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Competition for Light and Nutrients in Layered Communities of Aquatic Plants

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ABSTRACT: Dominance of free-floating plants poses a threat to biodiversity in many freshwater ecosystems. Here we propose a theoretical framework to understand this dominance, by modeling the competition for light and nutrients in a layered community of floating and submerged plants. The model shows that at high supply of light and nutrients, floating plants always dominate due to their primacy for light, even when submerged plants have lower minimal resource requirements. The model also shows that floating-plant dominance cannot be an alternative stable state in light-limited environments but only in nutrient-limited environments, depending on the plants' resource consumption traits. Compared to unlayered communities, the asymmetry in competition for light—coincident with symmetry in competition for nutrients—leads to fundamentally different results: competition outcomes can no longer be predicted from species traits such as minimal resource requirements (R^* rule) and resource consumption. Also, the same two species can, depending on the environment, coexist or be alternative stable states. When applied to two common plant species in temperate regions, both the model and field data suggest that floating-plant dominance is unlikely to be an alternative stable state.

Keywords: resource competition, macrophytes, coexistence, competitive exclusion, alternative stable states, theoretical model.

Introduction

Dense mats of free-floating plants are a threat to the biodiversity and ecological functioning of aquatic ecosystems, ranging from tropical lakes (Brendonck et al. 2003) to temperate ditches and ponds (Janse and van Puijenbroek 1998). Underneath these mats, the water often becomes too dark for submerged plants to photosynthesize (Morris et al. 2004) and too low in dissolved oxygen for macro-

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fauna and fish to survive (Portielje and Roijackers 1995). It is therefore crucial to know what drives the occurrence of these dense mats of floating plants and whether they are a self-enhancing (alternative) stable state, as suggested by Scheffer et al. (2003).

The in-water nutrient availability is of vital importance for the development of free-floating plants and is affected by submerged plants (Madsen and Cedergreen 2002). Therefore, the occurrence of free-floating plants can be understood by studying their competition with submerged plants for light and nutrients. Although there have been empirical studies on the competition between floating and submerged plants using laboratory experiments (Janes et al. 1996; Szabo et al. 2010), mesocosm experiments (Feuchtmayr et al. 2009; Netten et al. 2010; Lu et al. 2013; Smith 2014), and field experiments (Portielje and Roijackers 1995; Forchhammer 1999), the theoretical understanding of the competition between floating and submerged plants for light and nutrients is still limited.

Most mechanistic theory on competition for light and nutrients is developed for phytoplankton. For example, I_{out}^*-R^* theory describes the competition of phytoplankton species for light and nutrients in a mixed water column (Huisman and Weissing 1995). It is an extension of R^* theory, which describes competition of species for nutrients (Tilman 1982). An elegant feature of I_{out}^*-R^* theory (as well as R^* theory) is that one can predict the competition outcome from species traits, such as minimal resource requirements (R^* rule) and resource consumption. Yet this framework considers the competition between species that have the same position in the water column, while floating and submerged plants have different positions. The (vertical) position of a species matters when considering light, because light forms a gradient with depth due to light attenuation by biomass and background extinction (Kirk 1994). In a ver-

tically layered community, the competition for light, therefore, becomes asymmetric: the upper species (the floating plant) has the primacy for light and shades the lower species (the submerged plant) and thus has a competitive advantage. The competition for nutrients, on the other hand, is not asymmetric, as both floating and submerged plants compete for nutrients in the same medium (water column).

Mechanistic resource competition theory has been extended to include asymmetrical competition. Yet none of the available theoretical frameworks are suited to describe the competition between floating and submerged plants. Weissing and Huisman (1994), Huisman et al. (1999), and Perry et al. (2003) considered asymmetrical competition for light but did not take competition for nutrients into account. In cases where nutrients were explicitly modeled, either the mechanism underlying the layeredness differed or the competition was not only asymmetric for light but also for nutrients (double asymmetry).

For example, in pelagic phytoplankton communities, the layeredness emerges from limited vertical mixing of the water column (Yoshiyama et al. 2009; Ryabov and Blasius 2011; Ryabov 2012) and from extra movement of phytoplankton related to sinking or buoyancy regulation (Huisman et al. 2006; Ryabov et al. 2010), with vertical nutrient gradients as a result. For floating and submerged plants, however, the layeredness does not emerge—as they do not wander through the water column—but is directly imposed by their growth form. The model of Jäger and Diehl (2014) gives an example of double asymmetry: not only do the upper species (pelagic algae) have a primacy for light (similar to floating plants) but the lower species (benthic algae) have a primacy for nutrients, supplied from below, whereas floating and submerged plants directly compete for the same nutrients. Interestingly, these more complex examples of asymmetrical competition show that the competition outcome cannot simply be predicted anymore from species traits alone.

The only model that does describe the competition between floating and submerged plants is the model of Scheffer et al. (2003). However, this model is not fully mechanistic—for example, it does not have a closed nutrient and light balance—and is not embedded in classical resource competition theory. This motivated us to develop a model that does comply with these aspects.

Here we present a mechanistic model that describes the competition for light and nutrients in a layered community of floating and submerged plants. We hypothesize that the floating plant, due to its primacy for light, can outcompete the submerged plant, even when the submerged plant has lower resource requirements than the floating plant. This implies that the most parsimonious form of asymmetry in competition—asymmetry in competition for light but symmetry in competition for nutrients in a homogeneous nutrient environment—is sufficient to indicate that the competition outcome cannot be predicted anymore from species traits alone and, hence, that environmental conditions codetermine the competition outcome.

To test this and to better understand when floating plants dominate, we analyzed our model and its competition outcome for a wide range of species traits and environmental conditions, focusing on the requirements for single-species dominance, coexistence, or alternative stable states. Furthermore, we analyzed the competition outcome for floating and submerged plant species that are common in temperate regions and discuss the likelihood of floating-plant dominance as an alternative stable state.

Methods

Competition Model

Our model describes competition for light and nutrients in a layered community of floating plants (F) and submerged plants (S) in a vertical water column (fig. 1; table 1). The model extends I_{out}^*-R^* theory (Huisman and Weissing 1995), which describes the symmetric competition for nutrients and light among species with the same position, for species with a different fixed vertical position, resulting in asymmetrical competition for light. It consists of three differential equations, describing the dynamics of floating and submerged plant biomass (in g DW [dry weight] m^{-2}) and nutrients (in g N [nitrogen] m^{-3}). The plant biomass dynamics depend on the balance between loss rate m and growth rate p:

$$\frac{dF}{dt} = (p_F - m_F)F, \tag{1}$$

$$\frac{dS}{dt} = (p_S - m_S)S. \tag{2}$$

The growth rate $p(I, R)$ is colimited by nutrient concentration R and light intensity I:

$$p_i = f_{R,i}f_{I,i}p_{\max,i}, \tag{3}$$

where i stands for S or F, $p_{\max}$ is the maximum growth rate, $f_R(R)$ is the nutrient limitation factor, and $f_I(I)$ is the light limitation factor. Nutrient limitation is characterized by a Michaelis-Menten function with half-saturation constant M:

$$f_{R,i} = \frac{R}{R + M_i}. \tag{4}$$

Light limitation is also characterized by a Michaelis-Menten function, with half-saturation constant H. Since light forms a gradient with plant biomass and therefore varies with depth (Kirk 1994), the average light limitation
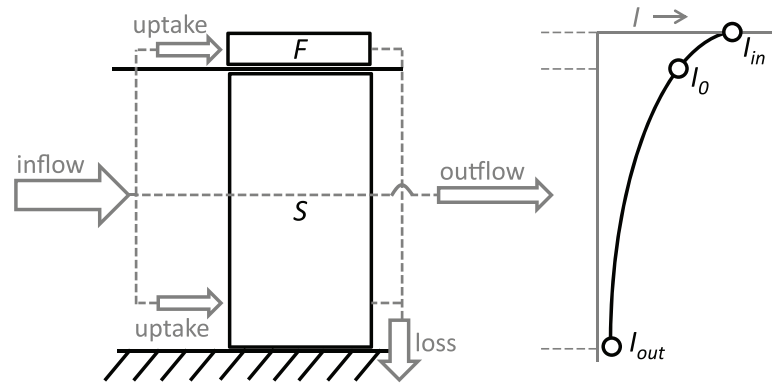
Figure 1: Competition model of floating plant F and submerged plant S in a vertical water column with nutrient fluxes (*left*) and light intensity (*right*).

is obtained by integrating over the depth covered by the plant, here expressed in terms of I, the light intensity at depth:

$$f_{I,F} = \frac{1}{k_F F} \int_{I_0}^{I_{in}} \frac{1}{H_F + I} dI = \frac{1}{k_F F} \ln\left(\frac{H_F + I_{in}}{H_F + I_0}\right), \tag{5}$$

$$f_{I,S} = \frac{1}{k_S S + K_{bg} z_B} \int_{I_{out}}^{I_0} \frac{1}{H_S + I} dI = \frac{1}{k_S S + K_{bg} z_B} \ln\left(\frac{H_S + I_0}{H_S + I_{out}}\right), \tag{6}$$

where in solving the integral, the plant biomass is assumed to be uniformly distributed with depth. For details on the derivation of the light limitation factor, see Huisman and Weissing (1994). Here I_{in} is the incoming light intensity, I_0 is the light intensity below the floating plants and above the submerged plants, and I_{out} is the light intensity below the submerged plants (fig. 1). I_0 and I_{out} depend on the light attenuation by plant biomass, according to Lambert-Beer's law:

$$I_0 = I_{in} e^{-k_F F}, \tag{7}$$

$$I_{out} = I_0 e^{-(k_S S + K_{bg} z_B)}, \tag{8}$$

where k is the light attenuation coefficient of the plant. Here I_{out} also depends on the background light attenuation K_{bg} of the water and the water column depth z_B.

The nutrient concentration R in the water column is assumed to be homogeneous over depth, which is a reasonable assumption for shallow waters. Nutrient dynamics depend on the nutrient consumption by the plants and on the input and output of nutrients related to water flow q:

$$\frac{dR}{dt} = \frac{q}{z_B}(R_{in} - R) - \frac{1}{z_B}(c_F p_F F + c_S p_S S) = \frac{r_{in}}{z_B} - DR$$
$$- \frac{1}{z_B}(c_F p_F F + c_S p_S), \tag{9}$$

where r_{in} is the nutrient loading, which can be converted to a nutrient concentration R_{in} of the inflowing water ($R_{in} = r_{in}/q$), D is the dilution rate of the water column ($D = q/z_B$), and the nutrient consumption by water plants equals the biomass growth multiplied by c, the nutrient content per unit of biomass. Division by z_B gives the nutrient consumption per unit volume.

Minimal Resource Requirements and Resource Consumption of the Plants

In general resource competition theory, such as R^* theory (Tilman 1980, 1982) and I_{out}^*-R^* theory (Huisman and Weissing 1995), the species' minimal resource requirements and resource consumption are important traits to predict the competition outcome. The minimal resource requirements are the lowest level of light and nutrients at which the plant can persist. The resource consumption is related to the consumption vector, which represents the proportion of resources consumed when the species is at equilibrium (Tilman 1980). We derived these traits from the model equations (see app. A; apps. A and B are available online) to analyze their importance when the competition is asymmetric for light.

Model Analysis

To test how asymmetry in light competition determines the competition outcome between submerged and floating plant species, we analyzed our model for a wide range of species traits and environmental conditions. We assumed nitrogen (N) to be the limiting nutrient. However, we could also have chosen phosphorus (P), because P limitation seems to be equally widespread for primary producers in freshwater ecosystems (Elser et al. 2007). We have checked by model simulations (not shown here) that the choice for N

Table 1: Model symbols and their definition

Type, symbol	Description	Unit	Default value (for F and S)	Common plants (*Lemna* sp., *Elodea* sp.)[a]
State variables:				
F	Floating plant biomass	g DW m^{-2}	...	...
S	Submerged plant biomass	g DW m^{-2}	...	...
R	Nutrient concentration in water column	g N m^{-3}	...	...
Light functions:				
I	Light intensity at depth	J m^{-2} s^{-1}	...	...
$I_0(F)$	Light intensity at top of water column	J m^{-2} s^{-1}	...	...
$I_{out}(S, F)$	Light intensity at bottom of water column	J m^{-2} s^{-1}	...	...
Plant species parameters and functions:				
$p_i(I, R)$	Growth rate of plant i	day^{-1}	...	...
$f_{R,i}(R)$	Nutrient limitation factor of growth	...	...	...
$f_{I,i}(I)$	Light limitation factor of growth	...	...	...
$p_{max,i}$	Maximum growth rate	day^{-1}	.3	.4, .32
m_i	Loss rate	day^{-1}	.05	.05, .029
k_i	Light attenuation coefficient	m^2 g DW^{-1}	.03	.03, .03
H_i	Half-saturation constant for light	J m^{-2} s^{-1}	30	32, 32
M_i (nitrogen)	Half-saturation constant for nutrient	g N m^{-3}	.5	2.5, .5
M_i (phosphorus)	Half-saturation constant for nutrient	g P m^{-3}	...	.25, .05
c_i (nitrogen)	Nutrient to dry weight ratio	g N g DW^{-1}	.03	.07, .0225
c_i (phosphorus)	Nutrient to dry weight ratio	g P g DW^{-1}	...	.015, .00215
Environmental parameters:				
r_{in}	Nutrient loading	g N m^{-2} day^{-1}	0–.5	...
I_{in}	Incoming light intensity	J m^{-2} s^{-1}	0–1,000	...
z_B	Water column depth	m	.1–1	...
D	Dilution rate of water column	day^{-1}	.01–.5	...
K_{bg}	Background light attenuation	m^{-1}	0–5	...

Note: DW = dry weight.

[a] From Janse 1998.

or P as a limiting nutrient does not affect the competition outcome qualitatively.

We performed the model analysis in several steps. We started our analysis by evaluating the competition outcome when both plants have equal traits (fig. 2A) by using the same default parameter values for each plant (table 1). These values were in the middle of ranges reported in the literature for common floating and submerged plants (Janse 1998, 2005; Scheffer et al. 2003). We plotted the competition outcome in the r_{in}–I_{in} plane, that is, for various combinations of light supply I_{in} and nutrient loading r_{in}, mimicking a wide range of environmental conditions.

Second, we analyzed the effect of different minimal resource requirements of the plants on the competition outcome in the r_{in}–I_{in} plane. This was done by varying the half-saturation constants for nutrient limitation (M) and light limitation (H; see eqq. [A1] and [A2] in app. A), such that the submerged plant has lower minimal requirements

for light (fig. 2B), nutrients (fig. 2C), or light and nutrients (fig. 2D). As it is often assumed that submerged plants have lower minimal resource requirements than floating plants, we continued our study focusing on this configuration. We aimed at obtaining a more thorough understanding of the competition outcome of this configuration by analyzing the equilibrium biomass of both plants along a gradient of light supply and nutrient loading (fig. 3). We zoomed in on these gradients that captured the most complex and interesting model outcomes.

Next, we were interested in the effect of the plant's resource consumption traits on the competition outcome in the r_{in}–I_{in} plane (fig. 4). Therefore, we varied the plant's ratio of light attenuation k to nutrient content c, as this ratio controls the resource consumption (see eqq. [A6] and [A7] in app. A). Also, we analyzed how the competition outcome depends on environmental conditions other than light and nutrient supply, such as water column depth z_B, dilution rate
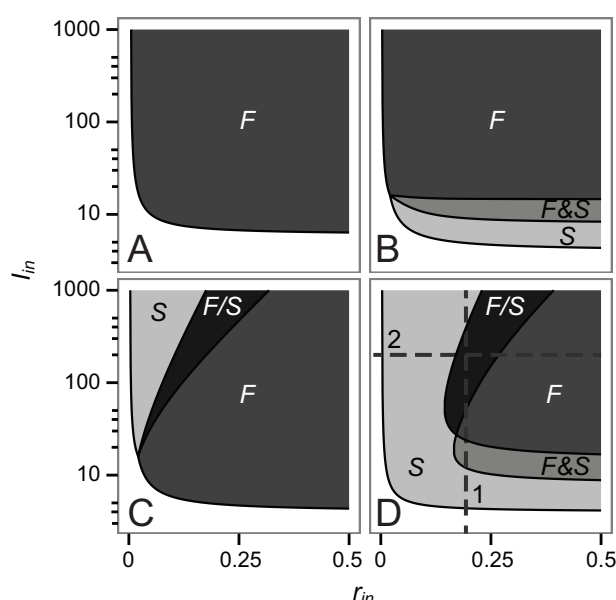
Figure 2: Outcome of the competition of floating plant *F* and submerged plant *S* for combinations of light supply I_{in} (W m^{-2}) and nutrient loading r_{in} (g N m^{-2} day^{-1}). F = regions where the floating plant persists, S = regions where the submerged plant persists, $F\&S$ = the plants coexist, F/S = the plants are alternative stable states. Note that at a low resource supply, both plants cannot persist. In *A*, the plants have equal traits, whereas in *B–D*, they have different resource requirements. The submerged plant has the lowest nutrient requirements in *C* and *D* and has the lowest light requirements in *B* and *D*. *D*, The dashed lines 1 and 2 are transects used for the bifurcation analysis in figure 3. Environmental parameters: $K_{bg} = 0$, $z_B = 0.5$, $D = 0.1$. The plant parameters equal the default values given in table 1, except for *M* and *H*, which determine the minimal resource requirements: A, $M_F = M_S = 0.5$, $H_F = H_S = 30$; B, $M_F = 0.3$, $M_S = 0.7$, $H_F = 40$, $H_S = 20$; C, $M_F = 0.7$, $M_S = 0.3$, $H_F = 20$, $H_S = 40$; D, $M_F = 0.7$, $M_S = 0.3$, $H_F = 40$, $H_S = 20$.

D, and water background light attenuation K_{bg} (fig. 5), by varying them within the ranges reported in table 1.

We concluded our analyses by evaluating the competition outcome for two floating and submerged plant species that are common in temperate regions, *Lemna* sp. (duckweed) and *Elodea* sp. (waterweed), respectively (fig. 6). We did this for both N and P as a limiting nutrient. We retrieved the parameter values (table 1) from the established ecosystem model PCDitch (Janse 1998), which simulates the competition between water plants with different growth forms. PCDitch provides a coherent set of vegetation parameters, derived from the literature and calibrated on experimental Dutch ditches. For *Lemna* sp., the light parameters *H* and *k* are not defined in PCDitch, because its light limitation is incorporated differently in PCDitch compared to our model. We assumed the half-saturation constant for light limitation *H* to be the same for *Lemna* sp. and *Elodea* sp. The light attenuation coefficient *k* for both plants was

chosen within realistic ranges (Krause-Jensen and Sand-Jensen 1998), such that the maximum plant biomasses are realistic. Furthermore, for the nutrient content *c* of the plants, we used the average of the minimum and maximum content provided by PCDitch.

Analysis Methods

We solved for the competition outcome numerically, since we did not find any simple expressions for the plants' equilibrium densities. We used the software packages AUTO (Doedel and Oldeman 2009) and R (R Core Team 2013) for numerical analyses and to determine the stability of the equilibria and the position of bifurcations in the r_{in}–I_{in} plane.

Supplementary to bifurcation analysis, we performed numerical invasion analysis to determine the competition outcome by calculating whether a species (the invader) can invade an equilibrium density of another species (the resident; Chesson 2000). In a two-species community such as ours, the species stably coexist when each species can invade (+) an equilibrium density of the other (++), and the species are alternative stable states when neither can invade (−) an equilibrium density of the other (− −), while (+ −) or (− +) leads to competitive exclusion of the species that cannot invade (e.g., Gerla et al. 2011). In the case of alternative stable states, the species that establishes first outcompetes the other.

Results

The Importance of Species Traits

When both plants have equal traits, the floating plant outcompetes the submerged plant for all combinations of light supply and nutrient loading (fig. 2*A*), provided that the resource supply is high enough for the plants to persist. This illustrates the asymmetry in light competition in layered communities and the resulting competitive advantage of the floating plant: it has the primacy for light, shades the submerged plant, and does not compete for light with the submerged plant.

The submerged plant can only outcompete the floating plant when it has lower minimal resource requirements for light (fig. 2*B*), nutrients (fig. 2*C*), or light and nutrients (fig. 2*D*), provided that the supply of the resource for which it has the lowest requirements is low enough. At a higher resource supply level, a submerged plant with lower resource requirements coexists or shows alternative states with—or is even outcompeted by—the floating plant. At a high enough supply of light and nutrients, the floating plant always outcompetes the submerged plant. For further analysis, we used the configuration where the sub-
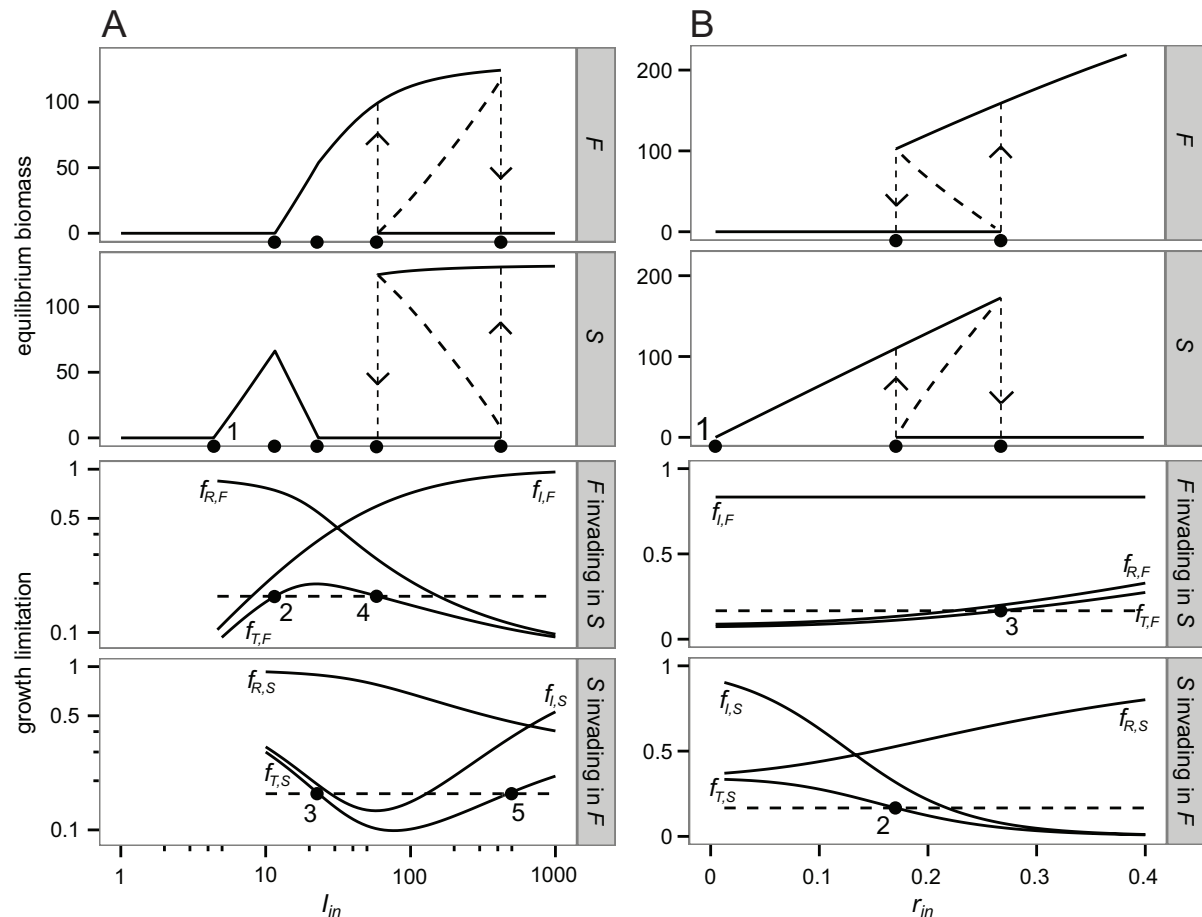
Figure 3: Effect of light supply I_{in} (W m^{-2}; *A*) and nutrient loading r_{in} (g N m^{-2} day^{-1}; *B*) on equilibrium biomass (g DW [dry weight] m^{-2}) of floating plant *F* and submerged plant *S* (upper panels) and on the growth limitation of the plant when invading an equilibrium density of the other (lower panels). Catastrophic shifts are indicated with arrows, and the dashed lines (upper panels) give the unstable coexistence equilibrium. The circles denote transcritical bifurcations. Bifurcations 2–5 are the invasion boundaries where the total growth limitation f_T of the invader ($f_T = f_R f_I$) equals the growth limitation level at which the invader can persist (dashed line). Note that the growth limitation is maximum at $f_T = 0$ and is absent at $f_T = 1$. The parameter values are the same as in figure 2*D*, with $r_{in} = 0.2$ in *A* (see transect 1 in fig. 2*D*) and $I_{in} = 200$ in *B* (see transect 2 in fig. 2*D*).

merged plant has the lowest requirements for both light and nutrients (fig. 2*D*) as a starting point, as this configuration is assumed to be the most common and gives the richest competition outcome.

To better understand the competition outcome, we analyzed the equilibrium biomass of both plants along a gradient of light supply (transect 1 in fig. 2*D*; results plotted in fig. 3*A*). The submerged plant can persist at a lower light supply (bifurcation 1), since it has the lowest light requirements. When the light supply is increased, there is enough light for the floating plant to persist (bifurcation 2), and the plants coexist until the floating plant reaches a critical biomass and intercepts too much light for the submerged plant to persist (bifurcation 3). With a further increasing light supply, nutrient limitation takes precedence

over light limitation. From bifurcation 4 onward, they are alternative states, since both plants cannot invade the equilibrium density of the other: the submerged plant reduces the nutrient concentration to levels too low for the floating plant to invade, and the floating plant intercepts too much light for the submerged plant to invade. At an even higher light supply level (above that of bifurcation 5), only the submerged plant persists because the floating plant no longer intercepts enough light to prevent the submerged plant from invading.

In a similar manner, we analyzed the competition outcome by regarding the equilibrium biomass along a gradient of nutrient loading (transect 2 in fig. 2*D*; results plotted in fig. 3*B*). The submerged plant persists at a lower nutrient loading (bifurcation 1), as it has the lowest nutri-
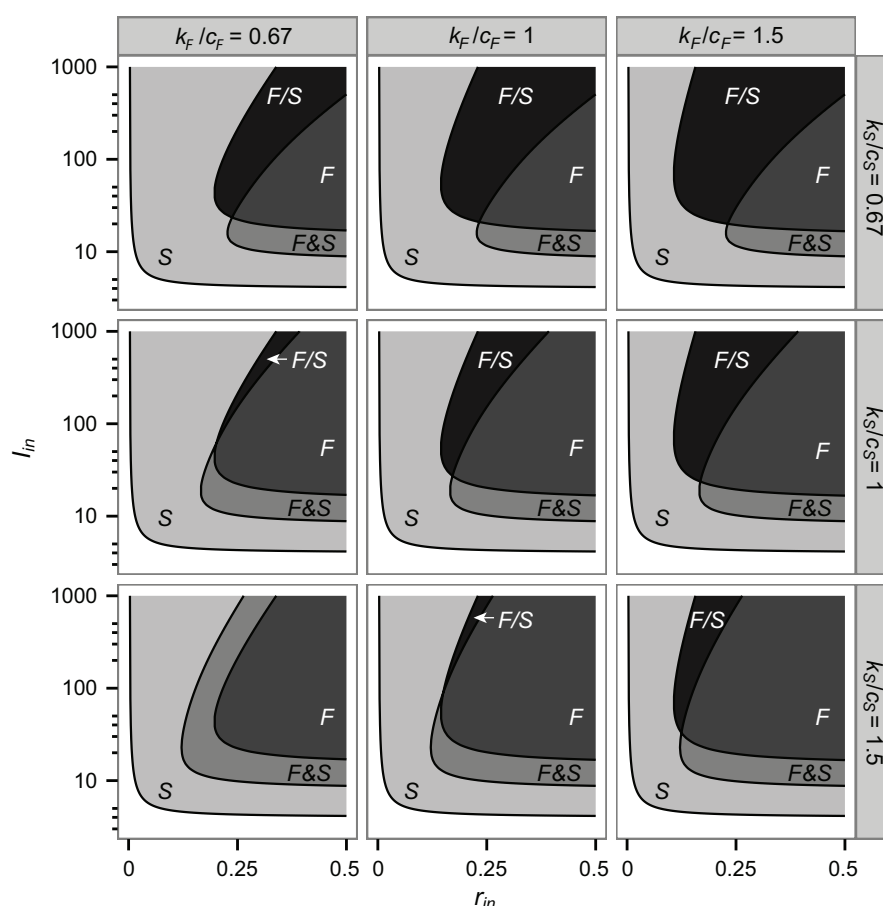
Figure 4: Outcome of the competition of floating plant *F* and submerged plant *S* when the plants have different resource consumption traits, resulting from different ratios of light attenuation coefficient *k* over nutrient to dry weight ratio *c*. Except for *k* and *c*, the parameter values are the same as in figure 2*D* (which equals the center graph).

ent requirements. With increasing nutrient loading (up to bifurcation 2), even if the floating plant is able to persist when alone, it is outcompeted by the submerged plant. From bifurcation 2 onward, they are alternative states since both plants cannot invade the equilibrium density of the other: the floating plant intercepts too much light for the submerged plant to invade, and the submerged plant keeps the nutrient concentration too low for the floating plant to invade. At a higher nutrient supply (from bifurcation 3 onward), only the floating plant persists, as the submerged plant cannot keep the nutrient concentration low enough to prevent the floating plant from invading.

When changing the resource consumption traits of both plants—by changing the ratio of light attenuation coefficient *k* over nutrient content *c*—the competition outcome is affected mainly in nutrient-limited environments (fig. 4). These are environments where nutrients are more limiting than light due to a low supply of nutrients relative to light. In these environments, the plants coexist or are alterna-

tive states depending on the consumption traits, where the chance of having alternative states increases when k_F/c_F relative to k_S/c_S increases. In light-limited environments, on the other hand, the competition outcome is hardly affected: the plants outcompete each other or coexist and do not show alternative states, irrespective of the consumption traits. Note that the competition outcome does not depend on the absolute values of *k* and *c*, as long as their ratio *k/c* is constant, because then the consumption vector does not change (see eqq. [A6] and [A7] in app. A). However, the absolute value of *k* does affect the equilibrium biomass: a higher value for *k* leads to a lower biomass due to more self-shading.

The Importance of Background Attenuation, Dilution Rate, and Water Depth

Varying the depth, dilution rate, and background attenuation of the water illustrates how the environment con-
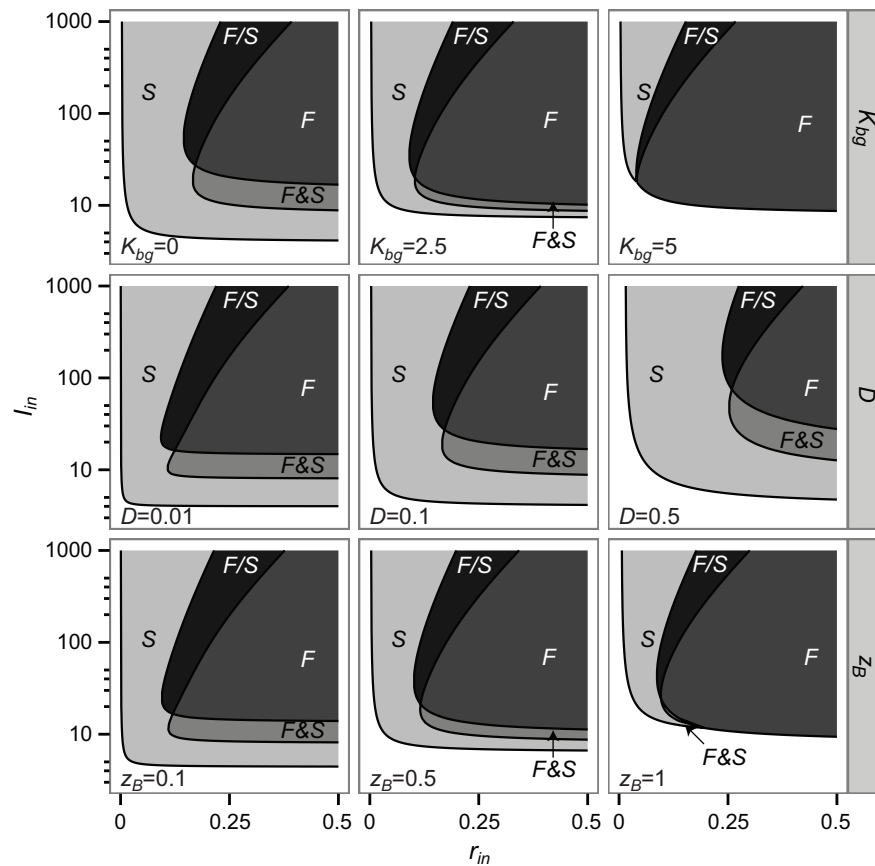
Figure 5: Outcome of the competition of floating plant F and submerged plant S for different background light attenuation K_{bg} (upper panels), dilution rate D (middle panels), and water column depth z_B (lower panels). The parameter values are the same as in figure 2D, except for the lower panels, where the background attenuation is nonzero ($K_{bg} = 2$), such that the water column depth influences the average light availability for the submerged plant.

trols the extent to which species can benefit from their specific position and traits. For example, a higher background light attenuation of the water reduces the competitive success of the submerged plant (fig. 5, upper panels), as the resulting lower light availability in the water column affects the submerged plant only. High background attenuation can even lead to the disappearance of submerged plants in light-limited environments, as the light availability in the water column becomes too low for the plants to persist.

An increased dilution rate enhances the competitive success of the plant with the lowest nutrient requirements (fig. 5, middle panels), which in our case is the submerged plant. This is because a higher dilution rate implies more water flow (see eq. [9]) and, thus, a lower nutrient concentration in the inflow for a given nutrient loading r_{in}. This lower concentration also implies that both plants need more light to persist.

An increase of the water depth simultaneously lowers the average light availability in the water column, which is detrimental to the submerged plant, and lowers the nutrient availability, as the nutrient loading has to be divided over a larger depth, which, in our case, is most detrimental to the floating plant. With the current model settings, the floating plant suffers less from deeper water (fig. 5, lower panels), as the adverse effect on the submerged plant takes precedence over the adverse effect on floating plants.

Competition Outcome for Common Macrophytes

When parameterizing the model for floating and submerged plant species common in temperate regions (*Lemna* sp. duckweed and *Elodea* sp. waterweed) for N or P as a limiting nutrient, the model predicts that waterweed outcompetes duckweed at a low resource supply, duckweed and waterweed coexist at an intermediate resource supply, and
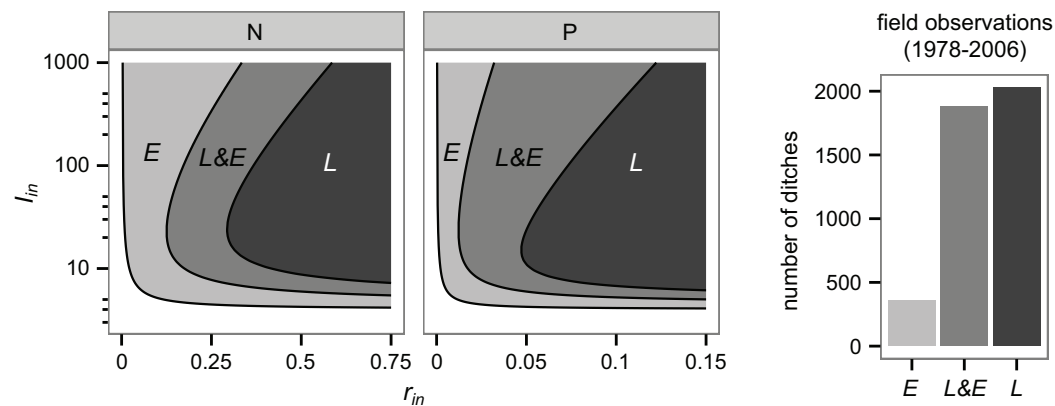
Figure 6: Outcome of the competition (left panels) of duckweed *L* (*Lemna* sp.) and waterweed *E* (*Elodea* sp.) for nitrogen (*left*, nutrient loading r_{in} is in g N m^{-2} day^{-1}) and phosphorus (*right*, r_{in} is in g P m^{-2} day^{-1}) as a limiting nutrient. The right panel shows the number of ditches in the Netherlands where duckweed and waterweed were observed in absence of each other or in coexistence. For plant parameter values in the left panels, see table 1. Environmental parameters in left panels: $K_{bg} = 0.5$, $z_B = 0.5$, $D = 0.1$.

duckweed outcompetes waterweed at a high resource supply (fig. 6, left panels). Thus, for these species, their asymmetrical competition for light does not lead to alternative stable states. We found this pattern to be robust as it is nearly insensitive (not shown here) to the chosen background attenuation and the chosen nutrient content of the plants, where in figure 6, we used the average of their reported minimal and maximal content. The found pattern is in line with an extensive data set on observed vegetation in Dutch ditches from 1978 to 2006, where in almost half of the ditches in which duckweed or waterweed were observed, they were found to coexist (fig. 6, right panel). This combination of model results and field data suggests that duckweed dominance is unlikely to be an alternative stable state.

Discussion

In many places around the world, floating-plant dominance is considered to be a true nuisance. Understanding when floating plants dominate, and particularly knowing whether their dominance can be a (self-enhancing) alternative stable state, is therefore a relevant issue for ecosystem management. Our model shows that the dominance of floating plants cannot be an alternative stable state in light-limited environments: when light limitation is reduced by an increase of light, the submerged plant—which can cope with the lowest light levels—starts to coexist with and is eventually "outshaded" by the floating plant. The fact that the plants coexist and do not show alternative stable states can be explained by the requirement for stable coexistence from classical competition theory, namely, that intraspecific competition must be greater than interspe-

cific competition (Williamson 1957). In other words, a species can coexist with another species when it suffers more from itself than from the other. In our model, the floating plant does not compete for light with the submerged plant, and therefore, in light-limited environments, the floating plant always suffers more from itself by self-shading (intraspecific competition) than from the other (interspecific competition), which leads to stable coexistence.

In nutrient-limited environments, the model predicts that with increasing nutrient levels, submerged plants are outcompeted by floating plants. This pattern was also found in field studies and mesocosm studies (Portielje and Roijackers 1995; Janes et al. 1996; Forchhammer 1999; Netten et al. 2010). At intermediate nutrient levels, floating and submerged plants can either coexist or are alternative stable states, depending on their resource consumption. The chance of alternative stable states increases when the submerged plant consumes more nutrients compared to the floating plant (the smaller k_S/c_S compared to k_F/c_F), thus, the more the floating plant suffers from the submerged plant than from itself. The semimechanistic model of Scheffer et al. (2003) gives comparable results: alternative stable states occur only as long as the submerged plant consumes more nutrients (per unit biomass) than the floating plant. Their model predicts no alternative stable states when the plants consume equal amounts of nutrients, which is not per se the case in our model. We found that for equal consumption traits ($k_S/c_S = k_F/c_F$), the plants can still be alternative stable states (fig. 2) or coexist (not shown here), depending on plant traits other than resource consumption.

Interestingly, for increasing supply of nutrients and light, the model predicts that the floating plant due to

its primacy for light can coexist with—or eventually out-compete—the submerged plant, even when the submerged plant has the lowest resource requirements. This is not possible in unlayered communities, as described in I_{out}^*-R^* theory (Huisman and Weissing 1995), where the species with the lowest minimal resource requirements always outcompetes the other (R^* rule). Another difference is that consumption traits that lead to coexistence in unlayered communities, namely, such that each species consumes more of the resource that most limits its growth, may in our layered community lead to alternative stable states, and vice versa (see fig. 4, where $k_F/c_F < k_S/c_S$ may lead to alternative stable states and $k_F/c_F > k_S/c_S$ may lead to coexistence). Related to this, the layeredness of species leads to a richer competition outcome in the sense that the same two species can, depending on the environmental conditions, coexist or be alternative stable states, whereas in unlayered communities, the same two species either coexist or be alternative stable states.

Thus, compared to unlayered communities as described in I_{out}^*-R^* theory, the layeredness—and associated asymmetry in competition for light—leads to fundamentally different results. Appendix B illustrates this by showing why the graphical isocline approach, which is used in I_{out}^*-R^* theory as well as in R^* theory (Tilman 1980) to predict the competition outcome, does not apply to layered communities.

Interestingly, more complex phytoplankton models of asymmetrical competition predict similar differences, although in these cases, there are, next to the primacy for light, more mechanisms at play that could cause these differences. For example, in the model of Jäger and Diehl (2014), asymmetrical competition for nutrients codetermines the competition outcome. In their double-asymmetric model, not only do the upper species (pelagic algae) have the primacy for light but the lower species (benthic algae) have the primacy for nutrients, as they assumed that the nutrients are supplied from below. Furthermore, Ryabov and Blasius (2011) found that differences in the dispersal ability of pelagic algae imply that a species with lower resource requirements can be outcompeted by a species with higher dispersal ability. In addition, the nonuniform nutrient environment in these models of pelagic algae—due to limited mixing of the water combined with nutrient supply from below—was found to explain that consumption traits that lead to coexistence in unlayered communities may lead to alternative stable states, and vice versa (Yoshiyama et al. 2009; Ryabov and Blasius 2011). However, our study shows that even in a uniform nutrient environment—that is, no nutrient gradient with depth—similar results can be found. We show that the most parsimonious form of asymmetrical competition—asymmetrical competition for light coincident with symmetry in competition for nutrients in a homogeneous nutrient environ-

ment—is sufficient to cause fundamentally different results compared to unlayered communities.

Our theoretical framework can also be used to study the competition between free-floating plants and phytoplankton. De Tezanos Pinto and O'Farrell (2014) state that field studies suggest that floating plants and phytoplankton are alternative stable states but that mathematical models are needed for more conclusive evidence. Our model may also be useful to study resource competition of terrestrial plants with different canopy positions.

For floating and submerged plant species that are common in temperate regions (*Lemna* sp. duckweed and *Elodea* sp. waterweed), both model and field data suggest that the occurrence of alternative stable states is unlikely. Instead, the species coexist or outcompete each other. This implies that floating-plant dominance may be a less persistent ecosystem state than suggested by Scheffer et al. (2003). We found similar model results (not shown here) when parameterizing both species directly from the literature, instead of from the ecosystem model PCDitch (Janse 1998). For both parameterizations, we kept the light attenuation coefficient k of *Lemna* sp. equal to that of *Elodea* sp. because little is known about k. In the model, we assumed that submerged plants take up nutrients only from the water column, whereas most submerged plants like waterweed can also take up nutrients from the sediment by their roots (Barko et al. 1991). Taking this into account will probably reduce the chance of alternative stable states even further, as a floating plant does not suffer from a submerged plant that takes up nutrients from the sediment only, which promotes coexistence instead of alternative stable states. We probably overestimated the nutrient loading needed for dominance of *Lemna* sp. because our model does not take into account nutrient recycling by water plants due to die-off. These processes, as well as other important phenomena in aquatic ecosystems such as variable stoichiometry, seasonal dynamics in light, nutrients, temperature, and phenology, are accounted for in more complex models such as PCDitch (Janse 1998) but at the cost of general insights into the dominant mechanisms and the way they interact.

Conclusions

The model presented here provides general insights into the competition for light and nutrients in layered communities of aquatic plants. At a high supply of light and nutrients, floating plants always outcompete submerged plants due to their primacy for light, even when submerged plants have lower resource requirements. The occurrence of coexistence or alternative stable states depends on the environmental conditions: in light-limited environments, the plants are never alternative stable states, whereas in nutrient-

limited environments, the plants coexist or are alternative stable states depending on their resource consumption traits. Compared to unlayered communities, the layeredness—and associated asymmetry in competition for light—leads to fundamentally different results: the competition outcome can no longer be predicted from species traits such as minimal resource requirement (R^* rule) and resource consumption. Also, it leads to a richer competition outcome in the sense that the same two species can, depending on the environment, coexist or be alternative stable states. For two common plant species in temperate regions, both the model and field data suggest that floating-plant dominance is unlikely to be a (self-enhancing) alternative stable state. This would ease ecosystem management that aims to reduce floating-plant dominance.

Acknowledgments

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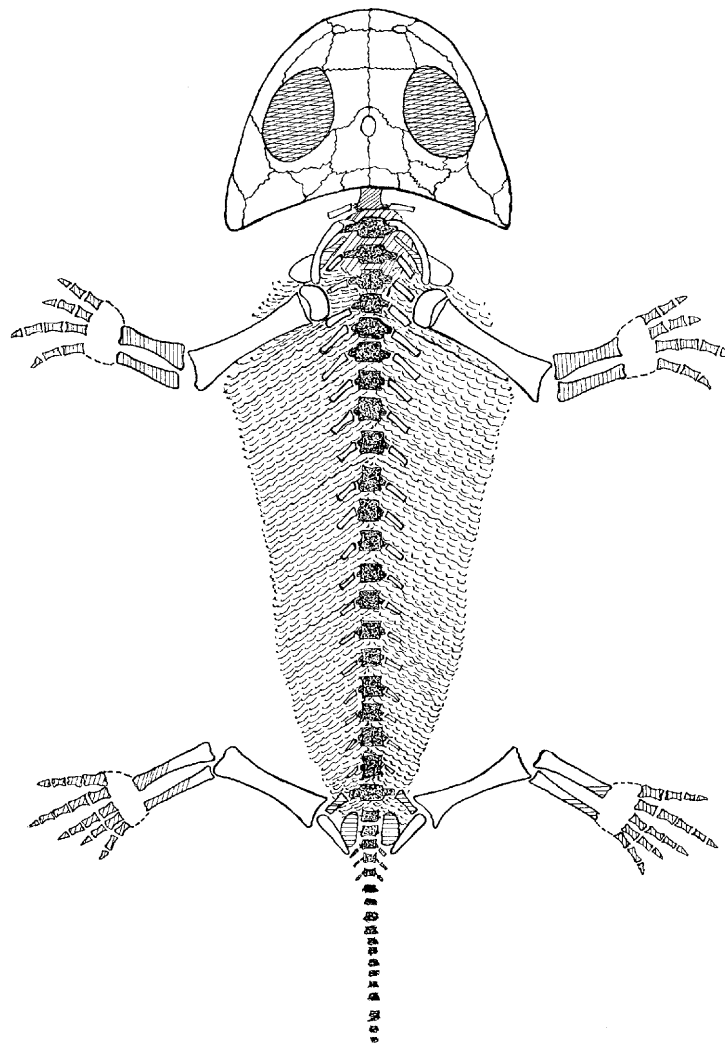
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