^{-2} s^{-1}	15−60
c_{ij}	Cellular content of nutrient i in species j	fmol cell^{-1}	2−160
k_j	Specific light attenuation coefficient of species j	μm^2 cell^{-1}	.5−10
R_{ij}^*	Critical concentration of nutrient i for species j	μmol L^{-1}	
$I_{\text{out},j}^*$	Critical light intensity for species j	μmol photons m^{-2} s^{-1}	
Environmental parameters:			
$R_{\text{in},i}$	Load of nutrient i	μmol L^{-1}	0−800
F	Flow rate	m day^{-1}	.1−0.25
I_{in}	Incident light intensity	μmol photons m^{-2} s^{-1}	100−600
z_{M}	Total depth of water column	m	1−100
K_{BG}	Background turbidity	m^{-1}	.05−.1

nutrient 1 or limited by nutrient 2 throughout the entire water column (as in fig. 1*A*):

$$\bar{\mu}_j = \mu_{\text{max},j} \min \left[f_{1j}(R_1), f_{2j}(R_2) \right]. \tag{10}$$

In this case, a species can establish a population only if the nutrient loads of both nutrients exceed a critical threshold value R_{ij}^* (fig. 2). These critical nutrient concentrations, R_{1j}^* and R_{2j}^*, can be derived by solving equation (6) for 0. With the help of equations (3) and (10), this yields (Tilman 1982)

$$R_{ij}^* = \frac{M_{ij}l_j}{\mu_{\text{max},j} - l_j}, \tag{11}$$

where $i = 1, 2$.

Hence, the values of these critical nutrient concentrations depend on species traits such as the maximum specific growth rate, loss rate, and half-saturation constants. In figure 2, the horizontal boundary line between the region of "no growth" and the region where the species is limited by nutrient 1 is given by $R_{\text{in},1} = R_{1j}^*$. Likewise, the vertical boundary line between the region of "no growth" and the region where the species is limited by nutrient 2 is given by $R_{\text{in},2} = R_{2j}^*$.

The region where growth is limited by nutrient 1 is separated from the region where growth is limited by nutrient 2 by a diagonal boundary line (fig. 2). At this diagonal boundary, both nutrients limit growth. Hence, the diagonal boundary line can be obtained by solving equations (6) and (7) at equilibrium, assuming $R_1 = R_{1j}^*$ and $R_2 = R_{2j}^*$. This yields

$$R_{\text{in},1} = R_{1j}^* + \frac{c_{1j}}{c_{2j}}(R_{\text{in},2} - R_{2j}^*). \tag{12}$$

This equation shows that the slope of the diagonal boundary line is given by the ratio c_{1j}/c_{2j}. Assuming $R_{\text{in},i} \gg R_{ij}^*$ for both nutrients, it follows that if $R_{\text{in},1}/R_{\text{in},2} > c_{1j}/c_{2j}$, the species is limited by nutrient 2. Conversely, if $R_{\text{in},1}/R_{\text{in},2} < c_{1j}/c_{2j}$, the species is limited by nutrient 1. In other words, the ratio at which the two nutrients are supplied determines which of the two nutrients limits phytoplankton growth. This reasoning lies at the heart of Tilman's resource-ratio hypothesis.

Colimitation. At intermediate nutrient loads, the upper part of the water column receives sufficient light such that local growth is nutrient limited, while growth deeper down in the water column is light limited (i.e., $I_{\text{out}} < I_{\text{co},j} < I_{\text{in}}$).

A Low nutrient load

B Moderate nutrient load

C High nutrient load
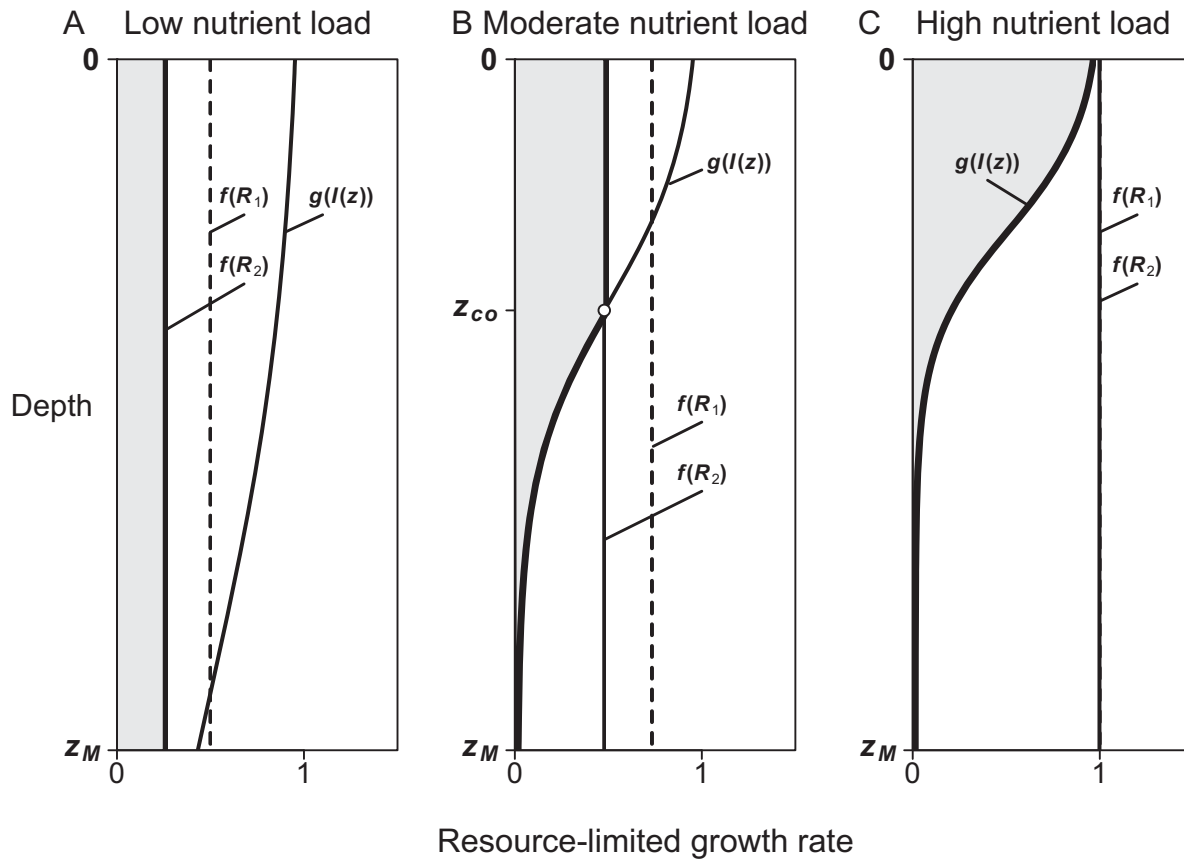
Resource-limited growth rate

Figure 1: Depth profiles of the local specific growth rate. Nutrient-limited growth is uniform over depth, as described by the functions $f(R_1)$ and $f(R_2)$. Light-limited growth, $g(I(z))$, decreases with depth. At each depth, the local specific growth rate (bold line) is determined by the most limiting resource. The depth-averaged specific growth rate is obtained by integrating these local specific growth rates over depth, as indicated by the shaded area. *A*, At low nutrient load, the specific growth rate is nutrient limited throughout the water column. *B*, At intermediate nutrient load, the specific growth rate is nutrient limited in the upper part and light limited in the lower part of the water column. The depth z_{co} marks the transition from nutrient limitation to light limitation. *C*, At high nutrient load, the specific growth rate is light limited throughout the water column.

This scenario is shown in figure 1*B*. In this case, one might say that the depth-averaged phytoplankton growth rate experiences colimitation by nutrients and light (fig. 2). That is, the depth-averaged specific growth rate of species j depends on the weighted average of nutrient-limited growth in the upper part and light-limited growth in the lower part of the water column:

$$\bar{\mu}_j = \mu_{\max,j}\frac{1}{z_M}\left\{\int_0^{z_{co,j}} \min\left[f_{1j}(R_1), f_{2j}(R_2)\right]\,dz\right.$$

$$\left. + \int_{z_{co,j}}^{z_M} g_j(I(z))dz\right\}. \tag{13}$$

The two depth integrals in this equation can be solved with the help of equations (1), (4), and (9). This yields

$$\bar{\mu}_j = \mu_{\max,j}\min[f_{1j}(R_1), f_{2j}(R_2)]$$

$$\times \left[\frac{\ln(I_{in}) - \ln(I_{co,j})}{\ln(I_{in}) - \ln(I_{out})}\right] \tag{14}$$

$$+ \mu_{\max,j}\left[\frac{\ln(H_j + I_{co,j}) - \ln(H_j + I_{out})}{\ln(I_{in}) - \ln(I_{out})}\right],$$

where $I_{co,j}$ is given by equation (8) and I_{out} is the light intensity at the bottom of the light gradient.

The two regions of nutrient limitation are separated from the two regions of colimitation by nutrients and light
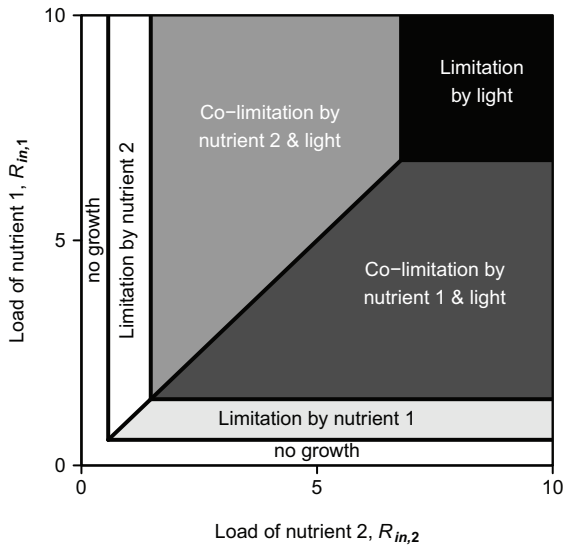
Figure 2: Resource limitation of a single species. In the "no growth" regions, nutrient availability is too low to support a phytoplankton population. At low nutrient loads, the growth rate is limited by either nutrient 1 or nutrient 2, depending on the ratio of the nutrient loads. At intermediate nutrient loads, growth is colimited either by nutrient 1 and light or by nutrient 2 and light, depending on the ratio of the nutrient loads. At high nutrient loads, growth is limited by light irrespective of the nutrient ratios. Parameter values are given in appendix C, available online.

by two boundary lines (fig. 2). Appendix A, available online, shows that these two boundary lines are given by

$$R_{\text{in},1} = R_{1j}^* + \frac{c_{1j}l_j}{k_jF}\left[\ln(I_{\text{in}}) - \ln\left(\frac{H_jR_{1j}^*}{M_{1j}}\right) - K_{\text{BG}}z_{\text{M}}\right], \quad (15a)$$

$$R_{\text{in},2} = R_{2j}^* + \frac{c_{2j}l_j}{k_jF}\left[\ln(I_{\text{in}}) - \ln\left(\frac{H_jR_{2j}^*}{M_{2j}}\right) - K_{\text{BG}}z_{\text{M}}\right]. \quad (15b)$$

Equation (15a) is independent of $R_{\text{in},2}$. Hence in figure 2, equation (15a) specifies the horizontal boundary line at the transition from limitation by nutrient 1 to colimitation by nutrient 1 and light. Likewise, equation (15b) specifies the vertical boundary line at the transition from limitation by nutrient 2 to colimitation by nutrient 2 and light. This implies that the transition from nutrient limitation to colimitation is not determined by nutrient ratios but by absolute nutrient loads (fig. 2). The diagonal boundary line separating the two colimitation regions indicates that the nutrient ratio does determine which of the two nutrients colimits growth.

Light limitation. At high nutrient loads, the specific growth rate is limited by light throughout the entire water column (i.e., $I_{\text{co},j} > I_{\text{in}}$). In this case, illustrated in figure 1C, the depth-averaged growth rate can be written as (Huisman and Weissing 1994):

$$\bar{\mu}_j = \mu_{\text{max},j}\frac{1}{z_{\text{M}}}\int_0^{z_{\text{M}}} g_j(I(z))dz$$
(16)
$$= \mu_{\text{max},j}\left[\frac{\ln(H_j + I_{\text{in}}) - \ln(H_j + I_{\text{out}})}{\ln(I_{\text{in}}) - \ln(I_{\text{out}})}\right].$$

It can be shown that, under light-limited conditions, the phytoplankton population will continue to increase until it has reduced the light intensity at the bottom of the water column to a critical light intensity $I_{\text{out},j}^*$ (Huisman and Weissing 1994, 1995). The critical light intensity has a similar interpretation as the critical nutrient concentrations R_{ij}^*. Different species have different critical light intensities, depending on their traits (Huisman et al. 1999). Contrary to R^*, the critical light intensity does not have an explicit analytical solution, but it can be solved numerically (i.e., by evaluating $\bar{\mu}_j - l_j = 0$ with the help of equation [16]).

The boundary lines separating the regions of colimitation by nutrients and light from the region of light limitation are given by (app. A):

$$R_{\text{in},1} = \frac{M_{1j}}{H_j}I_{\text{in}} + \frac{c_{1j}l_j}{k_jF}[\ln(I_{\text{in}}) - \ln(I_{\text{out},j}^*) - K_{\text{BG}}z_{\text{M}}], \quad (17a)$$

$$R_{\text{in},2} = \frac{M_{2j}}{H_j}I_{\text{in}} + \frac{c_{2j}l_j}{k_jF}[\ln(I_{\text{in}}) - \ln(I_{\text{out},j}^*) - K_{\text{BG}}z_{\text{M}}]. \quad (17b)$$

Equation (17a) specifies a horizontal boundary line, while equation (17b) specifies a vertical boundary line. Hence, the transition from colimitation to limitation by light is again determined by absolute nutrient loads (fig. 2).

In total, these results show that, at low to intermediate nutrient loads, the ratio of the nutrient loads determines which of the two nutrients will limit growth. However, the absolute nutrient loads determine the transition from nutrient limitation to colimitation by nutrients and light and also the transition from colimitation to light limitation. Furthermore, the boundary lines separating the different resource limitation regions also depend on species traits and on physical parameters affecting the underwater light field such as incident light intensity (I_{in}), background turbidity (K_{BG}) and mixing depth (z_{M}). More specifically, since the value of $I_{\text{out},j}^*$ decreases with I_{in} (Huisman and Weissing 1994), the nutrient thresholds specified by equations (15) and (17) increase with incident light intensity. This is illustrated in figure 3A–3C, which shows that the transitions from nutrient to colimitation and from colimitation to
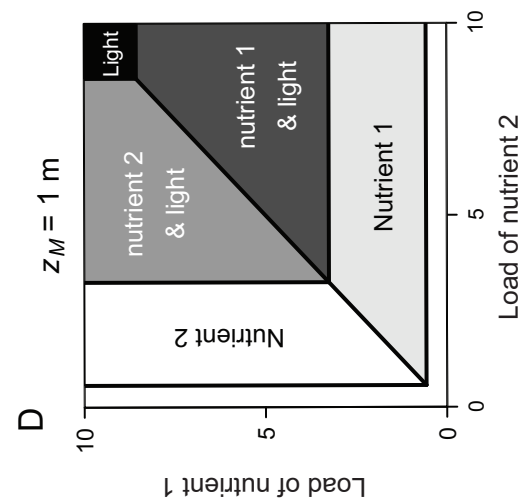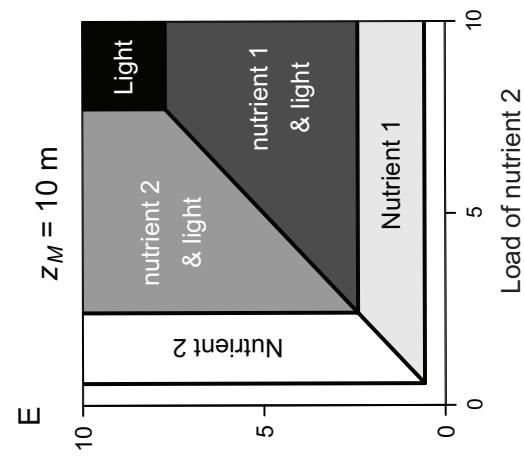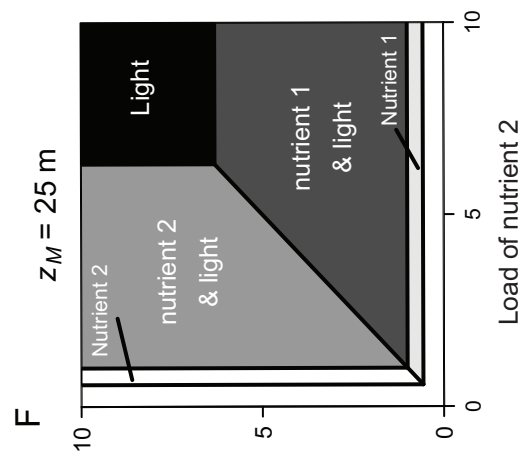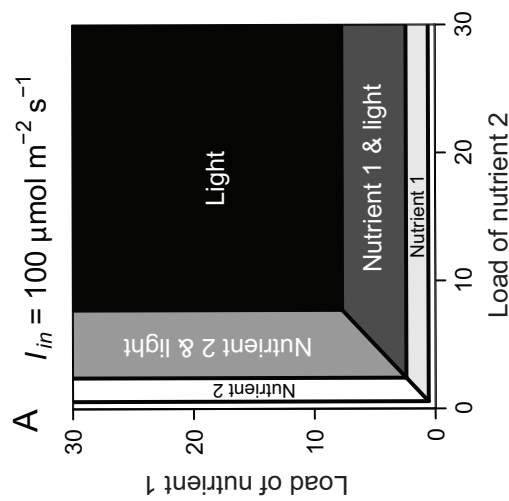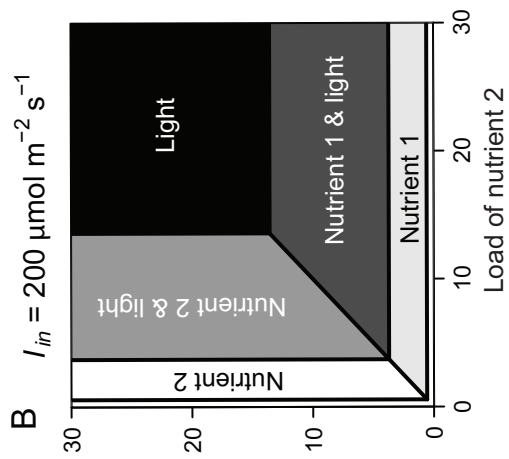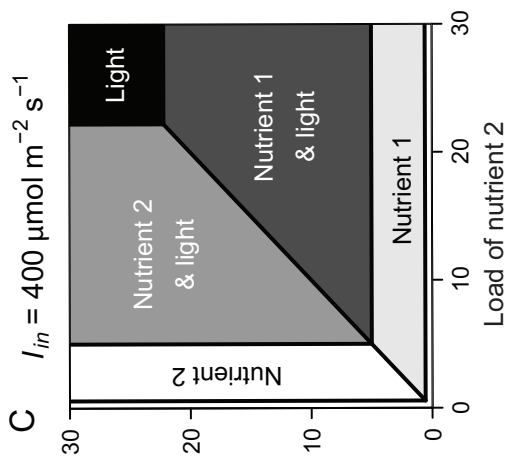
light limitation will occur at higher nutrient loads in ecosystems exposed to higher incident light intensities (e.g., tropical latitudes). Conversely, since $I_{\text{out},j}^*$ is independent of K_{BG} and z_{M} (Huisman and Weissing 1994), the nutrient thresholds specified by equations (15) and (17) decrease linearly with mixing depth and background turbidity. This is illustrated in figure 3D–3F, which shows that the transitions from nutrient to colimitation and from colimitation to light limitation occur at lower nutrient loads in deeply mixed waters than in shallow waters. Qualitatively similar results are obtained for changes in background turbidity. Accordingly, patterns of resource limitation show many similarities across ecosystems, yet quantitatively the values of the critical nutrient loads at which systems will shift from nutrient to light limitation will strongly depend on the local environmental setting.

Competition between Two Species

Resource competition among two species is well understood. If both species are limited by the same nutrient, the species with lowest R^* for that nutrient will be the superior competitor and will eventually exclude the other species (Armstrong and McGehee 1980; Tilman 1982). Likewise, under light limitation, the species with lowest I_{out}^* will be the superior competitor for light (Huisman and Weissing 1994; Huisman et al. 1999). When two resources are limiting, two species can coexist if each species is the superior competitor for another resource. The coexistence equilibrium is stable if each species consumes relatively more of that resource for which it is an inferior competitor (León and Tumpson 1975; Tilman 1982; Huisman and Weissing 1995). Conversely, the coexistence equilibrium is unstable, and the winner will depend on the initial conditions, if each species consumes relatively more of that resource for which it is a superior competitor.

For our model, the presence of a vertical light gradient complicates the mathematical analysis. Therefore, we first consider a simplified version of the model, in which the depth-averaged growth rate of equation (5) is replaced by

$$\bar{\mu}_j = \mu_{\text{max},j} \min\left[f_{1j}(R_1), f_{2j}(R_2), \frac{1}{z_{\text{M}}} \int_0^{z_{\text{M}}} g_j(I(z))dz \right]. \quad (18)$$

This equation differs from equation (5) in that the in-

tegral term is inside rather than outside the minimum function. Hence, the law of the minimum now acts at once over the entire depth rather than at each local depth separately. This assumption may particularly apply to terrestrial vegetation, where individual plants can integrate their photosynthetic activity over the entire depth of the canopy. The resource limitation pattern predicted by this simplified model resembles figure 2 but without colimitation of nutrients and light (fig. B1, available online). The simplified model has the advantage that the boundaries between different regions of competitive dominance can be derived analytically (see app. A). However, equation (5) is a more accurate description of local phytoplankton growth. Hence, we will return to the full model based on equation (5) at the end of this section, to compare the predictions of the simplified and full model.

We investigate three competition scenarios. The species parameters are chosen such that two-species coexistence is stable whenever it occurs (see app. C, available online, for parameter values). In the first scenario, species 1 is the superior competitor for nutrient 1 and light, and species 2 is the superior competitor for nutrient 2 (fig. 4A). In the intermediate region, the two species coexist because each species becomes limited by the resource for which it is an inferior competitor (fig. 4A). At low nutrient loads, the shape of this coexistence region resembles the classical cone form predicted by Tilman's (1982) resource-ratio hypothesis. Within this cone, species 1 is limited by nutrient 2, and species 2 is limited by nutrient 1. At high nutrient loads, the coexistence region extends vertically. Here, species 1 is still limited by nutrient 2, but species 2 has become limited by light. Hence, the change in orientation of the coexistence region occurs when the competitive interactions shift from competition for two nutrients to competition for nutrient 2 and light. Consequently, at low nutrient loads the outcome of competition depends on the ratio of the nutrient loads, but at high nutrient loads the outcome is determined by the absolute load of nutrient 2.

In the second scenario, species 1 is the superior competitor for nutrient 1, and species 2 is the superior competitor for nutrient 2 and light. The results resemble the first scenario. At high nutrient loads, however, the coexistence region now extends horizontally, where the two species compete for nutrient 1 and light (fig. 4B).

Figure 3: Resource limitation of a single species at different incident light intensities and mixing depths. *A–C,* With increasing incident light intensities, the transition from nutrient limitation to colimitation by nutrients and light and, also, the transition from colimitation to light limitation will occur at higher nutrient loads. *D–F,* With increasing mixing depths, the transition from nutrient limitation to colimitation and from colimitation to light limitation will occur at lower nutrient loads. Parameter values are given in appendix C, available online.

In the third scenario, species 1 is the superior competitor for both nutrients and species 2 is the superior competitor for light. In this case, the different regions are separated by L-shaped boundary lines that run parallel to the axes (fig. 4*C*). Species 1 wins at low nutrient loads, while species 2 wins at high nutrient loads. The two species coexist in the intermediate region, where they are colimited either by nutrient 1 and light or by nutrient 2 and light. Hence, in this scenario, the outcome of competition is never determined by the nutrient ratios. Instead, the species composition is determined by the absolute nutrient loads. The boundary lines in figure 4 are derived in appendix A.

Appendix B, available online, investigates the same competition scenarios, with the same parameter values as in figure 4 but now for the full model based on equation (5). Quantitatively, the predictions of the simplified and full model show several differences, but qualitatively their predictions are very similar (cf. figs. 4, B2). At low nutrient levels, the two species compete primarily for nutrients 1 and 2, and the outcome of competition is determined by the ratio of the nutrient loads. At high nutrient levels, the two species compete mainly for light, and the outcome of competition is determined by the absolute nutrient loads.

Competition between Three Species

This section investigates competition between three species for two nutrients and light. The number of theoretically possible scenarios is overwhelming. As Huisman and Weissing (2001) pointed out, three species can be ordered in six different ways according to their R^* values for a single resource. Hence, there are $6^3 = 216$ different ways to order the R^* values of three species for three resources. The stability of the coexistence equilibria depends on the resource consumption parameters of the species (i.e., the values of c_{1j}, c_{2j}, and k_j), and there are also 216 different ways to order the resource consumption parameters of three species for three resources. In case of three species competing for three resources one can thus distinguish $216 \times 216 = 46{,}656$ different model scenarios. Although some of these scenarios will be mathematically equivalent, it is clear that we cannot treat all possible scenarios here. Instead, we confine our analysis by the assumption that species 1 is the superior competitor for nutrient 1, species 2 is the superior competitor for nutrient 2, and species 3 is the superior competitor for light. We consider three cases with different configurations of the consumption parameters (fig. 5*A*–5*C*). With the help of the simplified model based on equation (18), the boundary lines can again be derived analytically (see app. A).

The results show that species 1 wins if all species are limited by nutrient 1, species 2 wins if all are limited by nutrient 2, and species 3 wins if all are limited by light

(fig. 5*A*–5*C*). Adjacent to these single-species regions are regions with either stable coexistence of two competitors (fig. 5*A*, 5*B*) or alternative stable states of two competitors (fig. 5*C*). In the center of each graph, where all three resources are limiting simultaneously, there is a stable or unstable three-species coexistence region (fig. 5*A*–5*C*). Huisman and Weissing (2001) demonstrated earlier that, in case of competition for three nutrients, the stability of the three-species coexistence equilibrium depends on the configuration of the consumption parameters. Our simulation results indicate that their "rules of thumb" also apply if three species compete for two nutrients and light. Coexistence of all three species is stable if each species consumes most of the resource for which it is the inferior competitor (fig. 5*A*). If each species consumes most of the resource for which it is the intermediate competitor, competition produces nontransitive interactions characterized by sustained species oscillations in the form of limit cycles (fig. 5*B*). This is an interesting case, because these nonequilibrium dynamics may enable the coexistence of many species on a few limiting resources (Huisman and Weissing 1999). If each species consumes most of the resource for which it is the best competitor, the species tend to monopolize the limiting resource, which leads to competitive exclusion where the winner depends on the initial conditions (fig. 5*C*).

Figure 6 investigates the same model scenarios, but now for the full model. In comparison to the simplified model, the boundaries separating the different dominance regions shift to other nutrient loads in the full model. Furthermore, several boundaries lines predicted by the full model are not linear but curved, reflecting the more gradual transition from nutrient to light limitation. Qualitatively, though, the predictions of the simplified and full model are again similar (cf. figs. 5, 6). Species 1 wins if all species compete only for nutrient 1, species 2 wins if they all compete for nutrient 2, species 3 wins if they all compete for light, competition for two resources leads to stable or unstable two-species coexistence, and there is a stable or unstable three-species coexistence region in the center.

Interestingly, however, we did not find limit cycles in the full model, at least not for the parameter values that generated limit cycles in the simplified model. Instead, the full model predicts stable coexistence of all three species (fig. 6*B*). A plausible explanation for this difference is that, in the simplified model, the growth rate of a species is limited by the same resource across the entire depth of the water column. Hence, nontransitive interactions between species play out over the entire depth of the water column. In contrast, in the full model, resource limitation is determined at each local depth. Accordingly, the species' growth rates will remain nutrient limited in the upper part and light limited in the lower part of the water column,

Competition for:

- ☐ R_2
- ☐ R_1
- ☐ R_1 & R_2
- ▨ R_2 & Light
- ▨ R_1 & Light
- ■ Light
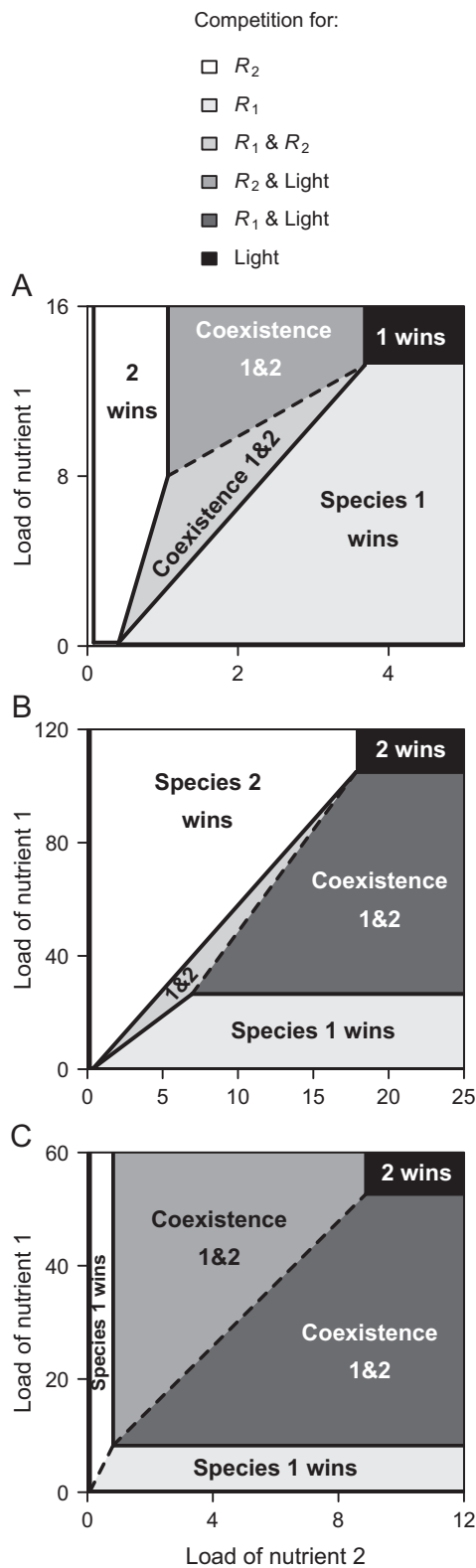
while their growth rates may fluctuate between nutrient and light limitation only at intermediate depth. Hence, any tendency for fluctuations in resource limitation generated by nontransitive interactions will be restricted to this narrow depth range only. We conjecture that this has a stabilizing effect on the population dynamics, suppressing the species oscillations in the full model.

Trait Combinations and Species Distributions

Natural communities often contain numerous species. This section therefore uses the full model to explore multispecies competition. Although the number of possible scenarios is daunting, some species traits may be physiologically or ecologically more plausible than others. Therefore, we confined our analysis to the following set of trait combinations:

Assumption 1. A three-way trade-off between competitive abilities for nitrogen, phosphorus, and light (see fig. C1, available online). In total, we consider 9 species. Species 1–5 are superior competitors for nutrients but inferior competitors for light, with species 1 the superior competitor for nitrogen (lowest R^* for nitrogen) and species 5 the superior competitor for phosphorus (lowest R^* for phosphorus). Species 6–8 are intermediate competitors for nutrients and light, with species 6 the better competitor for nitrogen and species 8 the better competitor for phosphorus. Species 9 is the superior competitor for light but an inferior competitor for both nutrients. The existence of a trade-off between competitive abilities for nitrogen and phosphorus is supported by the recent meta-analysis of Edwards et al. (2011), who showed that strong competitors for nitrogen are generally weak competitors for phosphorus, and vice versa. Less is known about trade-offs between competitive abilities for nutrients versus light (e.g., Passarge et al. 2006), although the existence of such trade-offs is suggested by the common observation that the species composition of phytoplankton communities changes along environmental gradients of nutrient and light availability (Sommer 1993; Reynolds 1997).

Assumption 2. Strong nutrient competitors (species with low R^* values) have low cellular contents of these nutrients

Figure 4: The outcome of competition between two species for two nutrients and light, predicted by the simplified model. *A,* Species 1 is the superior competitor for nutrient 1 and light, whereas species 2 is the superior competitor for nutrient 2. *B,* Species 1 is the superior competitor for nutrient 1, whereas species 2 is the superior competitor for nutrient 2 and light. *C,* Species 1 is the superior competitor for both nutrients, whereas species 2 is the superior competitor for light. Close to the *X*-axis and *Y*-axis, there is a region of "no growth" (as in fig. 2), but this region is often too narrow to be visible. Parameter values are given in appendix C, available online.
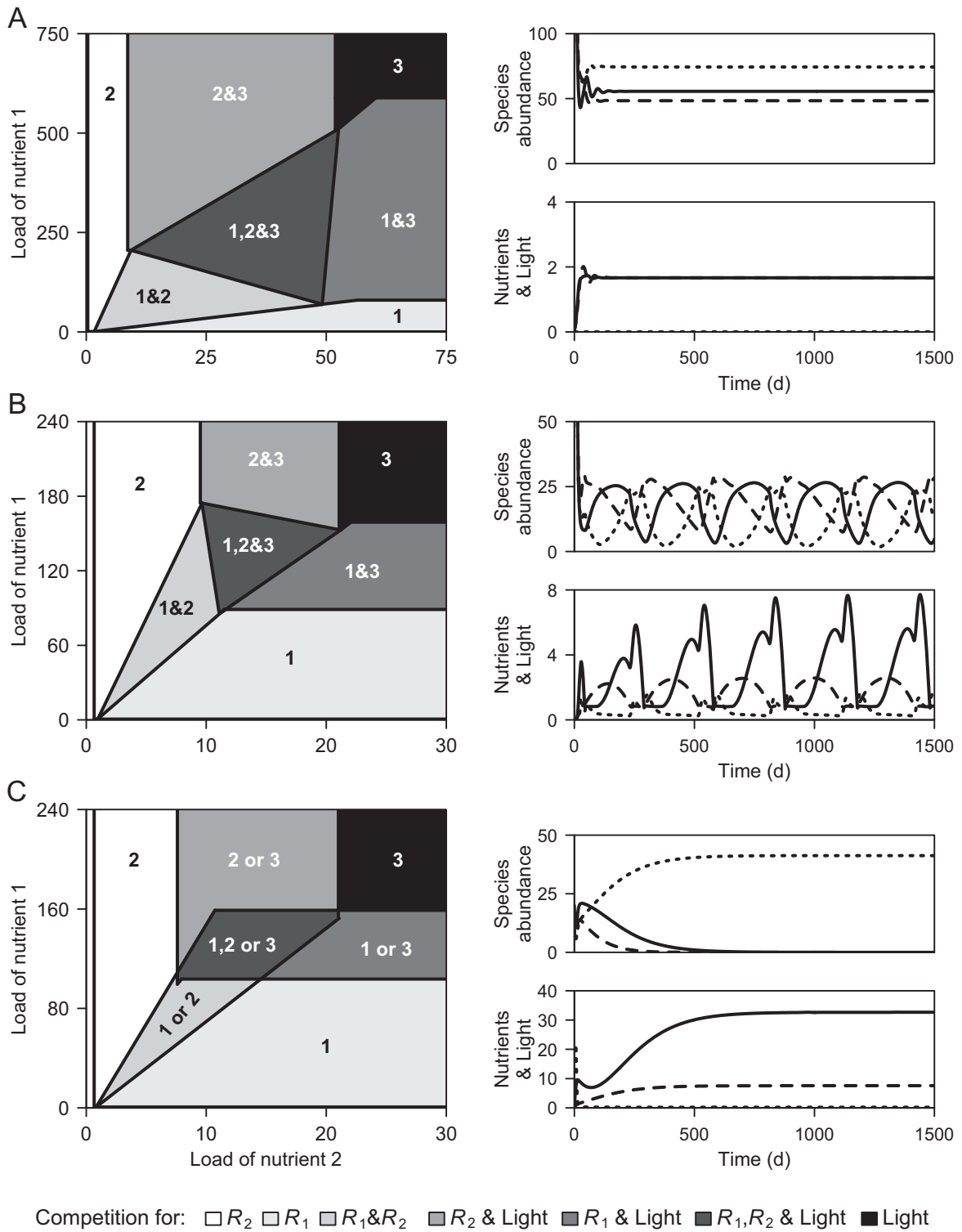
(low c_{ij}'s), reflecting the common observation that species of nutrient-poor habitats generally have higher nutrient use efficiencies than those of nutrient-rich habitats (e.g., Sterner et al. 1997). We incorporated this assumption through a positive correlation between the half-saturation constants for nutrient-limited growth and the cellular nutrient contents of the species, in line with empirical data reported by Litchman et al. (2007).

Assumption 3. Two different scenarios for the relationship between competitive ability for light and the light attenuation coefficients of species. The first scenario assumes that strong competitors for light (species with low I_{out}^*) have low light attenuation coefficients, while weak competitors for light have high light attenuation coefficients (figure C1*B*). Conversely, the second scenario assumes that strong competitors for light have high light attenuation coefficients, while weak competitors have low light attenuation coefficients (figure C1*C*).

The results show that the species composition predicted by this multispecies competition model is sensitive to changes in both nutrient ratios and nutrient loads (fig. 7). At low nutrient loads, species compete for nutrients and the species composition is largely determined by the N : P ratio. Species 1 and 2 are superior nitrogen competitors and win at low N : P ratio. Species 4 and 5 are superior phosphorus competitors and win at high N : P ratio. At high nutrient loads, community biomass increases and the competitive interactions are shifted toward competition for light. Here, species 9 is the superior light competitor and wins. At intermediate nutrient loads, multispecies competition generates a patchwork of different species combinations. The stability of the local coexistence equilibria within this patchwork depends on the two scenarios of assumption 3.

In the first scenario, strong competitors for light have low light attenuation coefficients, while weak competitors have high light attenuation coefficients. This trait combination has a stabilizing effect, generating a patchwork of stable two-species and three-species coexistence regions (fig. 7*A*).

In the second scenario, strong competitors for light have high light attenuation coefficients. This trait combination generates a patchwork of local alternative stable states in species composition (fig. 7*B*). In one state, the superior competitor for light creates low-light conditions that favor its own dominance and prevent invasion by strong nutrient competitors. In the alternative state, strong nutrient competitors deplete ambient nutrients to low levels, preventing invasion by the superior light competitor. In some regions, we even found three alternative stable states, where two intermediate competitors generated light conditions too low for invasion by stronger nutrient competitors, but nutrient conditions too low for invasion by stronger light competitors. Hence, the species composition in this scenario depends not only on the nutrient loads but is also sensitive to the initial species abundances.

Discussion

This article proposes the nutrient-load hypothesis to explain changes in species composition along productivity gradients. The nutrient-load hypothesis predicts that ratios of nutrient loads and absolute nutrient loads both have a major impact on the species composition of primary producers. Nutrient ratios are predicted to be a key determinant of the species composition in oligotrophic ecosystems, consistent with earlier resource competition theory (Tilman 1982; Grover 1997) and experiments (e.g., Tilman 1977; Sommer 1985; van Donk and Kilham 1990; Smith 1993). In contrast, absolute nutrient loads are predicted to be decisive for the outcome of competition in eutrophic ecosystems. High nutrient loads can produce high biomass, shifting the species interactions to competition for light. This favors the dominance of a superior light competitor that overshadows and excludes all other species. In mesotrophic ecosystems, communities can become colimited by two nutrients and light. This may enable stable coexistence of species but may also generate nonequilibrium coexistence or alternative stable states depending on the traits of the competing species. These results were obtained for two alternative formulations of the specific growth rate (eqq. [5], [18]). This indicates that, qualitatively, the nutrient-load hypothesis does not depend on highly specific model assumptions but reflects more general principles. Several insights suggested by our model results will be discussed below.

Figure 5: Competition between three species for two nutrients and light, predicted by the simplified model. Species 1 is the superior competitor for nutrient 1, species 2 for nutrient 2, and species 3 for light. Left panels show the winners of competition as function of the nutrient loads. Right panels show time series of species abundances and nutrient and light availability for the center region (region "1,2&3" in *A*, *B*; region "1,2 or 3" in *C*). Upper right panels show abundances of species 1 (solid line), species 2 (dashed line), and species 3 (dotted line). Lower right panels show concentrations of nutrient 1 (solid line), nutrient 2 (dashed line), and light penetration I_{out} (dotted line). The graphs consider three scenarios: *A*, Each species consumes most of the resource for which it is the inferior competitor; this produces stable coexistence. *B*, Each species consumes most of the resource for which it is the intermediate competitor; this produces limit cycles in the center region. *C*, Each species consumes most of the resource for which it is the superior competitor; this produces alternative stable states. Parameter values are given in appendix C, available online.
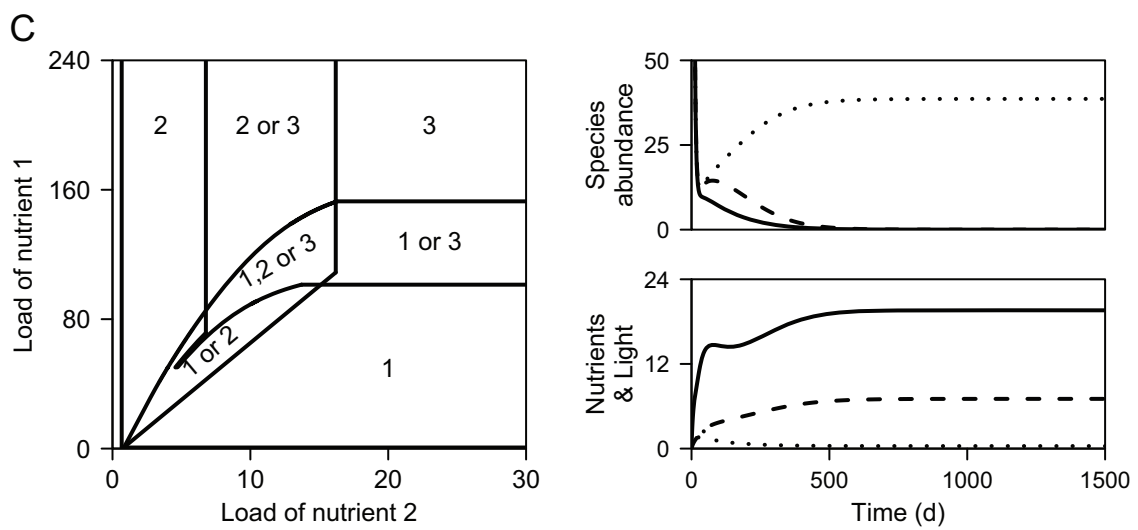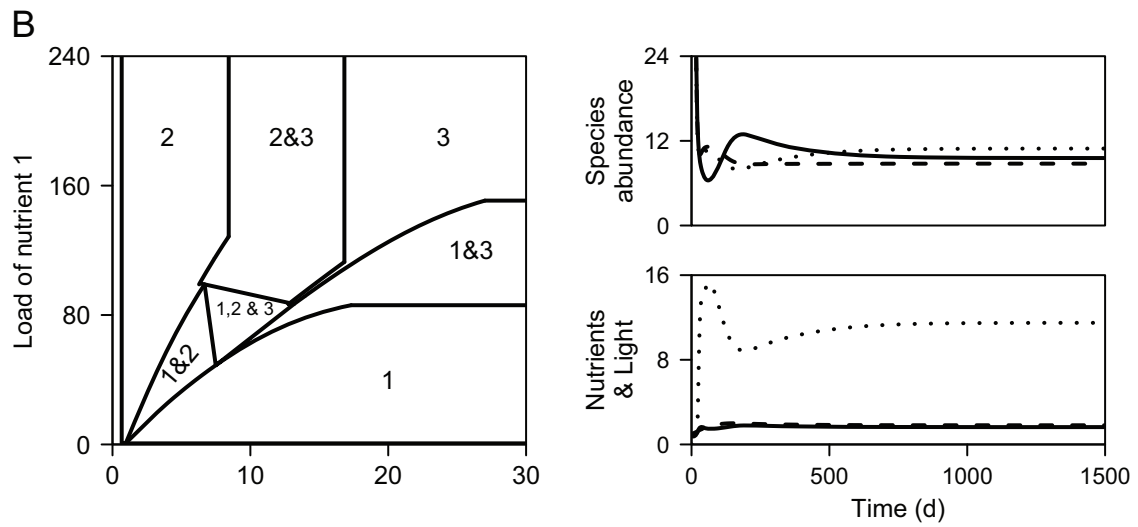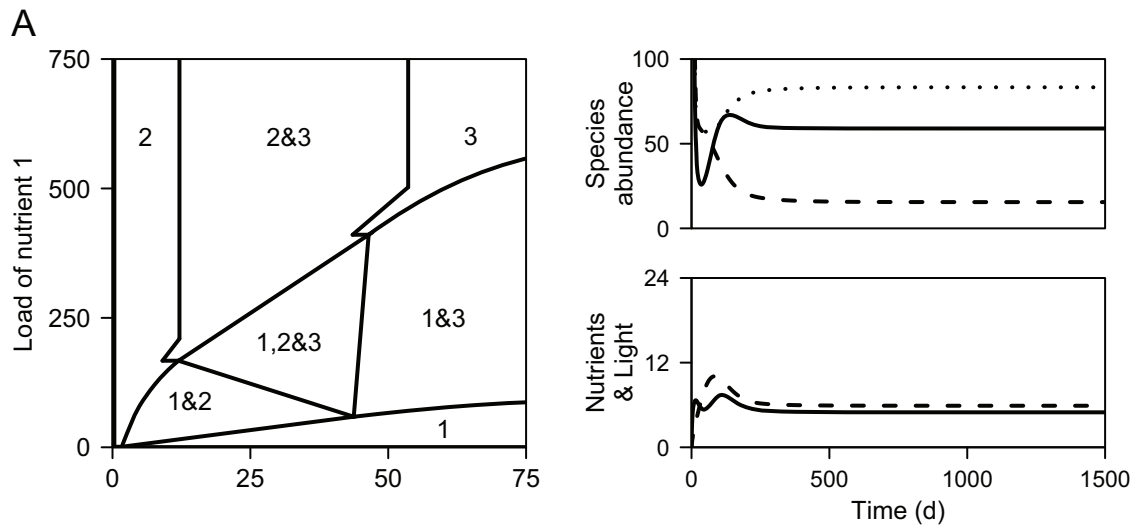
Nutrient Ratios versus Nutrient Loads

Our findings may help to reconcile the controversy over the role of nutrient ratios versus absolute nutrient levels in controlling the community composition of primary producers. For instance, several field studies have shown that the relative abundance of cyanobacteria in phytoplankton communities correlates well with the nitrogen-to-phosphorus ratio (Smith 1983; Smith and Bennett 1999; Havens et al. 2003; Nõges et al. 2008; Vrede et al. 2009), whereas other studies have shown that cyanobacterial dominance is more strongly associated with absolute nutrient concentrations (Trimbee and Prepas 1987; Canfield et al. 1989; Jensen et al. 1994; Reynolds 1998; Downing et al. 2001; McCarthy et al. 2009). To illustrate how our model predictions may explain these contrasting field observations, we consider a hypothetical scenario in which cyanobacteria compete against eukaryotic phytoplankton at different nitrogen and phosphorus supply concentrations. Our scenario assumes that eukaryotic phytoplankton are superior competitors for phosphorus (e.g., diatoms; Grover 1997), whereas cyanobacteria are superior competitors for nitrogen (Smith 1986; Tyrrell 1999) and for light (Mur et al. 1977; Schwaderer et al. 2011).

The outcome of competition between cyanobacteria and eukaryotic phytoplankton predicted from this hypothetical scenario is plotted in figure 8. The arrows indicate three gradients of nutrient enrichment. Interestingly, the replacement of eukaryotes by cyanobacteria is very similar along all three gradients (bottom panels in fig. 8). At low nutrient levels, enhanced phosphorus loads lead to an increase of the ambient P : N ratio, which shifts the species interactions from competition for phosphorus to competition for nitrogen. This favors the dominance of cyanobacteria at the expense of eukaryotic phytoplankton (gradient I). At high nutrient levels, the model also predicts that enhanced phosphorus loads lead to an increased P : N ratio, which again favors cyanobacteria over eukaryotic phytoplankton (gradient II). In this case, however, the correlation between the species composition and the P : N ratio is spurious, because the species interactions shift from competition for phosphorus to competition for light rather than to competition for nitrogen. The third gradient shows that cyanobacterial dominance also increases with combined nitrogen and phosphorus enrichment, even if the P : N ratio remains constant (gradient III). In this case, cyanobacteria become dominant again

because of their superior competitive ability for light. In total, our model thus predicts that cyanobacteria will be favored by low N : P ratios (high P : N ratios), and also by combined N + P enrichment (fig. 8). This offers a simple and straightforward solution for the long-standing controversy whether cyanobacterial dominance should be attributed to low N : P ratios or high nutrient loads (Smith 2003).

These predictions are supported by the few experimental studies that have investigated competition for two nutrients and light. Yang and Jin (2008) investigated competition between the non-nitrogen-fixing cyanobacterium *Microcystis aeruginosa*, a green alga and a diatom at different N : P : light levels. At low light levels, the cyanobacterium became dominant irrespective of the N : P ratio. At high light levels, the cyanobacterium coexisted with the green alga, and the relative abundances of the two species depended on the N : P ratio. De Tezanos Pinto and Litchman (2010) performed similar experiments with the nitrogen-fixing cyanobacterium *Anabaena flos-aquae* and several other species of cyanobacteria, green algae, diatoms, and cryptophytes. At low light levels, *Anabaena* became dominant irrespective of the N : P ratio. At high light levels, *Anabaena* dominated at low N : P ratios, while high N : P ratios resulted in a mixture of green algae. Hence, consistent with our model predictions, both studies found that nutrient ratios affected the species composition at high-light conditions but not at low-light conditions where light limitation controlled the competitive outcome.

Productivity and Diversity

Relations between productivity and biodiversity have been investigated in numerous theoretical and empirical studies. In this sense, our study builds on previous work, and integrates elements from several earlier theoretical studies (e.g., Tilman 1982; Huisman and Weissing 1995). Yet, our model study is the first to analyze competition for two nutrients and light in a systematic manner. It is therefore interesting to assess to what extent the model predictions can capture observed productivity-diversity relationships.

Figure 7 illustrates how different nutrient loads are predicted to affect the number of coexisting species. Dominance by one or two species is expected at low nutrient levels, where species compete for one or two nutrients but not for light. At intermediate nutrient loads, species com-

Figure 6: Competition between three species for two nutrients and light, predicted by the full model. Figure layout and parameter values are the same as in figure 5. The graphs consider three scenarios: *A*, Each species consumes most of the resource for which it is the inferior competitor; this produces stable coexistence. *B*, Each species consumes most of the resource for which it is the intermediate competitor; in the full model, this produces stable coexistence instead of limit cycles. *C*, Each species consumes most of the resource for which it is the superior competitor; this produces alternative stable states.
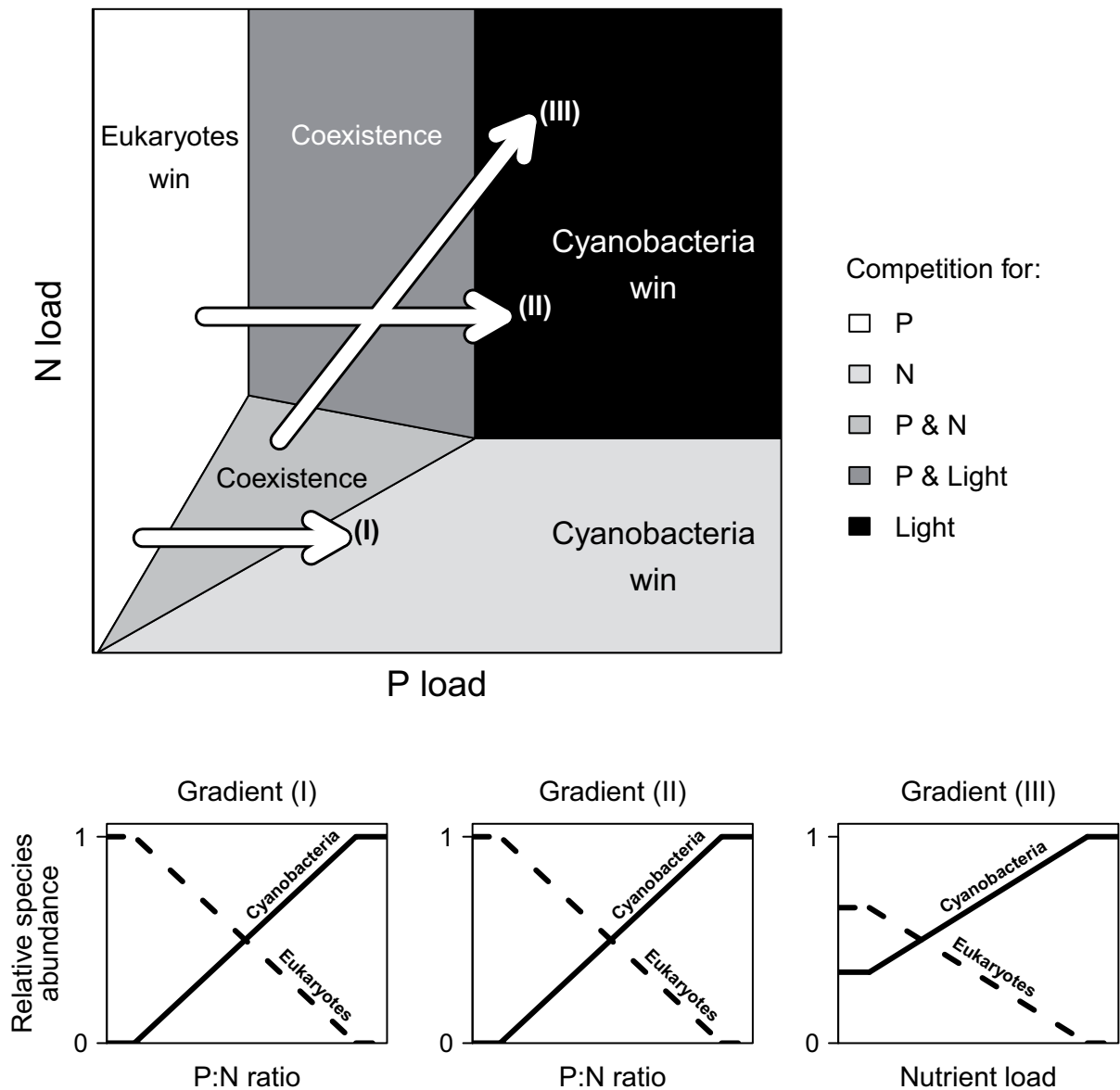
Figure 7: Competition between nine species for nitrogen, phosphorus, and light, predicted by the full model. The graphs show the winners of competition as function of the nitrogen and phosphorus loads for two different scenarios: *A*, Strong competitors for light have low light attenuation coefficients (see fig. C1*B*, available online). This produces a patchwork of local regions with stable coexistence of two or three species. *B*, Strong competitors for light have high light attenuation coefficients (see fig. C1*C*). This produces a patchwork of alternative stable states in species composition. Parameter values are given in appendix C, with a graphical illustration of the main traits of the species in figure C1.

pete for both nutrients and light, which can generate a patchwork of many local two-species and three-species coexistence areas (fig. 7*A*). In natural habitats, spatial heterogeneity or nonequilibrium conditions may span several of these local two-species and three-species areas, which will further enhance species diversity at larger spatial and temporal scales (cf. Tilman 1982). High nutrient loads lead to the lowest biodiversity, because the superior light competitor excludes all other species such that ultimately only a single species remains. Hence, in total, the model predicts that intermediate loads of both nutrients will favor high biodiversity, while high nutrient loads will strongly suppress biodiversity due to intense competition for light.

These model predictions are consistent with the unimodal productivity-diversity relationship observed for primary producers of many terrestrial, freshwater and marine ecosystems (Grime 1973; Tilman and Pacala 1993; Mittelbach et al. 2001; Irigoien et al. 2004; Stomp et al. 2011). They are also in line with field observations documenting a positive relation between the species diversity of primary producers and the number of limiting resources (Interlandi and Kilham 2001; Grover and Chrzanowski 2004; Harpole and Tilman 2007; Harpole and Suding 2011). Moreover, these model predictions may help to understand why eutrophication of ecosystems often leads to diversity loss and the dominance of only a few species (Grime 1973;

Carpenter et al. 1998; Hautier et al. 2009). The nutrient-load hypothesis may thus offer a simple conceptual framework to describe and understand how changes in productivity affect biodiversity.

Interestingly, however, our model results point out that intermediate nutrient loads do not necessarily yield high diversity. Instead of species coexistence, competition for two nutrients and light may also produce alternative stable states in species composition (figs. 5*C*, 6*C*). The latter occurs if strong competitors for light absorb more light per unit biomass than other species (as in fig. C1*C*), such that they can create the light-limited conditions that favor their own competitive dominance. Such a scenario seems physiologically quite plausible, since species with high light absorption per unit biomass will be able to cast substantial shade on other competitors while still capturing sufficient light energy themselves to survive under low-light conditions. Indeed, in laboratory experiments with five freshwater phytoplankton species, Passarge et al. (2006) found that the species with the highest light attenuation coefficients were the strongest competitors for light. In a multispecies context, this scenario produces a patchwork of alternative stable states, including regions with two and sometimes even three alternative stable states (fig. 7*B*). The presence of a patchwork of multiple alternative stable states implies that small differences in nutrient loads and initial

Figure 8: Competition between eukaryotic phytoplankton and cyanobacteria for nitrogen, phosphorus, and light. The graph assumes that eukaryotes are superior competitors for phosphorus, while cyanobacteria are superior competitors for nitrogen and light. The upper panel shows the outcome of competition as function of the nutrient loads; the arrows indicate environmental gradients. Gradient I: as the P load increases, the P : N ratio increases, and the species interaction shifts from competition for phosphorus to competition for nitrogen. Gradient II: as the P load increases, the P : N ratio again increases, but now the species interaction shifts from competition for phosphorus to competition for light. Gradient III: nitrogen and phosphorus loads both increase without changing the P : N ratio, shifting the species interaction from competition for nitrogen and phosphorus to competition for light. The three lower panels show the changes in species composition along these gradients (solid line, cyanobacteria; dashed line, eukaryotes).

species abundances will determine which species will ultimately gain the upper hand. This makes the species composition at intermediate nutrient loads rather unpredictable.

Suggestions for Future Work

Our model can be interpreted as a model of intermediate complexity. It adds further realism to classic resource com-

petition theory by incorporation of competition for light. Yet, the model still makes many simplifying assumptions. Our findings therefore suggest several avenues for further theoretical and experimental work.

One important simplification is the use of Von Liebig's (1840) law of the minimum. As a consequence, species shift abruptly from nutrient-limited to light-limited growth. We introduced this assumption because it facilitated the mathematical analysis. Yet, rates of photosynthesis are known to be sensitive to the nutrient status of organisms. Conversely, assimilation of nutrients into a wide range of cellular functions requires energy provided by photosynthesis. Hence, from a physiological perspective, it would be more realistic to assume interactive effects of light and nutrient availability on growth (Healey 1985; Evans 1989; Aguirre von Wobeser et al. 2011). This would result in a more gradual transition from nutrient to light limitation (Huisman and Weissing 1995). More detailed physiological models could certainly contribute to a better understanding of the interactions between competition for nutrients and competition for light.

Another important simplification is the assumption that species and nutrients are all homogeneously mixed. In a strict sense, this limits the applicability of our model to phytoplankton in turbulent waters, while incomplete mixing may lead to deviations from our model predictions. For instance, incomplete mixing may select for species that can exploit spatial variation in nutrient and light conditions (Huston and DeAngelis 1994; Huisman et al. 2006; Yoshiyama et al. 2009; Ryabov and Blasius 2011). Furthermore, species that overtop others will profit from enhanced light access while leaving competitors in their shade, which may foster founder control in terrestrial plant communities (Rees and Bergelson 1997; Perry et al. 2003). It will be interesting to investigate how such spatially extended growth strategies will affect the competitive interactions for nutrients and light.

Previous theory has shown that competition for three limiting resources can generate species oscillations induced by nontransitive interactions between the species (Huisman and Weissing 1999, 2001). These nonequilibrium dynamics may in turn favor high biodiversity (Huisman and Weissing 1999; Kerr et al. 2002; Laird and Schamp 2006). One might expect that competition for two nutrients and light would produce similar species oscillations. This was confirmed by the simplified model (fig. 5*B*), but surprisingly numerical simulations did not show species oscillations in the full model (fig. 6*B*). We conjecture that the vertical light gradient in combination with localized growth restricts nontransitive interactions to a narrow depth range, which has a stabilizing effect on the species dynamics. However, we have not explored this issue in

further detail, and more rigorous theoretical analysis may shed more light on this issue.

Testing predictions of resource competition models is laborious but relatively straightforward. Species can be grown in monoculture to measure their growth kinetics, and subsequently the competitive interactions between these species can be studied at a range of different nutrient and light conditions (Tilman 1977; Sommer 1985; Huisman et al. 1999; Passarge et al. 2006). Surprisingly, only a few experimental studies investigated the three-way interaction of competition for two nutrients and light (Yang and Jin 2008; De Tezanos Pinto and Litchman 2010). As discussed above, these studies confirmed that nutrient ratios affect the species composition at high-light conditions but not under light-limited conditions. However, these studies were not a priori designed to test the theory developed here, and more systematic tests of the theoretical predictions in controlled competition experiments would therefore certainly be warranted.

One aspect deserves particular attention. Theory predicts that competition for nutrients and light can produce either stable species coexistence (fig. 7*A*) or alternative stable states in species composition (fig. 7*B*), depending on the trait combinations of the competing species. Some empirical evidence indicates that strong competitors for light tend to have higher light attenuation coefficients (Passarge et al. 2006), which would favor alternative stable states. However, we still lack sufficient data to fully assess whether stable coexistence or alternative stable states will be more likely in natural communities. Moreover, in reality, the trait combinations might be fuzzier than the neat alignment of species traits assumed in our model simulations (fig. C1). In that case, the model predicts a complex mixture of the patterns in figure 7*A* and 7*B*, with some stable coexistence regions and other regions where alternative stable states prevail. These different scenarios have important implications for our general understanding of the productivity-diversity relationship and for the predictability of the species composition of natural communities. It will therefore be an important challenge for experimental studies to unravel which of these theoretically feasible scenarios are biologically most plausible.

Concluding Remarks

Human activities have modified nutrient availability in many aquatic and terrestrial ecosystems, for instance, through eutrophication, changes in land use, and climate change. The nutrient-load hypothesis offers a simple conceptual framework to interpret and communicate how such human-driven changes in nutrient availability may affect the biodiversity and species composition of aquatic and terrestrial plant communities. In particular, this hy-

pothesis incorporates the important role of nutrient ratios in oligotrophic environments, provides a mechanistic explanation for the high biodiversity commonly observed in mesotrophic environments and helps to explain why reduction of nutrient loads is essential to suppress superior light competitors and restore high biodiversity in ecosystems exposed to long-term eutrophication.

Acknowledgments

Literature Cited

Aerts, R., F. Berendse, H. de Caluwe, and M. Schmitz. 1990. Competition in heathland along an experimental gradient of nutrient availability. Oikos 57:310–318.

Agawin, N. S. R., S. Rabouille, M. J. W. Veldhuis, L. Servatius, S. Hol, H. M. J. van Overzee, and J. Huisman. 2007. Competition and facilitation between unicellular nitrogen-fixing cyanobacteria and non-nitrogen-fixing phytoplankton species. Limnology and Oceanography 52:2233–2248.

Aguirre von Wobeser, E., B. W. Ibelings, J. Bok, V. Krasikov, J. Huisman, and H. C. P. Matthijs. 2011. Concerted changes in gene expression and cell physiology of the cyanobacterium *Synechocystis* sp. strain PCC 6803 during transitions between nitrogen and light-limited growth. Plant Physiology 155:1445–1457.

Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist 115:151–170.

Berger, S. A., S. Diehl, T. J. Kunz, D. Albrecht, A. M. Oucible, and S. Ritzer. 2006. Light supply, plankton biomass, and seston stoichiometry in a gradient of lake mixing depths. Limnology and Oceanography 51:1898–1905.

Canfield, D. E., E. Phlips, and C. M. Duarte. 1989. Factors influencing the abundance of blue-green algae in Florida lakes. Canadian Journal of Fisheries and Aquatic Sciences 46:1232–1237.

Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications 8:559–568.

Ciros-Pérez, J., M. J. Carmona, and M. Serra. 2001. Resource competition between sympatric sibling rotifer species. Limnology and Oceanography 46:1511–1523.

De Tezanos Pinto, P., and E. Litchman. 2010. Interactive effects of N : P ratios and light on nitrogen-fixer abundance. Oikos 119:567–575.

Diehl, S., S. Berger, R. Ptacnik, and A. Wild. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. Ecology 83:399–411.

Donald, C. M. 1958. The interaction of competition for light and for nutrients. Australian Journal of Agricultural Research 9:421–435.

Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting cyanobacteria dominance in lakes. Canadian Journal of Fisheries and Aquatic Sciences 58:1905–1908.

Dybzinski, R., and D. Tilman. 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. American Naturalist 170:305–318.

Edwards, K. F., C. A. Klausmeier, and E. Litchman. 2011. Evidence for a three-way trade-off between nitrogen and phosphorus competitive abilities and cell size in phytoplankton. Ecology 92:2085–2095.

Evans, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. Oecologia (Berlin) 78:9–19.

Gerla, D. J., W. M. Wolf, and J. Huisman. 2011. Photoinhibition and the assembly of light-limited phytoplankton communities. Oikos 120:359–368.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

Grover, J. P. 1997. Resource competition. Chapman & Hall, London.

Grover, J. P., and T. H. Chrzanowski. 2004. Limiting resources, disturbance, and diversity in phytoplankton communities. Ecological Monographs 74:533–551.

Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. Nature 446:791–793.

Harpole, W. S., and K. N. Suding. 2011. A test of the niche dimension hypothesis in an arid annual grassland. Oecologia (Berlin) 166:197–205.

Hautier, Y., P. A. Niklaus, and A. Hector. 2009. Competition for light causes plant biodiversity loss after eutrophication. Science 324:636–638.

Havens, K. E., R. T. James, T. L. East, and V. H. Smith. 2003. N : P ratios, light limitation, and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution. Environmental Pollution 122:379–390.

Healey, F. P. 1985. Interacting effects of light and nutrient limitation on the growth rate of *Synechococcus linearis* (Cyanophyceae). Journal of Phycology 21:134–146.

Huisman, J., and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. Ecology 75:507–520.

———. 1995. Competition for nutrients and light in a mixed water column: a theoretical analysis. American Naturalist 146:536–564.

———. 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402:407–410.

———. 2001. Biological conditions for oscillations and chaos generated by multispecies competition. Ecology 82:2682–2695.

Huisman, J., R. R. Jonker, C. Zonneveld, and F. J. Weissing. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology 80:211–222.

Huisman, J., J. Sharples, J. M. Stroom, P. M. Visser, W. E. A. Kardinaal, J. M. H. Verspagen, and B. Sommeijer. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85:2960–2970.

Huisman, J., N. N. Pham Thi, D. M. Karl, and B. Sommeijer. 2006. Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. Nature 439:322–325.

Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. American Naturalist 144:954–977.

Inouye, R. S., N. J. Huntley, D. Tilman, J. Tester, M. Stillwell, and K. Zinnel. 1987. Old-field succession on a Minnesota sand plain. Ecology 68:12–26.

Interlandi, S. J., and S. S. Kilham. 2001. Limiting resources and the regulation of diversity in phytoplankton communities. Ecology 82: 1270–1282.

Irigoien, X., J. Huisman, and R. P. Harris. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. Nature 429: 863–867.

Jäger, C. G., S. Diehl, and G. M. Schmidt. 2008. Influence of water-column depth and mixing on phytoplankton biomass, community composition, and nutrients. Limnology and Oceanography 53: 2361–2373.

Jensen, J. P., E. Jeppesen, K. Olrik, and P. Kristensen. 1994. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. Canadian Journal of Fisheries and Aquatic Sciences 51:1692–1699.

Jöhnk, K. D., J. Huisman, J. Sharples, B. Sommeijer, P. M. Visser, and J. M. Stroom. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. Global Change Biology 14:495–512.

Kerr, B., M. A. Riley, M. W. Feldman, and B. J. M. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature 418:171–174.

Laird, R. A., and B. S. Schamp. 2006. Competitive intransitivity promotes species coexistence. American Naturalist 168:182–193.

León, J. A., and D. B. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. Journal of Theoretical Biology 50:185–201.

Litchman, E., and C. A. Klausmeier. 2001. Competition of phytoplankton under fluctuating light. American Naturalist 157:170–187.

Litchman, E., C. A. Klausmeier, and P. Bossard. 2004. Phytoplankton nutrient competition under dynamic light regimes. Limnology and Oceanography 49:1457–1462.

Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. Ecology Letters 10:1170–1181.

McCarthy, M. J., R. T. James, Y. Chen, T. L. East, and W. S. Gardner. 2009. Nutrient ratios and phytoplankton community structure in the large, shallow, eutrophic, subtropical Lakes Okeechobee (Florida, USA) and Taihu (China). Limnology 10:215–227.

Miller, T. E., J. H. Burns, P. Munguia, E. L. Walters, J. M. Kneitel, P. M. Richards, N. Mouquet, and H. L. Buckley. 2005. A critical review of twenty years' use of the resource-ratio theory. American Naturalist 165:439–448.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381–2396.

Monod, J. 1950. La technique de culture continue, théorie et applications. Annales de l'Institut Pasteur (Paris) 79:390–410.

Mur, L. R., H. J. Gons, and L. van Liere. 1977. Some experiments on competition between green algae and blue-green bacteria in light-limited environments. FEMS Microbiology Letters 1:335–338.

Nõges, T., R. Laugaste, P. Nõges, and I. Tõnno. 2008. Critical N : P ratio for cyanobacteria and N_2-fixing species in the large shallow temperate lakes Peipsi and Võrtsjärv, north-east Europe. Hydrobiologia 599:77–86.

Olff, H., J. Huisman, and B. F. van Tooren. 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. Journal of Ecology 81:693–706.

Passarge, J., S. Hol, M. Escher, and J. Huisman. 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? Ecological Monographs 76:57–72.

Perry, L. G., C. Neuhauser, and S. M. Galatowitsch. 2003. Founder control and coexistence in a simple model of asymmetric competition for light. Journal of Theoretical Biology 222:425–436.

Ptacnik, R., S. Diehl, and S. Berger. 2003. Performance of sinking and nonsinking phytoplankton taxa in a gradient of mixing depths. Limnology and Oceanography 48:1903–1912.

Rees, M., and J. Bergelson. 1997. Asymmetric light competition and founder control in plant communities. Journal of Theoretical Biology 184:353–358.

Reynolds, C. S. 1997. Vegetation processes in the pelagic: a model for ecosystem theory. Ecology Institute, Oldendorf.

———. 1998. What factors influence the species composition of phytoplankton in lakes of different trophic status? Hydrobiologia 369/370:11–26.

Rothhaupt, K. O. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature 333: 660–662.

Ryabov, A. B., and B. Blasius. 2011. A graphical theory of competition on spatial resource gradients. Ecology Letters 14:220–228.

Ryabov, A. B., L. Rudolf, and B. Blasius. 2010. Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer. Journal of Theoretical Biology 263:120–133.

Schwaderer, A. S., K. Yoshiyama, P. de Tezanos Pinto, N. G. Swenson, C. A. Klausmeier, and E. Litchman. 2011. Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton. Limnology and Oceanography 56:589–598.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221:669–670.

———. 1986. Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. Canadian Journal of Fisheries and Aquatic Sciences 43:148–153.

———. 1993. Applicability of resource-ratio theory to microbial ecology. Limnology and Oceanography 38:239–249.

———. 2003. Eutrophication of freshwater and coastal marine ecosystems: a global problem. Environmental Science and Pollution Research 10:126–139.

Smith, V. H., and S. J. Bennett. 1999. Nitrogen : phosphorus supply ratios and phytoplankton community structure in lakes. Archiv für Hydrobiologie 146:37–53.

Sommer, U. 1985. Comparison between steady-state and non-steady state competition: experiments with natural phytoplankton. Limnology and Oceanography 30:335–346.

———. 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnology and Oceanography 34:1162–1173.

———. 1993. Phytoplankton competition in Plußsee: a field test of the resource-ratio hypothesis. Limnology and Oceanography 38: 838–845.

Sterner, R. W., J. J. Elser, E. J. Fee, S. J. Guildford, and T. H. Chrzanowski. 1997. The light : nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. American Naturalist 150:663–684.

Stevens, C. J., N. B. Dise, J. O. Mountford, and D. J. Gowing. 2004.

Impact of nitrogen deposition on the species richness of grasslands. Science 303:1876–1879.

Stomp, M., J. Huisman, F. de Jongh, A. J. Veraart, D. Gerla, M. Rijkeboer, B. W. Ibelings, U. I. A. Wollenzien, and L. J. Stal. 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. Nature 432:104–107.

Stomp, M., J. Huisman, L. Vörös, F. R. Pick, M. Laamanen, T. Haverkamp, and L. J. Stal. 2007. Colourful coexistence of red and green picocyanobacteria in lakes and seas. Ecology Letters 10:290–298.

Stomp, M., J. Huisman, G. G. Mittelbach, E. Litchman, and C. A. Klausmeier. 2011. Large-scale biodiversity patterns in freshwater phytoplankton. Ecology 92:2096–2107.

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

Taylor, P. A., and P. J. LeB. Williams. 1975. Theoretical studies on the coexistence of competing species under continuous-flow conditions. Canadian Journal of Microbiology 21:90–98.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338–348.

———. 1980. Resources: a graphical-mechanistic approach to competition and predation. American Naturalist 116:362–393.

———. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

———. 1985. The resource-ratio hypothesis of plant succession. American Naturalist 125:827–852.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Trimbee, A. M., and E. E. Prepas. 1987. Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta Lakes. Canadian Journal of Fisheries and Aquatic Sciences 44:1337–1342.

Tyrrell, T. 1999. The relative influences of nitrogen and phosphorus on oceanic primary production. Nature 400:525–531.

Van de Waal, D. B., J. M. H. Verspagen, J. F. Finke, V. Vournazou, A. K. Immers, W. E. A. Kardinaal, L. Tonk, et al. 2011. Reversal in competitive dominance of a toxic versus non-toxic cyanobacterium in response to rising CO_2. ISME Journal 5:1438–1450.

Van Donk, E., and S. S. Kilham. 1990. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. Journal of Phycology 26:40–50.

Vojtech, E., L. A. Turnbull, and A. Hector. 2007. Differences in light interception in grass monocultures predict short-term competitive outcomes under productive conditions. PLoS ONE 2:e449.

Von Liebig, J. 1840. Die organische Chemie in ihrer Anwendung auf Agrikultur und Physiologie. Friedrich Vieweg, Braunschweig.

Vrede, T., A. Ballantyne, C. Mille-Lindblom, G. Algesten, C. Gudasz, S. Lindahl, and A. K. Brunberg. 2009. Effects of N : P loading ratios on phytoplankton community composition, primary production and N fixation in a eutrophic lake. Freshwater Biology 54:331–344.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecology & Evolution 5:360–364.

Yang, S., and X. Jin. 2008. Critical light intensities for *Microcystis aeruginosa*, *Scenedesmus quadricauda* and *Cyclotella* sp. and competitive growth patterns under different light : N : P ratios. Journal of Freshwater Ecology 23:387–396.

Yoshiyama, K., J. P. Mellard, E. Litchman, and C. A. Klausmeier. 2009. Phytoplankton competition for nutrients and light in a stratified water column. American Naturalist 174:190–203.

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High nutrient loads favor mass development of the cyanobacterium *Microcystis aeruginosa* in Lake Volkerak, The Netherlands. Photograph courtesy of the Province of Zeeland, holder of copyright.