Floating plant dominance as a stable state

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Invasion by mats of free-floating plants is among the most important threats to the functioning and biodiversity of freshwater ecosystems ranging from temperate ponds and ditches to tropical lakes. Dark, anoxic conditions under thick floating-plant cover leave little opportunity for animal or plant life, and they can have large negative impacts on fisheries and navigation in tropical lakes. Here, we demonstrate that floating-plant dominance can be a self-stabilizing ecosystem state, which may explain its notorious persistence in many situations. Our results, based on experiments, field data, and models, represent evidence for alternative domains of attraction in ecosystems. An implication of our findings is that nutrient enrichment reduces the resilience of freshwater systems against a shift to floating-plant dominance. On the other hand, our results also suggest that a single drastic harvest of floating plants can induce a permanent shift to an alternative state dominated by rooted, submerged growth forms.

Dense mats of free-floating plant have an adverse effect on freshwater ecosystems because they create anoxic conditions that strongly reduce animal biomass and diversity (1). Invasions by introduced exotic species are partly responsible for the increase of floating plant dominance. The problems caused by *Eichhornia crassipes*, *Pistia stratiotes*, and *Salvinia molesta* are notorious: they hamper fish production and navigation in tropical regions around the world (2–4). However, eutrophication is likely to have boosted the spread of free-floating plants, too. In temperate climate zones, it is known that dense beds of duckweeds (Lemnaceae) and small, floating water ferns (Azollaceae) are a symptom of high-nutrient loading in small water bodies, such as ponds and canals (5, 6). Just as in the case of tropical plant beds, the dark and anoxic conditions under thick duckweed cover leave little opportunity for animal or plant life (1).

The dependence of free-floating plants on high nutrient concentrations in the water is an obvious consequence of their growth form. They have no direct access to the sediment pool of nutrients, and they have a large portion of their leaf surface exposed to the atmosphere rather than to the water, thereby reducing the possibility of taking up nutrients other than carbon through their leaves. By contrast, rooted submerged macrophytes may take up a large part of their nutrients from the sediment (7, 8) and also use their shoots effectively for nutrient uptake from the water column (9, 10). Although floating plants are obviously superior competitors for light, submerged plants may affect the growth of free-floating plants through a reduction of available nutrients in the water column. Competition is likely to be especially strong for nitrogen. Although phosphorus availability in the water column can be reduced because of uptake by submerged macrophytes (11), many studies show unaltered or even increased ortho-P levels after increased macrophyte cover (12–15). By contrast, submerged nitrogen concentrations in the water column of submerged vegetation stands are often below detection levels (15, 16).

Methods

Model. The asymmetry in competition between free-floating and rooted submerged plants has three essential features: (*i*) floating plants have primacy for light, whereas (*ii*) submerged plants can grow at lower water-column nutrient concentrations, and (*iii*) they reduce water column nutrients to lower levels. We construct a simple model to explore the potential implications of this specific asymmetry:

$$\frac{dF}{dt} = r_f F \frac{n}{n + h_f} \frac{1}{1 + a_f F} - l_f F, \qquad [1]$$

$$\frac{dS}{dt} = r_s S \frac{n}{n + h_s} \frac{1}{1 + a_s S + bF + W} - l_s S. \qquad [2]$$

Changes over time of the biomass of floating plants, *F*, and submerged plants, *S*, are modeled as a function of their maximum growth rates, r_f and r_s, modified by nutrient and light limitation, and of their losses, l_f and l_s, caused by processes such as respiration and various mortality factors. Nutrient limitation is a saturating function of the total inorganic nitrogen concentration, *n*, in the water column, which is assumed to be a decreasing function of plant biomass:

$$n = \frac{N}{1 + q_s S + q_f F}, \qquad [3]$$

where the maximum concentration (*N*) in the absence of plants depends on the nutrient-loading of the system, and the parameters q_s and q_f represent the effect of submerged and floating plants on the nitrogen concentration in the water column. Light limitation is formulated in a simple fashion (17): where $1/a_f$ and $1/a_s$ are the densities of floating and submerged plants at which their growth rates become reduced by 50% because of intraspecific competition for light. In addition to this intraspecific competition, irradiation of submerged plants is reduced by light attenuation in the water column (*W*) and by shading by floating plants scaled by the parameter *b*.

Default values and dimensions for parameters are given in Table 1. The default value for h_s is 0, to mimic the situation in which nutrient supply from the sediment is sufficient to make submerged plant growth essentially independent of the nutrient concentration in the water column. The half-saturation concentration, h_f, for floating plants is chosen in the middle of the range of values reported in the literature on duckweed growth (18, 19). The default value for q_s implies that a submerged vegetation of 20 g of dry weight m^{-2} can reduce the nitrogen concentration in the water by 50% (15), whereas floating plants have a smaller impact ($q_f < q_s$). The self-shading parameters for floating and submerged plants a_f and a_s are set as equal and tuned in such a way that the maximum biomass in the absence of any nutrient limitation approaches a realistic value. Because, unlike the case of self-shading, in which all biomass of floating plants contributes to shading of all submerged plants, we chose the corresponding parameter *b* larger than the intraspecific competition

Table 1. Default values and dimensions of parameters and variables of the model

Variable	Value	Units
F	–	g dw m^{-2}
S	–	g dw m^{-2}
N	–	mg N liter^{-1}
n	–	mg N liter^{-1}
a_f	0.01	(g dw m^{-2})$^{-1}$
a_s	0.01	(g dw m^{-2})$^{-1}$
b	0.02	(g dw m^{-2})$^{-1}$
h_f	0.2	mg N liter^{-1}
h_s	0.0	mg N liter^{-1}
l_f	0.05	day^{-1}
l_s	0.05	day^{-1}
q_f	0.005	(g dw m^{-2})$^{-1}$
q_s	0.075	(g dw m^{-2})$^{-1}$
r_f	0.5	day^{-1}
W	0	–
r_s	0.5	day^{-1}

See text for parameter definitions and the way in which default values were obtained. dw, dry weight.

coefficient a. Note that, the default parameter values are just a starting point, as we will systematically analyze the sensitivity of the model to parameter values.
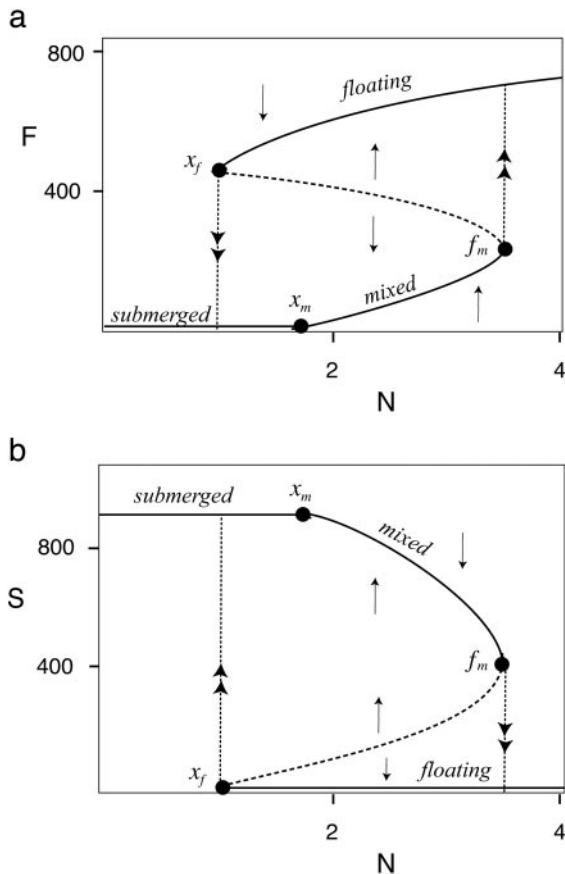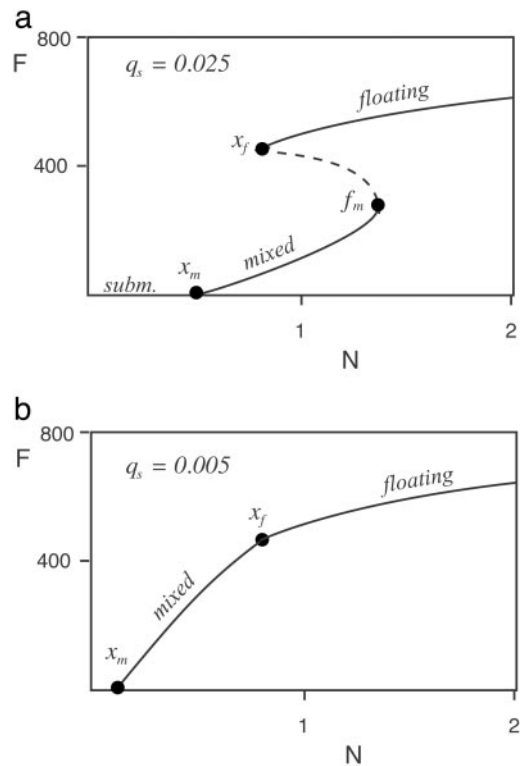

Fig. 1. Effect of nutrient loading on the equilibrium biomass of floating plants (*a*) and submerged plants (*b*). The arrows indicate the direction of change if the system is out of equilibrium. They illustrate that the dashed equilibrium (the saddle) is unstable. The vertical transitions with double arrows correspond to catastrophic shifts to an alternative equilibrium.

Results

Analysis of this model indicates that the competition is likely to lead to alternative stable states over a range of conditions (Fig. 1). At low-nutrient concentrations, the only stable state is an equilibrium with submerged plants (E$_s$). With increasing nutrient level, a monoculture of floating plants (E$_f$) appears as an alternative equilibrium. However, the submerged-plants state (E$_s$) also remains (locally) stable. Therefore, provided that no large disturbances occur, the system will remain dominated by submerged plants, until at the next bifurcation, floating plants start to coappear with the submerged plants in a stable mix (E$_m$). With increasing nutrient load, the share of floating plants in the mix increases gradually, until a bifurcation point (f_m) is reached at which the mixed equilibrium disappears and the system moves (Fig. 1, double arrow upward) to the only remaining stable state, the monoculture of floating plants. If, subsequently, the nutrient concentration is reduced, the system will not return to the mixed equilibrium along the same path. Instead, it remains on the floating plant-dominated upper branch of the folded curve until a bifurcation point (x_f) is reached where stability of the floating-plant monoculture ends, and the system switches back to the submerged plant-dominated state.

Robustness. The default parameter values are chosen in such a way that they seem likely to mimic certain field situations in a reasonable way. However, plant species and their environments differ widely, and different sets of parameter values or model formulations are obviously needed to represent different field settings. Here, we analyze how the results are affected by different assumptions about the competition for nutrients and light, and by taking a different model formulation.

Changing Competition for Nutrients. We have assumed that submerged plants reduce nutrient availability in the water column

Fig. 2. Effect of nutrient loading on the equilibrium biomass of floating plants as in Fig. 3*a* but for moderate (*a*: $q_s = 0.025$) and small (*b*: $q_s = 0.005$) reduction of nutrients in the water column by submerged plants.

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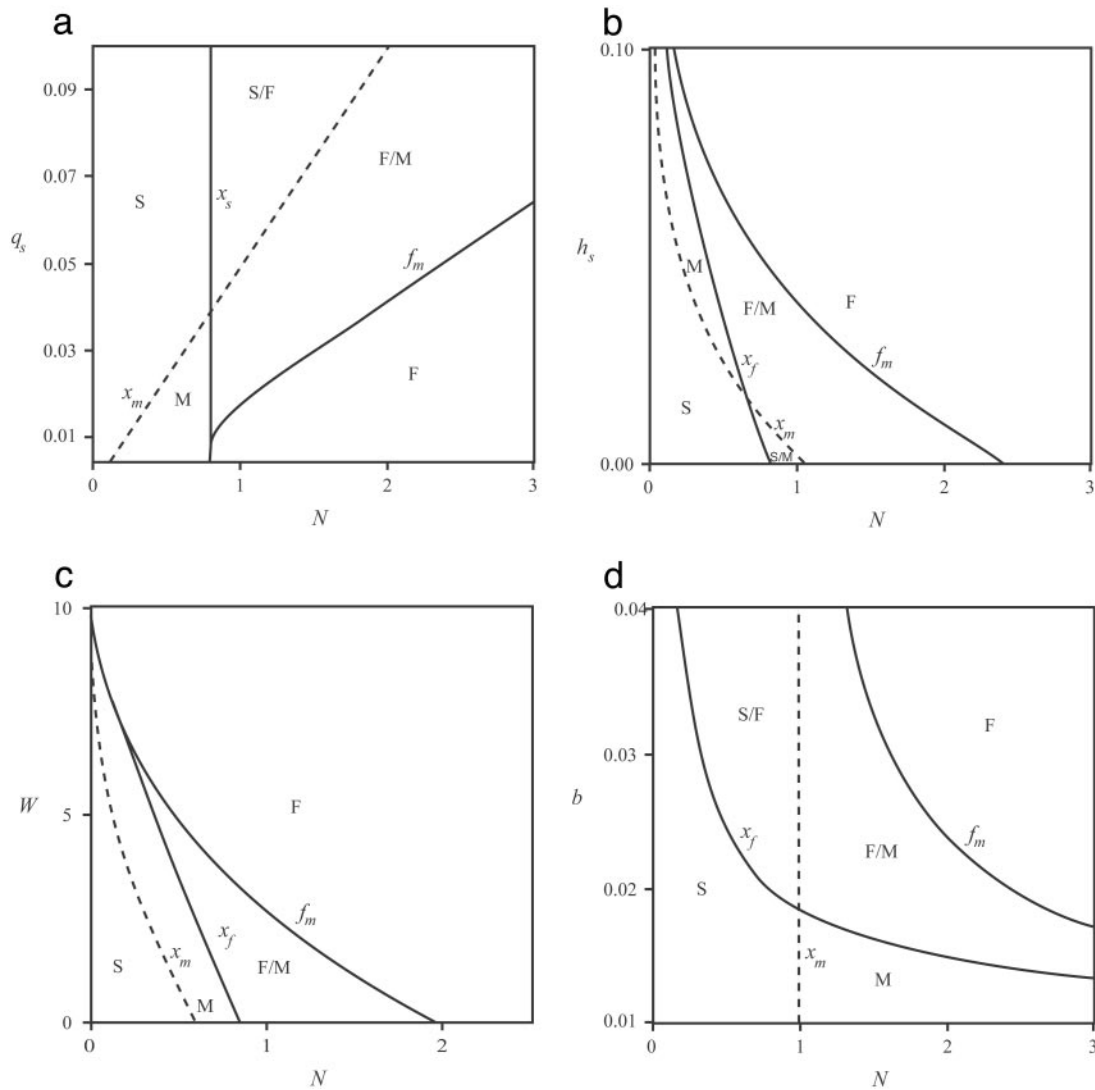
Fig. 3. Bifurcation graphs showing the effect of parameters q_s, h_s, W, and b (a, b, c, and d, respectively) on the nutrient loading (N) at which the different bifurcations (x_m, x_f, and f_m) in the model occur. The bifurcation lines delineate sections in the parameter plane with different sets of equilibria. Floating plant dominance (F), submerged plant dominance (S), or a stable mix of these groups (M) can occur as a unique equilibrium, but in some sections also as one of two alternative equilibria (indicated as S/F, F/M, or S/M). All depicted bifurcations are computed with the program LOCBIF (41).

to a greater extent than do floating plants ($q_s > q_f$), and that, essentially, growth of submerged plants does not depend on nutrients in the water column ($h_s = 0$). Relaxing the first assumption has several effects (Fig. 2). If the impact of submerged plants on nutrients is moderately but sufficiently reduced, a floating plant-dominated system switches first to a mixed equilibrium rather than directly to a pure submerged plant state in response to a decrease in nutrients. Secondly, hysteresis becomes less pronounced as the distance between the bifurcations x_f and f_m becomes smaller. Indeed, if we assume that the effect of submerged plants on nutrients is equal to that of floating plants, the hysteresis disappears entirely (Fig. 2b).

A more systematic way to analyze such effects of parameter values on the model behavior is to perform a bifurcation analysis (20). The idea in our case is to plot the critical nutrient levels at which the bifurcations occur as a function of the parameter of interest (Fig. 3). The first graph (Fig. 3a) shows the effect of altering the parameter (q_s) that represents the impact of submerged plants on nutrients (note that Figs. 1 and 2 represent the model behavior at different horizontal cross sections: $q_s = 0.075$, 0.025, and 0.005). The main thing to note is that the hysteresis

becomes smaller if the effect of submerged plants on nutrient levels (q_s) is reduced, and eventually disappears below the point where the two bifurcation curves (x_s and f_m) meet. Similarly, hysteresis becomes smaller if the dependence of submerged plant growth on nutrients (h_s) is increased (Fig. 3b). Other bifurcation analyses (not shown) reveal that decreasing q_f has qualitatively similar effects as increasing q_s, whereas increasing h_f is equivalent to decreasing h_s. In conclusion, the asymmetry in competition for nutrients ($q_s > q_f$ and $h_f > h_s$) is essential for causing the hysteresis.

Changing Competition for Light. Competition for light is the other major ingredient of our model. Although we did not model phytoplankton explicitly, a first point to note is that the chances decrease for submerged macrophytes to out-compete free-floating plants if light attenuation in the water column (represented by parameter W) becomes larger (Fig. 3c). Thus, lakes that are deeper and/or more turbid are predicted to have a lower probability of being dominated by submerged vegetation and show hysteresis.

The asymmetry in light competition between the two plant
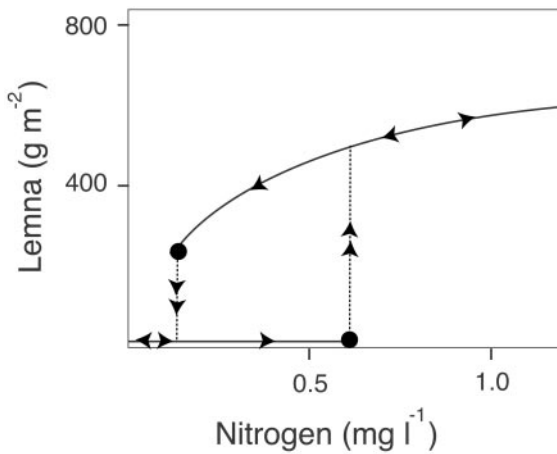
Fig. 4. Hysteresis in dominance by floating plants predicted from an elaborate seasonal simulation model of the competition between floating and submerged plants.

types is represented in our default parameter setting by assuming the shading effect (*b*) of floating plants on submerged plants to be twice as strong as intraspecific shading effects (*a*). The rationale is that, on average, only 50% of the biomass of submerged plants casts shade on a given submerged plant leaf, whereas all floating plant biomass contributes to shade on a submerged leaf. This logic sounds reasonable at first, but holds exactly only for the unlikely case in which the photosynthesis decreases linearly with shading biomass. Reducing *b* to relax this assumption moves the hysteresis to higher nutrient levels (Fig. 3*d*). However, it is not easy to assess what would be the most realistic value for *b*. In fact, there are more fundamental problems with the formulation of light competition. The way in which photosynthesis decreases with shading biomass depends upon light attenuation in plant biomass and the photosynthetic response to light.

Changing the Model. To check whether the predicted hysteresis is an artifact of simplifying assumptions such as the simple formu-

lation of light competition and the absence of seasonality and reproduction, we formulated an elaborate individual-based spatially explicit simulation model for the competition between rooted submerged plants and duckweed. This model is an extension of an earlier submerged plant growth model (21), and its characteristics and analysis will be presented elsewhere in detail. The model describes the seasonal dynamics of aquatic plant growth in temperate regions, including overwintering as dormant stages and regrowth in spring. Although nutrient competition is formulated simply as in our simple model, light competition is described in a much more realistic way in the simulation model. Irradiance follows a sine wave over both a year and a daily cycle. Photosynthesis on a given part of the plant depends on *in situ* light and the distance from the tissue to the top of the plant; the latter is because of the decrease in activity with tissue aging. *In situ* light on any site depends on shading by plant biomass in higher strata and turbidity in the water layer. The response of this elaborate model to nutrient loading (Fig. 4) is characterized by hysteresis that does not include the mixed state but is otherwise much like the one found in the simple model (Fig. 1). This result indicates that the hysteresis is at least not an artifact of the simple formulation of light competition used in the simple model, nor of the absence of seasonality in the simple model.

Evidence

Competition Experiments. To test whether alternative equilibria may really result from competition between the two growth forms, we performed a set of controlled experiments in which we let the submerged plant *Elodea nuttallii* and the floating duckweed *Lemna gibba* compete. All plants were acclimatized for 14 days in nutrient poor (0.5 mg per liter of N, 0.08 mg per liter of P) water under the same temperature and light regime before the experiments. Subsequently, plants were allowed to compete for 57 days in 8-liter containers. The initial nutrient level was the same for all tanks (5 mg per liter of N, 0.83 mg per liter of P). Water temperature was maintained at 23–25°C, and the tanks were exposed to a daily 16-h dark/8-h light cycle (180 μmol·m^{-2}· s^{-1}). Parallel experiments were started from four different initial conditions, each one represented by two replicate aquaria. If there is only one equilibrium, such experiments are expected to
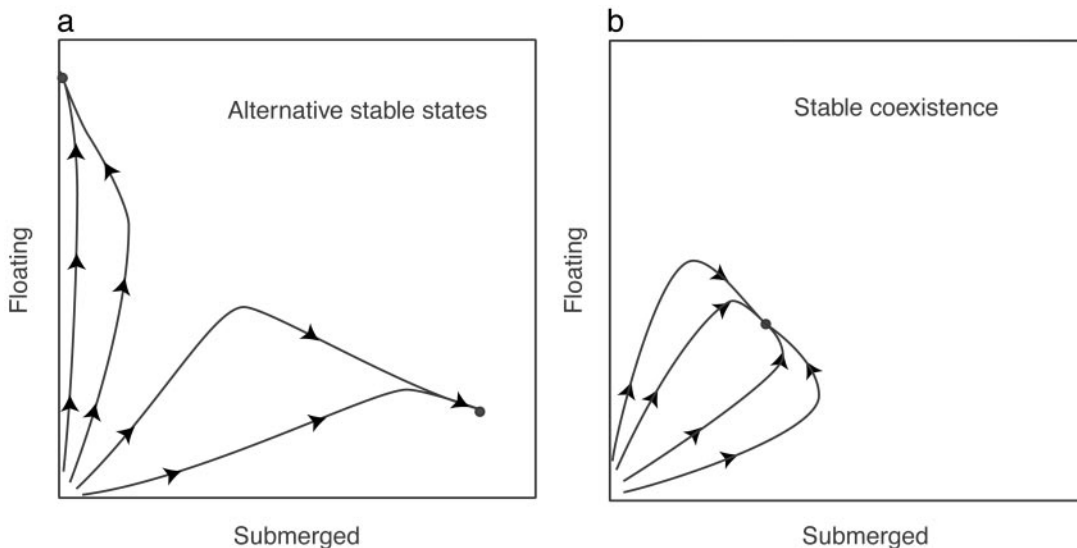
**Fig. 5.** (*a*) If two stable states exist, trajectories of simulations with our model end in either of the two states, depending on initial conditions. (*b*) By contrast, trajectories of simulations converge to the same point if there is a single equilibrium. The latter simulations are performed with h_s = 0.2, r_s = 1.2, and the other parameters at default values (see Table 1).

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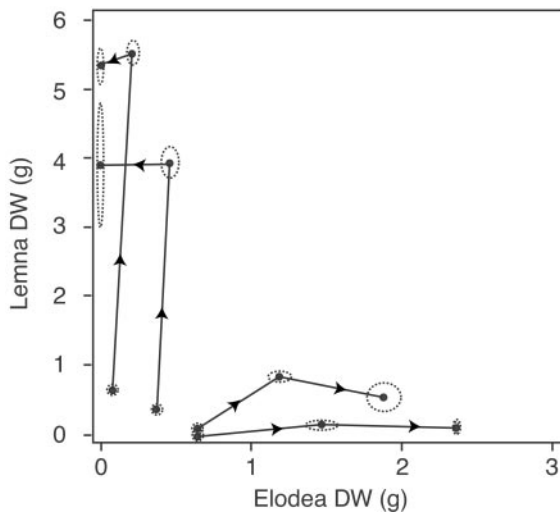
Fig. 6. Growth trajectories in competition experiments of a submerged plant (*Elodea*) and a floating plant (*Lemna*) tend to different final states, depending on the initial plant densities. All experiments were performed under the same conditions. Biomass is plotted for all experiments at the 1st, 23rd, and 57th day. Dashed ellipses indicate SDs of replicate experiments.

converge to it, whereas they are predicted to end in either of the alternative equilibrium states if those exist (Fig. 5). Our replicated experiments clearly ended in alternative states, depending on the initial biomass of both species (Fig. 6), thus confirming the alternative equilibrium hypothesis. Similar experiments performed at various nutrient levels showed that *Lemna* was increasingly likely to out-compete *Elodea* at higher nutrient levels (not shown), which is also in line with the model predictions.

Patterns of Duckweed Dominance in Dutch Ditches. To check whether evidence of alternative stable states can also be found in the field, we analyzed an extensive dataset of vegetation censuses and water quality from 641 Dutch ditches. Routinely, vegetation is nonselectively removed from such ditches once or twice a year to prevent them from becoming clogged by vegetation. Obviously, vegetation biomass, and therefore competition, increases steadily from the (not recorded) moment of removal. Therefore, we arbitrarily divided the dataset in a sparsely vegetated subset (total cover of all taxa <50%), a
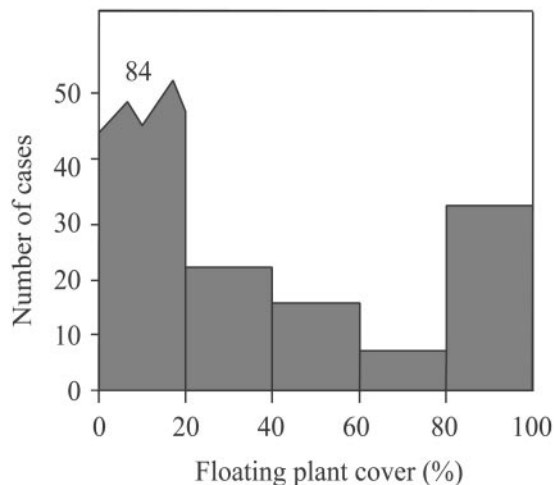
Fig. 7. Bimodal frequency distribution of free-floating plants in a set of 158 densely vegetated (total vegetation cover >80%) Dutch ditches.

Table 2. Spearman rank correlations: dense vegetation

Dense vegetations	Floating plants	Submerged plants	N_{tot}
Submerged plants	−0.58** (204)	–	–
N_{tot}	+0.28** (141)	−0.24** (141)	–
P_{tot}	+0.34** (169)	−0.29** (169)	+0.49** (141)

Spearman rank correlations between percentage coverage of free-floating and submerged plants and the total N and P water column concentrations in densely vegetated ditches (total coverage of floating and submerged plants >50%). Double asterisks denote two-tailed $P < 0.01$; numbers of ditches are given in parentheses.

densely vegetated subset (total cover >50%) and a very densely vegetated subset (total cover >80%). In line with the theory, the frequency distribution of free-floating plants at higher vegetation densities was bi-modal (Fig. 7). Also, as predicted, cover by floaters was negatively correlated to submerged plant abundance, and floaters showed a positive correlation to nutrient levels of the water column, whereas submerged plants were negatively related to nutrient levels (Table 2). By contrast, in the sparsely vegetated subset of ditches (Table 3), correlations between growth forms and nutrient concentrations are less pronounced, and abundances of floating and submerged plants are positively correlated as would be expected in a phase of regrowth after removal of vegetation, when biomass reflects the recovery time since clearing rather than competition between growth forms (Fig. 5*a*).

Shifts Between Floating and Submerged Plants in an African Lake. On a completely different scale, the tendency to alternative stable states is illustrated by the history of Lake Kariba, the largest manmade African lake, created by the damming of the Zambezi river in 1958. During the filling, there was a population explosion of floating *Salvinia molesta* and other floating plants (22–24). Floating vegetation remained abundant until a decade later, when an explosion of benthic vegetation and mussels occurred that locked up large amounts of nutrients (24). *Salvinia* cover rapidly dropped to <5% in 1973 and to <1% from 1980 onward (23). In 1996–1999, there was a new increase of floating vegetation, this time of *Eichhornia crassipes*. Most probably, the shifts between the alternate states had been driven by the amplitude of water-level fluctuations. Strong fluctuations favor floating plants as they suppress submerged plants (25) and enhance nutrient input from flooded land (23, 26). The history of this lake again illustrates a tendency to dominance by either submerged or floating plants, the latter being associated with high-nutrient levels and increased mortality of submerged plants driven, in this case, by water-level fluctuation.

Discussion

Although alternative stable states are considered essential to the understanding and management of ecosystems ranging from

Table 3. Spearman rank correlations: sparse vegetation

Sparse vegetations	Floating plants	Submerged plants	N_{tot}
Submerged plants	+0.23** (436)		
N_{tot}	+0.15** (454)	−0.17** (354)	
P_{tot}	+0.25** (382)	−0.09 (382)	+0.54** (353)

Spearman rank correlations between percentage coverage of free-floating and submerged plants and the total N and P water column concentrations in sparsely vegetated ditches (total coverage of floating and submerged plants <50%). Double asterisks denote two-tailed $P < 0.01$; numbers of ditches are given in parentheses.

coral reefs (27) and open ocean systems (28) to dry lands (29) and forests (30), their presence in field situations has been remarkably hard to prove. Typically, strong cases require a combination of approaches (31, 32). This has been the approach in this study.

The models form the basis of our analysis. However, even though the individual-based simulation model contains more detail than the simple model, many mechanisms that may affect the competition have still not been included. For instance, anoxia under floating plant beds may boost the decline of submerged plants. Also, growth of duckweed species can be inhibited at higher pH (33–35), which may arise from photosynthesis in submerged weed beds. Although these specific mechanisms will tend to enhance rather than weaken the hysteresis, other mechanisms that we did not consider could potentially work the opposite way.

An important factor that we have not addressed is the role of phytoplankton. In temperate shallow lakes, submerged plants are out-competed by phytoplankton at higher nutrient levels, and a phytoplankton-dominated state and submerged-plant dominance seem likely to represent alternative attractors (25, 36–38). Thus, an important question is whether submerged plants will be replaced by floating plants or phytoplankton at high-nutrient loading. Obviously, floating plants are in the best position for competition for light. Therefore, one should logically expect floating plants to ultimately become dominant when nutrients are not limiting. Although this may indeed be the case in tropical lakes (2) and temperate ponds and ditches (5), free-floating plants never seem to become dominant in larger temperate lakes. The most likely explanation is that the small duckweeds and other free-floating plants that occur in temperate regions are simply washed ashore in exposed waters, restricting their distribution to sheltered sites. By contrast, the larger growth forms of free-floating plants that can develop massively in tropical lakes apparently survive much more exposed conditions (2). Obviously, development of a truly general framework

for predicting which conditions give rise to dominance by floating plants, phytoplankton, or submerged plants remains a major challenge. Meanwhile, the results of our current study apply to situations in which dominance by floating plants is not prevented by factors other than nutrients.

Overall, the different lines of evidence we present seem to make a rather strong case for the hypothesis that competition between floating and submerged plants can cause alternative attractors. The model approach shows that this hypothesis can be deduced in a robust way from the assumptions that floating plants have primacy for light, whereas submerged plants can grow at lower water column-nutrient concentrations and reduce water-column nutrients to lower levels. The controlled competition experiments demonstrate alternative attractors in a straightforward way on a small temporal and spatial scale, and the patterns in Dutch ditches and Lake Kariba suggest that the phenomenon also may be important in field situations. None of these approaches in themselves can be seen as proof. Interpretations of models, controlled experiments, and field patterns all have their specific caveats (39). Thus, our central result is merely an approximation of "truth as the intersection of independent lies" (40).

Probably the most useful complementary type of evidence could be obtained through large-scale field experiments. Because the final state of the system depends on the initial biomass of floating plants (Figs. 6 and 7), our results imply that in shallow waters that have some submerged plants and are not too high in nutrient level, a single harvest of floating plants may lead to a permanent switch to submerged-plant dominance. The critical harvest needed for a shift is predicted to increase with the nutrient level. Actual critical levels will differ between ecosystems, but could be detected experimentally. In general, the best way to manage ecosystems with alternative stable states is to enhance the resilience of the preferred state (32). Translated to our case, this conclusion implies that nutrient control may be an important strategy to reduce the risk of invasion by native or exotic floating plants.

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