

Regime shifts between free-floating plants and phytoplankton: a review

Paula de Tezanos Pinto · Inés O'Farrell

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Abstract Field studies evidence shifts between phytoplankton and free-floating plant regimes; yet, it is unclear what drives these shifts and if they are critical transitions (alternative stable states). In this review, we synthesized field and experimental data on free-floating plants (of varying size and phylogenies) and phytoplankton regimes, to assess the effects of these producers on the environment. Nutrient-rich environments promote free-floating plants dominance—regardless of life form—which causes dark and anoxic environments, and nutrient release from sediments. This reinforces free-floating plants dominance, but controls phytoplankton biomass by strong shading (despite high nutrients and low grazing). Phytoplankton dominance renders turbid and oxygen-rich (when producing) environments. We also searched for case studies of regime shifts for free-floating plants and phytoplankton dominance. Most studies showed that when free-floating plants dominance was interrupted, phytoplankton biomass (usually Cyanobacteria) rose steeply. Likewise, when phytoplankton-dominated, the development of dense

mats of free-floating plants covers usually controlled phytoplankton. Field evidence that suggests critical transitions include abrupt regime transitions in time and space; yet, evidence including indoor controlled experiments and mathematical models is needed for conclusive evidence of alternative stable states to be drawn.

Keywords Phytoplankton · Free-floating plants · Alternative stable states · Regime shifts

Introduction

The hypothesis that shallow lakes have alternative stable states was recognized for shifts between submerged plants and phytoplankton communities (Scheffer et al., 1993) and submerged plants and free-floating plants communities (Scheffer et al., 2003). Field patterns also evidence alternation between phytoplankton and free-floating plant communities, both in space (Abdel-Tawwab, 1998; Izaguirre et al., 2004) and time (O'Farrell et al., 2011); however, it is unclear what drives these regime shifts, and whether they are triggered by alternative stable states (critical transitions sensu Scheffer, 2009).

Dense mats of free-floating plants result in low phytoplankton biomass (Abdel-Tawwab, 1998; O'Farrell et al., 2003; Ayala et al., 2007) and diversity (O'Farrell et al., 2009), mostly because of the dark

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P. de Tezanos Pinto (✉) · I. O'Farrell
Departamento de Ecología, Genética y Evolución,
Facultad de Ciencias Exactas y Naturales, IEGEBA
(CONICET-UBA), Universidad de Buenos Aires,
C1428EHA Buenos Aires, Argentina
e-mail: paulatezanos@ege.fcen.uba.ar

conditions that prevail below dense free-floating plants. Probably other mechanisms, such as competition for nutrients, secretion of allelochemicals, and provision of refuge for predators may also be responsible for the low phytoplankton biomass at free-floating plant dominance. Because free-floating plants differ in size and phylogeny, it is uncertain if their effects on phytoplankton and the environment change with plant life form.

The evidence from the literature showed that when free-floating plant dominance is interrupted, either by natural causes (O'Farrell et al., 2011), management programs (Mangas-Ramirez & Elías-Gutierrez, 2004; Ayala et al., 2007; Bicudo et al., 2007; Crosetti & Bicudo, 2008), or experimentally (de Tezanos Pinto et al., 2007), it mostly resulted in marked increases in phytoplankton biomass. Free-floating plant removal could also stimulate the growth of submerged plants, however, this is rare at high nutrient load (Meerhoff & Jeppesen, 2009, p. 647, Fig. 2). In space, we also found evidence of sharp boundaries between contrasting sites characterized by free-floating plant dominance and scarce phytoplankton biomass, and phytoplankton dominance with scarce free-floating plant biomass, both among similar environments (Abdel-Tawwab, 1998) and within the same environment (Izaguirre et al., 2004).

A community can be considered locally stable either if it persists some period of time in spite of forces potentially capable of altering its structure (Sutherland, 1974) or if it returns to equilibrium when perturbed (Connell & Sousa, 1983). An ecological system formally exhibits alternative stable states when its state variable responds to environmental change by a backwards folding curve (hysteresis) (May, 1977). Thus, in an identical environment, the system can be in either one of two contrasting stable states (Schröder et al., 2005). Regime shifts describe a sudden jump from one regime to another one: this jump can be smooth or non linear (threshold or hysteretic) (Scheffer, 2009). Critical transitions are the subset of regime shifts where the system is pushed over a threshold where a positive feedback causes a self-propagating shift to an alternative regime (Scheffer, 2009). Hysteresis-driven systems are predicted to show abrupt state transitions over time, sharp boundaries between contrasting sites, bimodal state variable frequency distribution, or dual response to driving parameters (Schröder et al., 2005).

Table 1 Free-floating plants sizes, names, and phylogeny

Size	Scientific name	Common name	Phylogeny
Small (1–5 cm)	<i>Lemna</i> L.	Duckweed	Angiosperm
	<i>Spirodella</i> Schleid.	Duckweed	Angiosperm
	<i>Ricciocarpus natans</i> L.	Duckweed	Livewort
	<i>Salvina</i> Seguirer	Water fern	Fern
	<i>Azolla</i> Lam.	Water fern	Fern
Medium (5–20 cm)	<i>Wolffia</i> Hornerl ex Schleid.	Water meal	Angiosperm
	<i>Pistia stratiotes</i> L.	Water lettuce	Angiosperm
Large (5–20 cm)	<i>Eichhornia crassipes</i> (Mart.) Solms	Water hyacinth	Angiosperm

In this review, we compiled and synthesized available studies dealing with free-floating plants (of varying size and phylogenies) and phytoplankton dominance, and their corresponding regime shifts. We aimed to identify: (a) the behavior/feedback of the system's components for each regime, (b) the driver(s) leading to their regime shifts, and (c) evidence for critical transitions. Most of the information about regime shifts was found from tropical, subtropical, and warm temperate shallow environments, probably reflecting the natural distribution of most free-floating plants.

Free-floating plant and phytoplankton regimes

Free-floating plant regime

Free-floating plants lie suspended on the water surface and can be distributed by wind and water movements (Lacoul & Freedman, 2006). Many free-floating plants are native to South America—mostly in tropical and subtropical areas—due to their sensitivity to low air temperature and freezing (Sculthorpe, 1967). The small-sized *Lemna*, *Wolffia*, and *Wolffiella* have cosmopolitan distribution (Sculthorpe, 1967).

Free-floating plants range in size and phylogeny (Table 1), have high growth temperature optima (van der Heide et al., 2006), and grow well at high nutrients concentrations (Portielje & Roijackers, 1995). The

Table 2 Effects of dense free-floating plant cover of different life forms on the environment. Numbers denote references

Common name	Duckweed	Water fern	Water lettuce	Water hyacinth
Species	<i>Lemna</i> spp.	<i>Azolla</i> spp. <i>Salvinia</i> spp.	<i>Pistia stratiotes</i>	<i>Eichhornia crassipes</i>
Plant size	Small	Small	Medium	Large
Effects on the abiotic variables				
Decreased light availability	1, 2	2, 5	9	23
Decreased nutrient concentration		4, 6, 7	9	14, 15, 16 ^b , 17, 18
Increased nutrient concentration	3		10	
Decreased suspended sediments		6	11	17,18
Secretion of allelochemicals		8	13	19
Decreased oxygen concentration	1, 2, 3	2, 5, 6, 7	9, 10	16 ^b , 18, 20, 21
Decreased temperature		7	9, 10	20
Decreased pH	1,3, 4	2, 6, 7	9, 11	17
Effects on the biotic variables				
Decreased phytoplankton biomass	1, 4	6, 7	11, 12 ^a	16 ^b , 17
Phytoplankton dominated by	Cyanobacteria 1		Cyanobacteria and diatoms 10	Cryptomonas, Cyanobacteria and euglenoids 22
Decreased zooplankton biomass		6	12	20 ^a
Decreased fish biomass		6		14 ^a , 18

(1) de Tezanos Pinto et al. (2007), pp. 51–53, Figs. 2–4), (2) Janes et al. (1996, p. 24, Table 2), (3) Boedeltje et al. (2005, p. 354, Fig. 1), (4) Portielje & Roijackers (1995, pp. 132,146; Fig. 3, 6), (5) Netten et al. (2010), (6) Abdel-Tawwab (2006, p. 27, Table 2), (7) Abdel-Tawwab (1998, pp. 36, 43, Table 1; Fig. 2), (8) Gopal & Goel (1993), (9) Izaguirre et al. (2012, p. 225, Table 1), (10) Izaguirre et al. (2004, pp. 30, 32, Table 1; Fig. 4), (11) O'Farrell et al. (2011, p. 280, Fig. 3), (12) Ayala et al. (2007, p. 626, Fig. 5), (13) Wu et al. (2013), (14) Meerhoff et al. (2002, p. 73, Fig 7), (15) Petrucio & Esteves (2000, p. 376, Table 1), (16) Villamagna & Murphy (2010), (17) Bicudo et al. (2007, p. 1125, Fig. 3), (18) Mc Vea & Boyd (1975), (19) Sharma et al. (1996), (20) Meerhoff et al. (2003), (21) Maine et al. (1999, p. 134, Table 1), (22) Zalocar de Domitrovic (2003)

^a Compared to sites with submerged plants

^b Reviewed in Villamagna & Murphy (2010)

experiments of Abdel-Tawwab (2006) showed that when free-floating plants covered most of the surface (50–75%) of 250 m² fish ponds, there was a significant decrease in phytoplankton biomass, oxygen, and nutrient (ammonia, nitrate, and phosphate) availability, compared to covers <50%. The results of this field experiment suggest that there may be a threshold of free-floating plant cover needed to cause significant effects in the environment. Such threshold would probably change with water body characteristics (shallow lake, ditch) and latitude (tropical, temperate).

Table 2 shows that dense mats of free-floating plants—regardless of their life form—cause similar effects on the environment. They attenuate most of the incoming light, immobilize nutrients in their biomass, enhance sedimentation of suspended solids, and can secrete allelochemicals (dashed arrows in Fig. 1a; Table 2). The water column is anoxic or has low

oxygen availability (Fig. 1a; Table 2) mostly because of the strong light attenuation (which hinders photosynthesis, but see other reasons below). Sediment oxygen demand can play an important role in the oxygen budget, however, in sub-oxic or anoxic situations the sediment oxygen demand is low (Belanger, 1981). Also, the water column has lower temperatures, and lower pH (Table 2) than surrounding habitats without free-floating plants.

Free-floating plants have primacy in competition for light; their shading seems to be the major driver controlling phytoplankton biomass (Fig. 1a) (Roijackers et al., 2004; de Tezanos Pinto et al., 2007) and diversity (O'Farrell et al., 2009). The low light availability under dense free-floating plants cover (75–100%) favors Cyanobacteria, diatoms, cryptophytes, and euglenoids (Table 2) which have physiological and morphological traits that improve fitness at

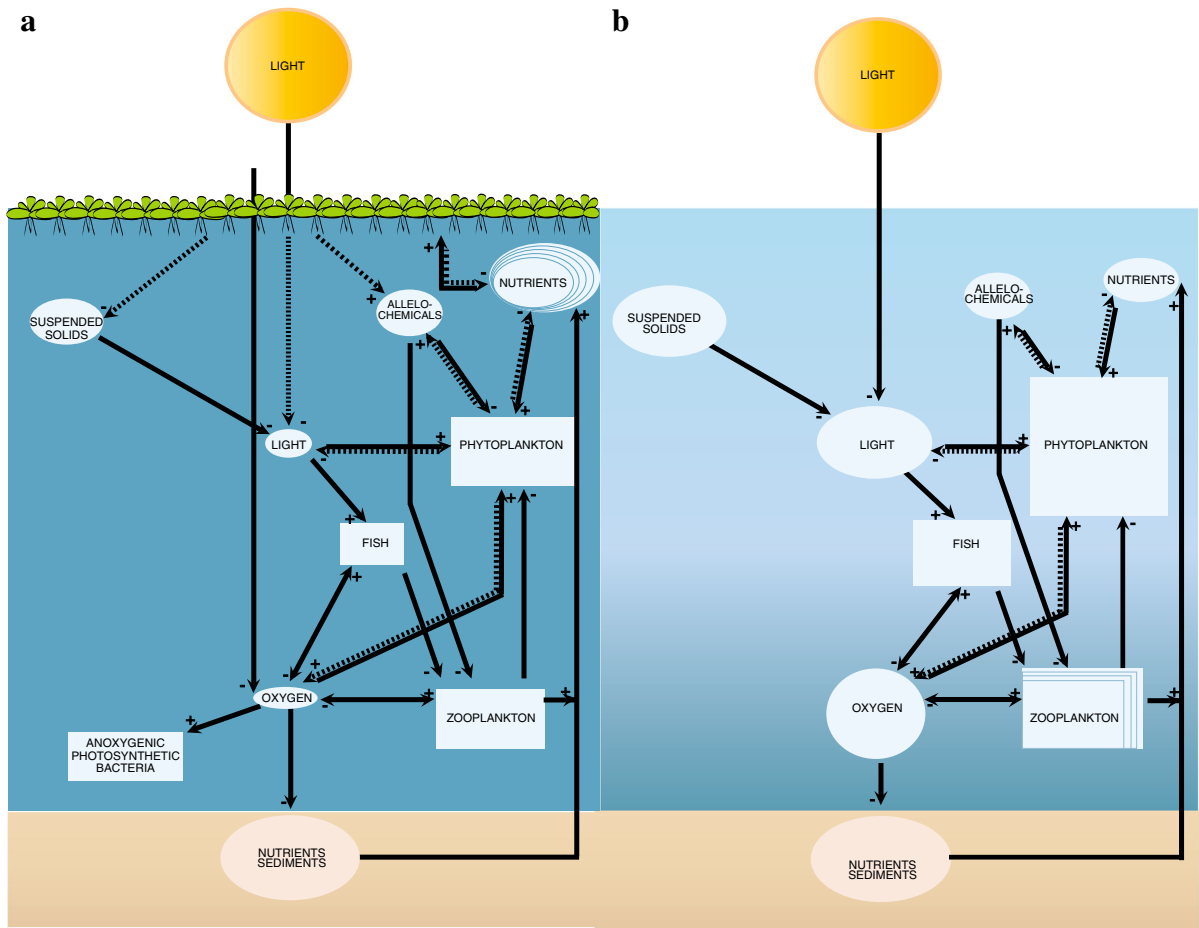


Fig. 1 Main effects of free-floating plants (a) and phytoplankton (b) regimes in vegetated shallow lakes. Compartment sizes indicate the importance of the variable in the ecosystem; biotic variables are in rectangles and abiotic variables in ovals. Dashed arrows depict direct effects of the producers on the environment and full arrows cascading effects. The plus and minus symbols indicate the qualitative effects of each component on each other.

low light. Cyanobacteria is the best low light-adapted phytoplankton group as it has the highest light efficiency, followed by diatoms (Schwaderer et al., 2011). Mixotrophs—euglenoids and cryptophytes—may ingest prey allowing cell maintenance at low light (Jones, 2000). Motility, provided by gas vesicles (in Cyanobacteria) and flagella (in cryptophytes and euglenoids), decreases the risk of loss by sedimentation. Morphologies such as small size, low volume, high surface to volume ratios, and organism elongation characterize phytoplankton communities under complete cover with duckweed (O’Farrell et al., 2007), suggesting that these traits enhance fitness in low light

Note that the water column is darker at free-floating plants regime (a) as most of the incoming light is attenuated; at phytoplankton dominance (b) light attenuates with depth. Compartments containing lines denote variability (e.g., nutrients, and zooplankton + invertebrates). The information synthesized was compiled from bibliographic references cited on the main text and on Table 2

scenarios. Free-floating plant dominance also causes low biomass of picoplankton (Izaguirre et al., 2010, 2012), periphyton (Portielje & Roijackers, 1995), and submerged plants (Janes et al., 1996), probably related to the strong attenuation of incoming light.

Even though different free-floating plant life forms have similar effects on physical variables, they exert different effects on nutrient availability. Experiments in tanks showed that the growth of the small *Salvinia molesta* D. Mitch was less affected by low nitrogen and phosphorus concentrations than the medium-sized *Pistia stratiotes*, and both these species grew better at low nutrients compared to the large *Eichhornia*

crassipes (*Salvinia molesta* < *Pistia stratiotes* < *Eichhornia crassipes*) (Henry-Silva et al., 2008, p. 156, Fig. 2). Hence, phytoplankton growing below dense mats of small-sized free-floating plants would be light-limited but have sufficient nutrients, as observed in field experiments with duckweed dominating (de Tezanos Pinto et al., 2007). But, phytoplankton growing below dense mats of big-sized free-floating plants—which consume high nutrients (Table 2)—would be limited both by low light and low dissolved inorganic nutrient availability. For example, in the Garças reservoir (Brazil) soluble reactive phosphorus concentrations remained close to zero during years with dense *E. crassipes* cover (Bicudo et al., 2007, p. 1127, Fig. 5b), providing evidence for phosphate limitation for phytoplankton (in addition to light limitation). The nutrient uptake by *E. crassipes* may change with season, being high in warm periods and low in cold periods (Maine et al., 1999; Meerhoff et al., 2002). In these cases, phytoplankton growing below dense *E. crassipes* mats could be either limited by light and nutrients (in warm periods) or by light (in the cold season).

Free-floating plants seem to uptake phosphorus (P) more efficiently than nitrogen (N). In an experiment conducted in outdoor tanks dominated either by *E. crassipes*, *P. stratiotes*, or *S. molesta*, free-floating plants were observed to remove most of the total P and phosphate (averages: 80 and 74%, respectively) but only half of the total N, ammonia, and nitrate (averages: 44, 55, and 55%, respectively) from effluents (average TN and TP at the inlet, 370 and 77 $\mu\text{g l}^{-1}$, respectively) (Henry-Silva et al., 2008, p. 156, Table 1). Mesocosm experiments with nutrient additions showed that *E. crassipes* biomass and TP content in the plant tissue were highest when amended with P or P + N doses, but not by N additions (Kobayashi et al., 2008). Conversely, phytoplankton exposed during a month to high shading—in a field experiment mimicking the effect of dense free-floating plants mats—only consumed dissolved inorganic nitrogen (phosphate concentrations remained unchanged) (O’Farrell et al., 2009). At low light, light-limited phytoplankton increases its nitrogen quota (minimum needs of a resource) (Rhee & Gotham, 1980), probably consequence of an increase in chlorophyll per unit of biomass to maximize photosynthesis (Dubinsky & Stambler, 2009). More evidence—including stoichiometry analyses—is

needed to ascertain that free-floating plants use more P and that light-limited phytoplankton uses more N. If this is so, at free-floating plant dominance the competition for nutrients with phytoplankton may lead to coexistence. Indeed, in 16 cold wetlands dominated by free-floating plants, phytoplankton chlorophyll concentrations were mostly intermediate (ca. 20–80 $\mu\text{g l}^{-1}$, 11 wetlands) and rarely high ($\geq 100 \mu\text{g l}^{-1}$, 3 wetlands) (Smith, 2012, p. 681, Fig. 4). Also, in warm shallow lakes and reservoirs, phytoplankton chlorophyll was high under duckweed (ca. 50–70 $\mu\text{g l}^{-1}$) (de Tezanos Pinto et al., 2007, p. 52, Fig. 3; O’Farrell et al., 2011, p. 280, Fig. 3), water lettuce (ca. 30–60 $\mu\text{g l}^{-1}$) (Ayala et al., 2007, p. 626, Fig. 5), and water hyacinth (ca. 50 $\mu\text{g l}^{-1}$) (Bicudo et al., 2007, p. 1125, Fig. 3) dominance. Interestingly, lakes dominated by submerged plants (>75% cover) have one order of magnitude lower chlorophyll concentrations (1.6–2.7 $\mu\text{g l}^{-1}$) (Allende et al., 2009) compared to those in the free-floating plant regime, suggesting that submerged plants outcompete phytoplankton (probably due to low nutrient availability). Though the evidence presented for free-floating plant regimes suggest coexistence of free-floating plants and phytoplankton, the phytoplankton biomass increased at least three times whenever free-floating plants disappeared (Ayala et al., 2007, p. 626, Fig. 5; Bicudo et al., 2007, p. 1125, Fig. 3; de Tezanos Pinto et al., 2007, p. 52, Fig. 3; O’Farrell et al., 2011, p. 280, Fig. 3). This emphasizes the interactive effects of competition for light (where free-floating plants should outcompete phytoplankton) and perhaps nutrients (which may lead to coexistence) between producers.

The anoxia below dense free-floating plants mats (Table 2) is mostly a consequence of decreased phytoplankton photosynthesis (Rodríguez et al., 2012), decreased diffusion of oxygen through the mats (Morris & Barker, 1977; Hamilton et al., 1995), increased respiration and macrophyte decomposition (Bianchini Junior, 2003), and high oxygen demand from sediments (Belanger, 1981) (Fig. 1a). The anoxia plays an important role in the release of nutrients (Søndergaard et al., 1990; Beutel, 2006; O’Farrell et al., 2009) from the sediments (Fig. 1a), which potentially fuel the growth of free-floating plants and phytoplankton. Phytoplankton levels remain relatively low because of the strong light limitation, however.

Anoxia seems to exert a minor control on phytoplankton biomass (de Tezanos Pinto et al., 2007) but

favors development of anoxygenic photosynthetic bacteria (Izaguirre et al., 2010) (Fig. 1a). Zooplankton biomass declined with anoxia (Fontanarrosa et al., 2010) (Fig. 1a). Also, zooplankton biomass was lower at sites dominated by free-floating plants (Table 2) than at sites without free-floating plants. Under *E. crassipes* beds, omnivore-piscivores were more abundant than to omnivore-planktivorous fish, hence cascading effects on phytoplankton are not likely to be strong (Meerhoff et al., 2003).

Based on the evidence compiled from our literature search, we suggest that when free-floating plants dominate there is a strong positive feedback between macrophytes and the environment (shading, anoxia, and high nutrient availability) that facilitates the self-replacement of free-floating plants but hinder phytoplankton development (Fig. 1a). We further suggest that dense cover of free-floating plants causes low(er) phytoplankton biomass by the strong shading they engineer. The shading effect overrides the high nutrient availability and low grazing pressure that should promote phytoplankton growth.

Phytoplankton regime

Dense phytoplankton biomass creates turbid waters, but still light availability is usually sufficient for phytoplankton growth. Phytoplankton immobilizes nutrients in its biomass, oxygenates the water column when photosynthesizing (but consume oxygen during respiration), potentially secretes allelochemicals (dashed arrows in Fig. 1b), and leads to increased pH due to high photosynthesis. Because of high nutrient consumption at light sufficiency (Litchman et al., 2004), the availability of dissolved inorganic nutrients can be limiting or scarce (Fig. 1b). The secretion of nutrients from the sediments is depressed at high oxygen availability compared to anaerobic conditions (Søndergaard et al., 2003; Beutel, 2006). Nevertheless in eutrophic shallow lakes the release of nutrients can also be high at oxygen saturation (Søndergaard et al., 1990, p. 141, Fig. 1), or during the night because of low oxygen. Phytoplankton biomass is likely to increase with trophic status. At light-sufficient conditions, laboratory (de Tezanos Pinto & Litchman, 2010) and lake-scale (Schindler et al., 2008) experiments show that light-nutrient availability plays an important role in shaping the phytoplankton community composition. At low

nitrogen to phosphorus ratios, Cyanobacteria prevail, whereas at high ratios green algae dominate (Schindler et al., 2008; de Tezanos Pinto & Litchman, 2010). Also, laboratory experiments show that increased temperatures should favor Cyanobacteria and green algae (Lürling et al., 2012). Yet, field studies found that at high temperatures Cyanobacteria out-compete green algae (Jeppesen et al., 2009, p. 1936, Fig. 8) and that the percentage of the total phytoplankton biovolume attributable to Cyanobacteria increases steeply (Kosten et al., 2012). Also, the interaction of increased temperatures and eutrophication should favor Cyanobacteria over other phytoplankton (Paerl & Huisman, 2009; Wagner & Adrian, 2009).

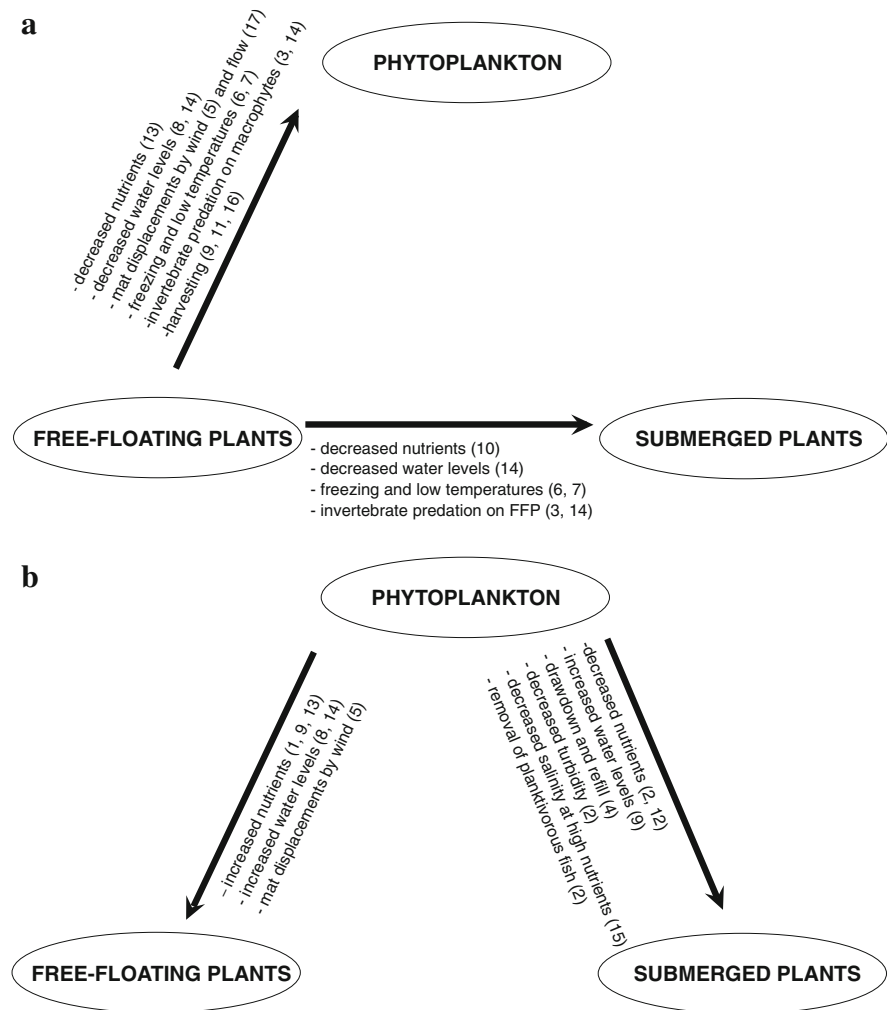
Laboratory experiments show that phytoplankton hinders duckweed (*Lemna gibba* L.) growth and biomass, mostly because of nutrient competition (and also because of increased pH) (Szabó et al., 1999, 2005). The competition for nutrients decreases with increased duckweed cover (Szabó et al., 1998) probably as light-limited phytoplankton is unable to use nutrients at high rates.

At phytoplankton dominance (blooms) inedible taxa—unpalatable or toxic—may prevail, decreasing the grazer-mediated recycling of nutrients and thus causing low nutrient availability (Sunda et al., 2006) (Fig. 1b). In tropical and subtropical lakes, because of the high predation pressure of omnivorous-planktivorous fishes, the zooplankton community is characterized by small-sized zooplankton, including rotifers, and small-sized cladocerans, and copepods (Meerhoff et al., 2003; Iglesias et al., 2008), which exert low control on phytoplankton. In temperate lakes, however, the zooplankton community is characterized by large-sized zooplankton, including *Daphnia* spp. (Meerhoff et al., 2007a), which exert strong control on phytoplankton, provided that fish predation is low. Also, zooplankton abundances are generally higher in temperate than in subtropical lakes, (probably) due to the high fish predation in subtropical lakes (Meerhoff et al., 2007a, b).

Stability of the free-floating plants and phytoplankton regimes

A community can be considered locally stable either if it persists some period of time in spite of forces potentially capable of altering its structure (Sutherland,

Fig. 2 Perturbations that may trigger shifts in free-floating plants (**a**) and phytoplankton (**b**) regimes. FFP free-floating plants. Numbers in brackets indicate references: (1) Portielje & Roijackers (1995), (2) Scheffer et al. (1993), (3) Sosa et al. (2007), (4) Van Geest et al. (2007), (5) O'Farrell et al. (2009), (6) Sculthorpe (1967), (7) van der Heide et al. (2006), (8) O'Farrell et al. (2011), (9) Ayala et al. (2007), (10) Scheffer et al. (2003), (11) de Tezanos Pinto et al. (2007), (12) Ibelings et al. (2007), (13) Roijackers et al. (2004), (14) Marshall & Junor (1981), (15) Jeppesen et al. (2007), (16) Bicudo et al. (2007), (17) Lacoul & Freedman (2006)



1974) or if it returns to equilibrium when perturbed (Connell & Sousa, 1983). Many examples demonstrate the ecological stability of free-floating plants in the face of perturbations. In Mexico, the water hyacinth *E. crassipes* dominated for more than 12 years in the Guadalupe Dam despite herbicides application (Lugo et al., 1998) and for more than 30 years in the Valsequillo reservoir despite herbicides application and plant shredding (Mangas-Ramirez & Elías-Gutierrez, 2004). In Bolivia, the water lettuce *P. stratiotes* recovered after two annual massive harvests in laguna Alalay (Ayala et al., 2007). In Zambia and Zimbabwe, the small water fern *S. molesta* dominated for more than a decade in Lake Kariba, despite floods, drops in water level, introduction of fish, and use of grasshoppers for biological control (Marshall & Junor, 1981). Regarding phytoplankton dominance, plenty of

evidence supports its stability in shallow lakes (Naselli-Flores et al., 2003).

Case studies: perturbations that may cause shifts between free-floating plants and phytoplankton regimes

True critical transitions can be caused by a tiny but critical change in conditions (Scheffer, 2009), and/or by a disturbance pushing the system across the border of a basin of attraction (Beisner et al., 2003; Scheffer, 2009). Figure 2 summarizes the current evidence on disturbances that may cause shifts in free-floating plants and phytoplankton regimes.

Perturbations that may interrupt a free-floating plant regime—and cause a regime shift toward either

phytoplankton or submerged plants regime—include high wind, flow and/or rains, freezing, predation, decreased nutrients, decreased water levels, and/or harvesting (reviewed in Fig. 2a).

In a long-term field study (1998–2009), the natural disappearance of duckweeds and water lettuce—linked to marked drops in water level (drought)—resulted in dominance by bloom-forming Cyanobacteria and major changes in the environment (significant increases in pH, humic acids, and suspended solids) (O'Farrell et al., 2011, p. 280, Fig. 3).

The Garças reservoir (526 ha, eutrophic and shallow, Brazil), which was sampled monthly during 8 years (1997–2004), is a case study of a free-floating plant-phytoplankton regime shift driven by harvesting. From June to September 1999, the large *E. crassipes* (water hyacinth) was removed—from 40 to 70% cover to almost 0%—to avoid mosquitos' proliferation. This resulted in a catastrophic (within ca. 1 month) and a permanent (1999–2004) regime shift to phytoplankton dominance (an approximate five-fold increase in chlorophyll) with heavy cyanobacteria blooms, and significant increases in turbidity and pH (Bicudo et al., 2007). The harvesting of water hyacinth markedly accelerated the process of eutrophication in this reservoir, with significant increases in TN and TP (Bicudo et al., 2007). Though a shift toward submerged plants is in theory plausible, Bicudo et al. (2007) described a lack of submerged vegetation during the study period.

The study of Laguna Alalay (219 ha, shallow and eutrophic, in Bolivia) between the years 1989 and 2006 is another example of a regime shift caused by harvesting. Between years 1989 and 1991, the lake periodically shifted from phytoplankton to submerged vegetation, linked to changes in water level. But, after a restoration project (run in 1997) involving sediment and fish removal, the submerged vegetation disappeared permanently. Phytoplankton dominated until the medium-sized *P. stratiotes* started to achieve high biomasses. During 2004–2006, a total of 5,331 tons of water lettuce were harvested to use as a fertilizer. Within 2 months, phytoplankton chlorophyll increased at least two-folds (Ayala et al., 2007, p. 626, Fig. 5). The biomass of the water lettuce *P. stratiotes* recovered after the two annual harvests; whenever *P. stratiotes* was abundant, the phytoplankton chlorophyll quickly decreased (within 1 month) (Ayala et al., 2007).

Harvesting of small-sized *Lemna* spp. (duckweeds) mats in a field experiment in Laguna Grande (Argentina) (from 100 to 0% cover) caused, within 1 week, a ca. eightfold increase in phytoplankton biomass, a significant drop in dissolved inorganic nutrients, a reversion of anoxia, and an increase in pH (de Tezanos Pinto et al., 2007, pp. 51–52, Figs. 2, 3).

Scheffer et al. (2003) suggested that if nutrient levels have been sufficiently decreased, a one-time removal of floating plants might tip the balance to an alternative stable state dominated by submerged plants. Nevertheless, in all the case studies presented here, the harvesting of free-floating plants resulted in either permanent or periodic shifts to phytoplankton dominance, with lack of submerged vegetation, probably as these systems are eutrophic.

We found only few cases of shifts from free-floating to submerged plant dominance. The man-made Lake Kariba (Zambia and Zimbabwe) shifted from *S. molesta* D. Mitch dominance (20% cover, 600–1,000 km² for more than a decade) to submerged plant dominance (Marshall & Junor, 1981, p. 479, Fig. 2), but back to free-floating plant dominance (*E. crassipes*) 10 years later (1996–1999) (reviewed in Scheffer et al., 2003); what drove these community shifts, is, however, unclear. Also, Smith (2012) studied inter-annual variation in vegetation community composition in cold temperate wetlands, and found that only one of the 19 wetlands dominated with free-floating plant shifted to submerged plant dominance. Ponds dominated by free-floating plants were more frequent, than ponds dominated by submerged plants (Smith, 2012). Submerged plant lakes occurred at TP concentrations below ca. 125 $\mu\text{g l}^{-1}$ and TN concentrations below ca. 2,000 $\mu\text{g l}^{-1}$, whereas free-floating plant dominance occurred at TP concentrations above ca. 125 $\mu\text{g l}^{-1}$ and within a broad range of TN concentrations (ca. 1,200–5,500 $\mu\text{g l}^{-1}$) (Smith, 2014, p. 3, Fig. 1). This suggests that a shift from a free-floating plant to a submerged plants regime would happen if nutrients (mostly TP) are decreased.

The potential drivers of community shifts from a phytoplankton to free-floating plant regime include increased nutrients and water level, and wind displacement of mats (Fig. 2b). Phytoplankton was outcompeted by *P. stratiotes* in a eutrophicated reservoir, probably due to increased total phosphorus availability (Ayala et al., 2007, p. 625, Fig. 3a). Decreases in water level followed by refill promoted growth of free-

floating plants (*E. crassipes* and *Salvinia herzogii* Raddi), probably through increased P availability (Thomaz et al., 2006). Likewise, increased water levels seem to favor the development of water lettuce (O'Farrell et al., 2011) and water fern (Mitchell, 1969). This, in turn, should decrease phytoplankton biomass through dilution and shading.

In field mesocosms, O'Farrell et al. (2009) placed dark meshes over a phytoplankton-dominated regime—mimicking the shading generated by dense free-floating plants mats—and after 2 weeks they observed a decrease in phytoplankton biomass (ca. 27%) and disappearance of many species (30). In the same study, periodic shifts in the shading—simulating a dynamic effect of wind in displacing the mats of free-floating plants—were unable to control the phytoplankton biomass (O'Farrell et al. 2009).

A wide body of studies assessed the drivers of regime shift between phytoplankton and submerged vegetation (Fig. 2b). These drivers include, biomanipulation, decreased nutrients, turbidity and salinity (at high nutrients), and changes in water levels (reviewed in Fig. 2b). Remarkably, regime shifts from phytoplankton to submerged plant dominance seem to happen less frequently than in the reverse direction. For example, in a comparative study of 70 lakes, Van Geest et al. (2007, p. 42, Table 4) found that (generally) inter-annual vegetation community shifts from submerged plant rich lakes to submerged plant poor lakes occurred up to three times more frequently than in the reverse direction.

Meerhoff & Jeppesen (2009) predicted that increased eutrophication and temperatures will enhance phytoplankton and free-floating plant regimes over submerged plants. Indeed, studies show that increased nutrients in the water column favor phytoplankton (Bornette & Puijalon, 2011) or free-floating plants (Portielje & Roijackers, 1995; Netten et al., 2010) over submerged plants. Field experiments showed that increased temperatures and nitrogen promoted free-floating plant growth (*Lemna* spp. and *Spirodella*) without excluding submerged plant biomass (*Potamogeton* spp., *Ceratophyllum demersum*, *E. muttalli*) (Feuchtmayr et al., 2009). Also, using field data and a mathematical model, Peeters et al. (2013) showed an advance in the onset of duckweeds dominance by 2 weeks in 25 years, consequence of a 1 °C increase in average maximum daily winter temperatures. Finally, the probability of

Cyanobacteria dominance (within a TP range of 70–215 $\mu\text{g l}^{-1}$) increased because of climate-induced changes in thermal regimes, rather than direct temperature effects (Wagner & Adrian, 2009).

Is there enough evidence to acknowledge critical transitions for free-floating plants and phytoplankton shifts?

Patterns in field data that suggest the possibility of alternative stable states include abrupt state transitions over time, sharp boundaries between contrasting sites, bimodal state variable frequency distribution, or dual response to driving parameters (Schröder et al., 2005; Scheffer, 2009). Nevertheless, none of these are conclusive of alternative stable states (Scheffer, 2009).

The empirical evidence compiled in our review shows abrupt regime transitions over time in the same system, as shown in several descriptive studies (Ayala et al., 2007; Bicudo et al., 2007; Crosetti & Bicudo, 2007; O'Farrell et al., 2011) and sharp boundaries between communities in space in the same system, observed both in field surveys (Abdel-Tawwab, 1998; Izaguirre et al., 2004) and mesocosm experiments (Abdel-Tawwab, 2006; de Tezanos Pinto et al., 2007). The contrasting differences between regimes in terms of light availability, oxygen concentration, and pH resulted from the influence of the dominant producer on the environment, which increased the probability of its own persistence and decreased the chances of development of the alternative producer.

Though the evidence gathered in this review suggests that the contrasting regimes may represent stable states, more hints of the existence of alternative attractors (e.g., dual relationship to a control factor (Scheffer, 2009)), plus manipulation experiments and mathematical models are needed to draw conclusive evidence of the existence of critical transitions among free-floating plants and phytoplankton.

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