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LETTER

Evolutionary emergence of alternative stable states in shallow lakes

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Abstract

Ecosystems under stress may respond abruptly and irreversibly through tipping points. Although mechanisms leading to alternative stable states are much studied, little is known about how such ecosystems could have emerged in the first place. We investigate whether evolution by natural selection along resource gradients leads to bistability, using shallow lakes as an example. There, tipping points occur between two alternative states dominated by either submersed or floating macrophytes depending on nutrient loading. We model the evolution of macrophyte depth in the lake, identify the conditions under which the ancestor population diversifies and investigate whether alternative stable states dominated by different macrophyte phenotypes occur. We find that eco-evolutionary dynamics may lead to alternative stable states, but under restrictive conditions. Such dynamics require sufficient asymmetries in the acquisition of both light and nutrient. Our analysis suggests that competitive asymmetries along opposing resource gradients may allow bistability to emerge by natural selection.

KEY WORDS

adaptive dynamics, bistability, diversification, eco-evolutionary model, macrophyte, phytoplankton, tipping points

INTRODUCTION

Ecosystems are exposed to increasing anthropogenic stress (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019). Under such stress, ecosystems could possibly respond in an abrupt and irreversible way which may be a concern for future conservation (Scheffer et al., 2001). Theoretically, evolution may affect the stability of ecosystems (Kondoh, 2003; Loeuille, 2010). Evolution by natural selection could prevent the extinction of a species, through evolutionary rescue (Gomulkiewicz & Holt, 1995). Evolutionary trajectories can themselves exhibit bistability; in such cases, the endpoint of evolution depends on initial trait values (Lu & Hedin, 2019). Dakos et al. have postulated that trait variation could alter the bistability of an ecosystem, either by hastening the tipping point, delaying it or even removing bistability (Dakos et al., 2019). However, could natural selection, instead of having a rescue effect, allow the emergence of the very dynamics that threaten ecosystems with

tipping points? That question does not hold only for the shallow lake ecosystem which we take as an example, but also for other ecosystems exposed to opposing gradients of resources (seagrass beds (Williams, 1987), grasslands (Olf et al., 1990) or wetland (Sanderson et al., 2008)). Identifying the conditions under which ecosystems would evolve to a more fragile state would allow better ecosystem management, by preventing tipping point responses.

In ecosystems with tipping points, strong positive feedbacks are responsible for alternative stable states (van Nes et al., 2016), meaning that at least two equilibria are locally stable in a given range of environmental conditions. The transition from one stable equilibrium to another is abrupt: a small environmental perturbation past a threshold can push the ecosystem into a qualitatively different state (Holling, 1973). The management of ecosystems with alternative stable states is difficult since a large restoration is needed to return to the pre-collapsed (and often desirable) state. Examples of ecosystems with alternative stable states include drylands which can shift

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from shrub vegetation to desert (Kéfi et al., 2007), tropical forests that can switch from forest to savanna and back (Scheffer et al., 2014; Staver et al., 2011) and coral reefs that can shift from healthy coral dominance to being overgrown by macro-algae (Knowlton, 1992). Yet, the most studied examples of alternative states are found in shallow lakes (Gsell et al., 2016).

In shallow lakes, tipping responses can be found between two stable states dominated by either submersed or floating macrophytes. Submersed macrophytes remove nutrients from the water and maintain a clear water state. The positive feedback responsible for alternative stable states is the following: when nutrient loading exceeds a certain threshold, floating macrophytes are able to grow, shade submersed macrophytes and hinder submersed macrophyte growth. As a result, more nutrients become available to floating macrophytes, floating macrophytes grow more, further shade and eventually outcompete the submersed macrophytes (Scheffer et al., 2003). Such strong positive feedback may favour the emergence of hysteresis, implying that a large reduction in nutrient loading is required to restore the dominance of submersed macrophytes and the clear water state in the lake.

Evolution can interact with the stability of ecosystems in at least three ways: changing their persistence (number of species lost), resistance (amount of environmental change that a system can take before shifting to another state) and resilience (return time to equilibrium). Models of evolutionary rescue suggest that a population's heritable variability may promote its persistence in a changed environment (Gomulkiewicz & Holt, 1995). In larger communities, Cortez et al. found contrasting effects of eco-evolutionary feedbacks: evolution of predator traits can prevent the loss of species, while the evolution of consumed species tends to do the opposite. There, evolution increased persistence at the ecosystem level (Cortez et al., 2020). Regarding the return time to equilibrium, evolution tends to increase resilience in small communities and decrease it in large communities (Loeuille, 2010). However, only recently are we beginning to examine whether evolution could also alter the stability properties of ecosystems with tipping points (Chaparro Pedraza et al., 2021; Dakos et al., 2019).

We hypothesise that evolution could affect the presence of alternative stable states, by modifying the strength of interactions that are at the very basis of some positive feedback loops. Chaparro-Pedraza et al. showed that a minor ecological change can trigger a future tipping point. In that study, a momentary decrease in mortality triggers the evolution of body size, resulting in a population shift in the long run (Chaparro-Pedraza & de Roos, 2020). This study focuses on the impact of evolution in ecosystems with tipping points, but the role of evolution in the emergence of positive feedbacks that is responsible for the existence of tipping points is, to our knowledge, unaddressed.

How could ecosystems with tipping points have emerged in the first place? The literature that looks at ecosystems

with tipping points from an ecological perspective, without evolution, examines the conditions that are necessary for alternative stable states to occur in different systems (De Roos & Persson, 2002; Kéfi et al., 2007; Mumby et al., 2007; Scheffer et al., 2003). However, we do not know if and under which conditions alternative stable states will emerge in an ecosystem after its long-term evolution. Put differently, the question is: when does evolution lead to the emergence of the strong positive feedbacks responsible for the observed tipping points in ecosystems around us?

Here, we tackle this question in the case of stable states between the dominance of two competing phenotypes in the shallow lake. We model the adaptive dynamics of a macrophyte population whose depth can evolve. The living depth of a macrophyte can be under the genetic control of the length of its stem or the buoyancy of its leaves. We first study the conditions under which a macrophyte population diversifies to at least two phenotypes that are needed to dominate alternatively. We expect that the way nutrients and light are distributed in the water column and the type of competition between diversified phenotypes should be a strong determinant of evolutionary outcomes. Second, we study how the evolved community responds to increased nutrient loading. If coexisting phenotypic populations are indeed differentiated in terms of the competitive ability for light and nutrients, this difference should determine the response of the lake to perturbations. We hypothesise that in sufficiently differentiated phenotypic populations, asymmetries in competitive abilities for light and nutrients should create strong positive feedbacks that could lead to the establishment of alternative stable states.

We use three evolutionary scenarios combining three mechanisms present in a shallow lake (Figure 1). In the first scenario, depth determines the quantity of light and nutrients that a macrophyte population has access to. In the second scenario, we add asymmetric competition created by shading: shallower macrophyte populations shade deeper populations. In the third scenario, we add a higher nutrient exploitation efficiency for macrophyte populations that grow closer to the sediment. In what follows, we define the ecological dynamics of a single macrophyte population, describe the ecological mechanisms that can affect evolutionary trajectories in the macrophyte populations and then present results structured along the three described evolutionary scenarios.

MATERIALS AND METHODS

Bistability can be found for different types of aquatic organisms: submersed vs. floating macrophytes (Scheffer et al., 2003), or different phytoplankton layers (Bengfort & Malchow, 2016; Huisman & Weissing, 1995). In both cases, organisms live at different depths, which determine their competitive abilities for light and nutrients, and potential asymmetries between phenotypes. We, thus, model the eco-evolutionary dynamics of a

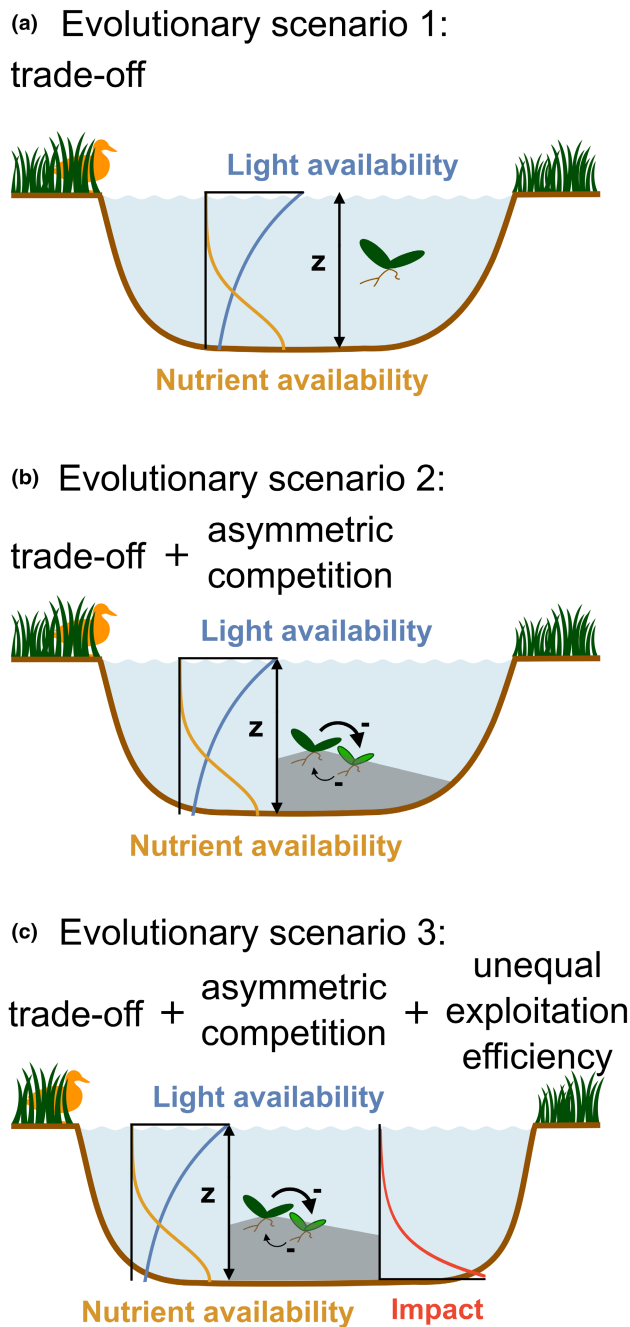


FIGURE 1 Three evolutionary scenarios based on different combinations of ecological mechanisms in a shallow lake model. (a) In scenario 1, the depth at which a macrophyte population settles is simply associated with a trade-off between access to light and nutrients. (b) In scenario 2, in addition to the trade-off, we introduce asymmetric competition for light, that is, a phenotype that grows higher in the water column shades all phenotypes below it. (c) In Scenario 3, on top of the two previous mechanisms, we consider different nutrient exploitation efficiencies whereby phenotypes that grow deeper in the water column are more efficient at removing nutrients. (z denotes water column depth, arrows the light competition between macrophyte phenotypes and impact is the effect of macrophytes on nutrient content in the water column).

photosynthetic organism whose depth in the water column of a lake, z , evolves. For a rooted macrophyte, depth corresponds to the height that its canopy reaches,

which is controlled by the length of its stem (Arthaud et al., 2012). The depth at which phytoplankton layers form depends on phytoplankton size, density and propensity to form colonies (Alexander & Imberger, 2008). In the rest of the paper, for simplicity, we refer to the photosynthetic organism as the macrophyte.

Depth in the lake, z , varies from the surface ($z = 0$) to the bottom ($z = z_b$). In the rest of the paper, small values of z are closer to the surface and are referred to as “shallower” or “above”. Larger values of z are deeper and referred to as “below”.

Ecological dynamical model of a macrophyte population

We modelled the growth rate of a single macrophyte population following Scheffer et al. (2003):

$$f(M) = \frac{dM}{dt} = M \left(g \frac{n}{n+h} \frac{1}{1+aM+W} - l \right) \quad (1)$$

with

$$n = \frac{N}{1+qM} \quad (2)$$

Change in a macrophyte population biomass, M , over time depends on the maximum production rate g , which is limited by nutrients and light, and on a loss rate l (Equation 1). Nutrient limitation and light limitation are two multiplied Monod terms. Light limitation depends on W , water background turbidity, and the shading induced by conspecifics, aM . Nutrient limitation depends on the amount of available nutrients in the water column, n , with half-saturation constant h , which represents the competitive ability to acquire nutrients. We do not explicitly model nutrient dynamics, but the feedback between plant growth and nutrient concentration is captured by Equation 2. The amount of nutrients available for macrophyte uptake n depends on the quantity of nutrients N that would be present in the absence of macrophytes, and on the density of macrophytes that take up nutrient from the water at rate q (Equation 2). A list of parameters is presented in Appendix a, Table a1.

Evolutionary analysis using adaptive dynamics

We analyse the evolution of a macrophyte population, characterised by a trait z , depth in the lake, using adaptive dynamics (Dieckmann & Law, 1996; Geritz et al., 1998; Metz et al., 1992). From the ecological model (Equations 1 and 2), we derive the dynamics of a dominant population M with a trait z interacting with a mutant population M_m with trait z_m . Depth determines different competitive abilities for light and nutrient, and depend on the scenario in which the population evolves, so N , W , a and q become functions of depth, z (Equations 8–11):

$$\frac{dM}{dt} = g M \frac{n(z, z_m)}{n(z, z_m) + h} \frac{1}{1 + a(z, z) M + a(z, z_m) M_m + W(z)} - l M \quad (3)$$

$$\frac{dM_m}{dt} = g M_m \frac{n(z_m, z)}{n(z_m, z) + h} \frac{1}{1 + a(z_m, z) M + a(z_m, z_m) M_m + W(z_m)} - l M_m \quad (4)$$

where

$$n(z, z_m) = \frac{N(z)}{1 + q(z) M(z) + q(z_m) M_m(z_m)}, \quad (5)$$

$$n(z_m, z) = \frac{N(z_m)}{1 + q(z) M(z) + q(z_m) M_m(z_m)}$$

The main assumption of adaptive dynamics is the separation of evolutionary and ecological timescales. The introduced mutant is assumed to be rare ($M_m \approx 0$) while the resident has time to reach its equilibrium (M^*). Using these two assumptions in Equations 3, 4 and 5, we write the invasion fitness of a mutant, that is, the per capita growth rate of a rare mutant of trait z_m in the stationary conditions set by the resident population of trait value z :

$$s(z_m, z) = g \frac{n(z_m, z)}{n(z_m, z) + h} \frac{1}{1 + a(z_m, z) M^* + W(z_m)} - l \quad (6)$$

with

$$n(z_m, z) = \frac{N(z_m)}{1 + q(z) M^*(z)} \quad (7)$$

Whether a mutant is able to invade the resident population depends on the sign of the invasion fitness (Equation 6). Identical phenotypes can neither invade nor be invaded by the resident population and have a null invasion fitness: $s(z, z) = 0$. Mutants with a negative invasion fitness die out. Mutants with a positive invasion fitness successfully invade the resident population.

From the invasion fitness equation (Equation 6), we derive the fitness gradient and find long-term evolutionary outcomes, or evolutionary singularities, which are then classified by deriving the convergence and invasibility criteria from fitness second derivatives (Geritz et al., 1998).

The three ecological mechanisms explored in the three evolutionary scenarios

Vertical trade-off for light and nutrients (evolutionary scenarios 1, 2 and 3)

In every scenario, we model light attenuation underwater following the Beer–Lambert law as in (Huisman &

Weissing, 1995) and assume that nutrients are stored in the sediment and brought into the water column by eddy diffusion as in Klausmeier and Litchman (Klausmeier & Litchman, 2001). These assumptions translate into the following expressions (Figure 2a,b):

$$N(z) = \frac{N_0}{u\sqrt{2\pi}} e^{-(z_b - z)^2 / (2u^2)} \quad (8)$$

where N_0 is the total nutrient content in the water and u controls the strength of nutrient diffusion (Figure 2a). A high u implies that nutrients are more homogeneously distributed, while a low u corresponds to strong stratification of nutrients in the water column. The total quantity of nutrients N_0 is constant.

$$W(z) = W_0(e^{wz} - 1) \quad (9)$$

W_0 is the baseline turbidity and w controls the strength of light attenuation (Figure 2b). A low w implies that luminosity barely changes with depth z , while a high w means that the bottom of the lake is darker than the surface.

Asymmetric competition by shading (evolutionary scenarios 2 and 3)

We consider a second mechanism, that of asymmetric competition for light (i.e. shading, Figure 2c), by assuming that the shading coefficient a varies with the relative depth between two populations:

$$a(z_m, z) = \frac{2a_0 e^{b(z_m - z)}}{1 + e^{b(z_m - z)}} \quad (10)$$

The intensity of such asymmetric competition depends on the depth difference between the two competing populations and the sensitivity parameter b (Figure 2c). We study this mechanism in the second and third evolutionary scenarios.

Unequal nutrient efficiency (evolutionary scenario 3)

The third mechanism introduces the fact that macrophytes living at different depths have different competitive abilities for nutrients. (Figure 2d). Deeper macrophytes remove nutrients more effectively than shallower macrophytes because they prevent the resuspension of sediment by intercepting nutrients diffusing from the bottom with their shoots. We include this mechanism in scenario 3 by letting the parameter q increase with macrophyte depth z :

$$q(z) = q_0 e^{pz} \quad (11)$$

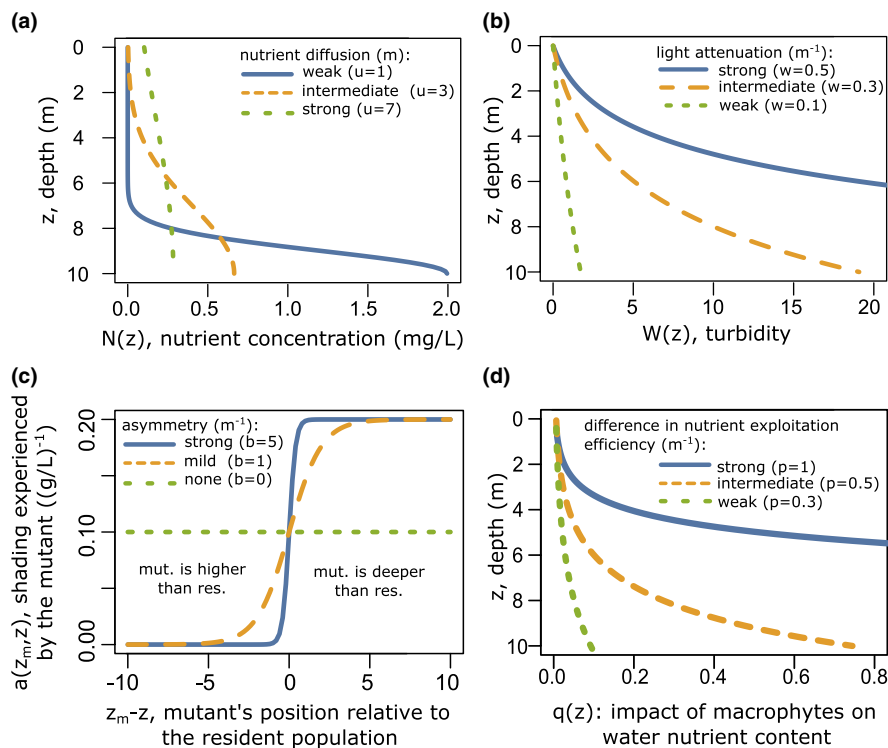


FIGURE 2 Functions used to model each mechanism. (a) Trade-off between nutrients and light: nutrients are diffused from the bottom of the lake with strength u , but the total quantity of nutrients in the water is constant ($N_0 = 5 \text{ mg/m}^2$). (b) Trade-off between nutrients and light: turbidity increases with depth at a different pace depending on w , the strength of attenuation ($W_0 = 1$). (c) Asymmetric competition by shading: parameter b controls how steep the asymmetric competition between two populations is ($a_0 = 0.01 (\text{g/L})^{-1}$). (d) Unequal exploitation efficiency: Macrophytes ability to retain nutrients increases with depth ($q_0 = 0.005 (\text{g/L})^{-1}$).

Deep macrophytes have a stronger impact on water nutrient content than shallower macrophytes. Setting $p = 0$ is equivalent to turning off this difference in exploitation efficiencies, which is the case in scenarios 1 and 2 (Figure 2d).

Identifying conditions for diversification

We obtain two types of evolutionary singularities in the model: strategies that are convergent and non-invasible, that is, selected strategies towards which the population evolves, and convergent but invasible strategies, or branching points. Branching points correspond to depths at which disruptive selection acts and polymorphism emerges. Evolution to a branching point leads to diversification and thus satisfies the first condition for the emergence of a system with alternative stable states: the existence of at least two phenotypes.

The sign plot of the invasion fitness (Equation 6) according to the mutant trait z_m and the resident trait z is a Pairwise Invasibility Plot (PIP) and is used to visualise long-term evolutionary singularities. We numerically computed the value of z^* for different combinations of nutrient diffusion u and light attenuation w using the invasion fitness equation. We present how the singularity varies with environmental conditions

in E^3 -diagrams (Ferrière & Legendre, 2013), which are plots showing the value of the singularity as a function of parameters u , w , b and p . The range of parameters used is sufficiently large to capture extreme strategies (macrophyte population evolving to the bottom or to the surface of the lake).

When diversification is possible, we ran simulations of the eco-evolutionary dynamics for combinations of parameters that yielded a branching point. The parameters for which we ran simulations were sampled at regular intervals of u and w to cover the diversification region. Population densities are integrated continuously, with discrete mutation events. They start with a single ancestor phenotype ($z = 1$) at its equilibrium density. At every time step, potential parent populations mutate at a rate of 10^{-4} times their density. If the parent population does mutate, the mutant trait is drawn from a normal distribution centred around the parent trait with a standard deviation of 0.05 meters. The mutant is then introduced with an initial density of 10^{-2} g/L ($\approx 0.01\%$ of resident population density). The mutant population grows depending on its population dynamics described in Equations 3 and 4, experiencing light and nutrient competition from all other populations. Populations falling below the density of 10^{-2} g/L are considered extinct. At the next mutation event, populations above that threshold are potential candidates for generating

mutants, and evolution proceeds with the sequential replacement of populations.

Identifying the emergence of alternative stable states after evolution

To assess whether evolution leads to the emergence of alternative stable states, we model an ecological perturbation after the system has reached an evolutionary equilibrium. We assume that the system responds at an ecological timescale, that is, faster than evolution, so that only the equilibrium density is affected. After the eco-evolutionary simulations reach a quasi-equilibrium (when trait z values did not change by more than 0.1 meters during 2×10^7 timesteps), we retrieve the value of the depth z_1 and z_2 of the two phenotypes. We then analyse their corresponding ecological dynamics using the same model as described before, with the growth of the phenotype i depending on the phenotype j :

$$\frac{dM_i(z_i)}{dt} = M_i \left(g \frac{n(z_i, z_j)}{n(z_i, z_j) + h} \frac{1}{1 + a(z_i, z_j)} \frac{1}{M_j + a(z_i, z_i)} \frac{1}{M_i + W(z_i)} - l \right) \quad (12)$$

with

$$n(z_i, z_j) = \frac{N(z_i)}{1 + q(z_j)} \frac{1}{M_j(z_j) + q(z_i)} \frac{1}{M_i(z_i)} \quad (13)$$

with $i = 1, j = 2$ for the growth of phenotype 1 and $i = 2, j = 1$ for the growth of phenotype 2. Then, we determine the ecological equilibria and their stability from the eigenvalues of the Jacobian matrix for a gradient of the total amount of nutrients in the lake N_0 from 0 to 10 mg/m².

Ecological equilibria and evolutionary singularities were computed using Wolfram Mathematica 12.2, and eco-evolutionary simulations were run in R using the Isoda integration method.

RESULTS

Evolutionary scenario 1: Light and nutrients determine the evolution of a macrophyte's depth in the lake

In the first scenario, where light is attenuated with depth and nutrients are diffused from the bottom of the lake (Figure 1a), depth simply determines the quantity of light and nutrients a macrophyte population had access to. As a result, the macrophyte population systematically evolves towards a selected depth (Figures 3a, 4a).

For example, in our $z_b = 10$ meter deep model lake, with strong light attenuation ($w = 0.3$) and intermediate

nutrient diffusion ($u = 3$), no population survives shallower than 2 meters (because of nutrient limitation, Appendix b), and no population survives deeper than 7 meters (because of light limitation, Figure 3a1). The macrophyte population evolves towards a depth of 5 m (Figure 3a). This trait value z^* is the evolutionary singularity, in other words, the point where the selection gradient is null (star in Figure 3a1). At the singularity, no mutant population can invade below or above the resident population. Put differently, in a resident population established above the singularity, any deeper mutant can invade and replace the resident population, whereas in a resident population established below the singularity, any mutant population slightly above can invade. Thus, the evolutionary singularity is convergent and stable, as illustrated by the corresponding simulation (Figure 3a2).

Figure 4a1 shows in a E^3 -diagram the effect of nutrient diffusion u on the evolutionary singularity. As nutrient diffusion u increases, the evolved depth in the lake z^* decreases. As nutrients are more homogeneously distributed, macrophytes evolve closer to the surface where they make the most of the available light.

Finally, we explore the combined effect of nutrient diffusion and light attenuation (Figure 4a2). For every value of u and w (Figure 4a2), the singularity is always a selected strategy. The corners of the figure correspond to the extreme combinations of nutrient and light availability: in the top left corner, low nutrient diffusion and strong light attenuation render life impossible. In the bottom left corner, high light availability leads the population to evolve to the bottom of the lake (deep blue). In the top right corner, nutrients are strongly diffused so the population evolves to the surface (light grey). For any intermediate combination, macrophytes evolve to intermediate depths corresponding to the best trade-off between access to light and nutrients. When considering only a light–nutrient trade-off, evolution is not able to lead to an ecosystem with alternative states as the ecosystem is always dominated by a single, best-adapted, macrophyte population (Figure 4a2).

Evolutionary scenario 2: Asymmetric competition by shading enables macrophyte diversification

In the second scenario, in addition to the light–nutrient trade-off, we consider the effect of asymmetry in competition for light. Adding this mechanism enables the macrophyte population to diversify, meaning that more than one phenotype can be supported in the lake.

The PIP illustrates how such a diversification arises (Figure 3b1). The population converges again towards the singularity (positive invasion fitness above the diagonal for mutants below z^* , positive invasion fitness below the diagonal for mutants above z^*). However, once at z^* , both shallower and deeper mutants have a positive

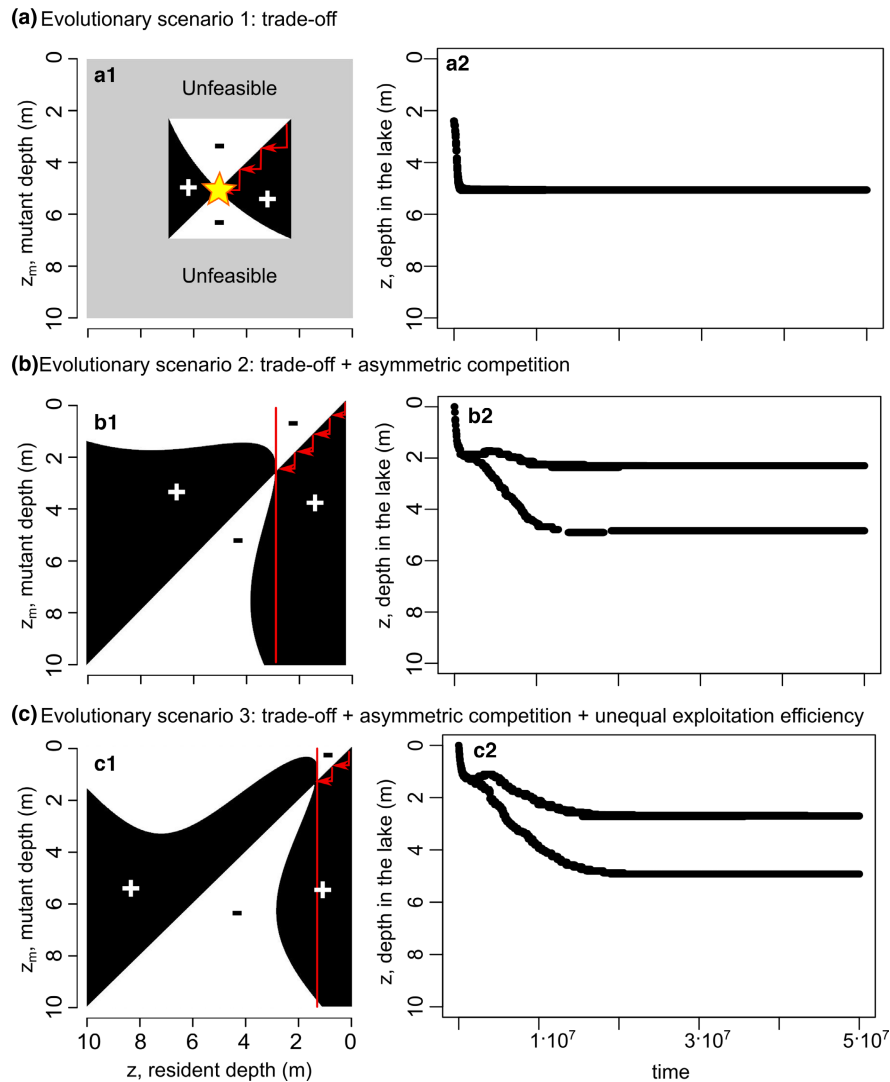


FIGURE 3 (Left panels): Pairwise Invasibility Plots (PIPs) showing the invasion fitness' sign depending on resident and mutant traits. Red arrows show the direction of evolution due to selected mutations. Star denotes the selected strategy. Vertical red lines serve as guides to see the positive invasion fitness of mutants around Branching Points. Grey area denotes the trait values where the population growth is not feasible. (Right panels): Simulation of the eco-evolutionary dynamics corresponding to the red arrows and evolutionary singularity found in the PIPs. (a) Evolutionary scenario 1 ($u = 3, w = 0.3$): the population converges to a selected depth. (b) Evolutionary scenario 2 ($u = 5.1, w = 0.1$): the singularity corresponds to a branching point where disruptive selection acts, and the population diverges into two phenotypes. (c) evolutionary scenario 3 ($u = 4.5, w = 0.15$): as in scenario 2, diversification occurs.

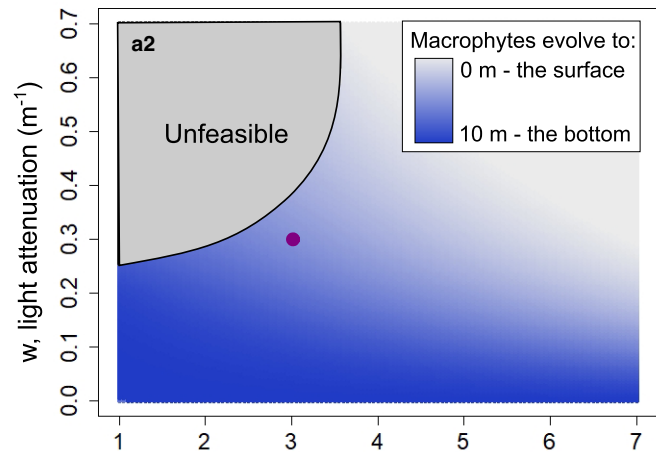
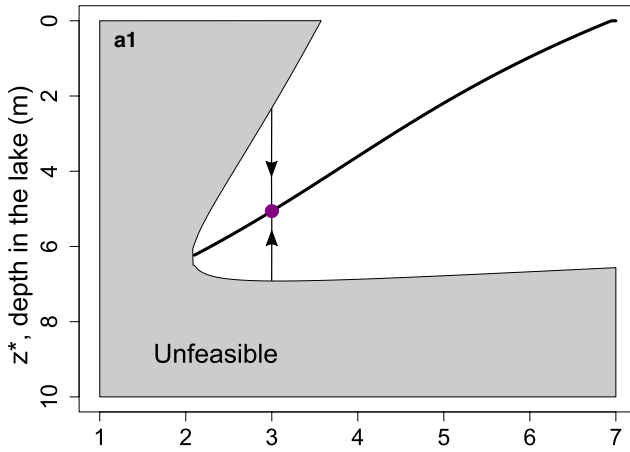
fitness (the vertical line passing through z^* is in black regions in the vicinity of z^*). At this point, the selection is disruptive: the singularity is inviable. The eco-evolutionary simulation illustrates how two populations with distinct phenotypes evolve from a monomorphic population (Figure 3b2).

Figure 4b1 and 4b2 show that diversification is only possible in a subset of light attenuation and nutrient diffusion conditions. Within the branching region, macrophytes diversify into two phenotypes in the most restrictive light and nutrient conditions (crosses situated at the upper left boundary of the branching region), while as conditions become less restrictive (lower light attenuation and higher nutrient diffusion) the population diversifies in more than two phenotypes. For sufficient

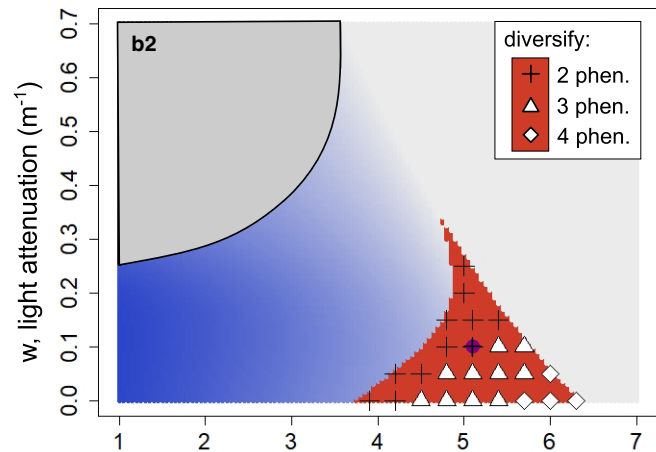
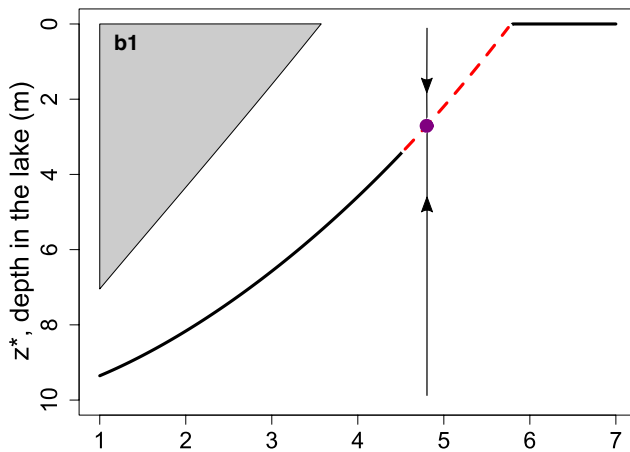
nutrient diffusion ($u > 6.2$), the population systematically evolves towards the surface. The region of diversification changes shape and becomes larger with a stronger asymmetric competition (higher b , presented in Appendix c), and leads to increased diversity at the end of the simulation, emphasising that asymmetric competition drives disruptive selection.

We study whether the diversified ecosystem with multiple phenotypes could show alternative states when responding to a perturbation (Appendix d). In the 25 simulated cases (marked in the diversification subset of Figure 4b2), whether the system diversified into 2, 3 or 4 phenotypes, an increase in nutrient concentration in the lake (N_0) caused only gradual transitions from the dominance of a single phenotype to the coexistence of

(a) Evolutionary scenario 1: trade-off



(b) Evolutionary scenario 2: trade-off + asymmetric competition



(c) Evolutionary scenario 3: trade-off + asymmetric competition + unequal exploitation efficiency

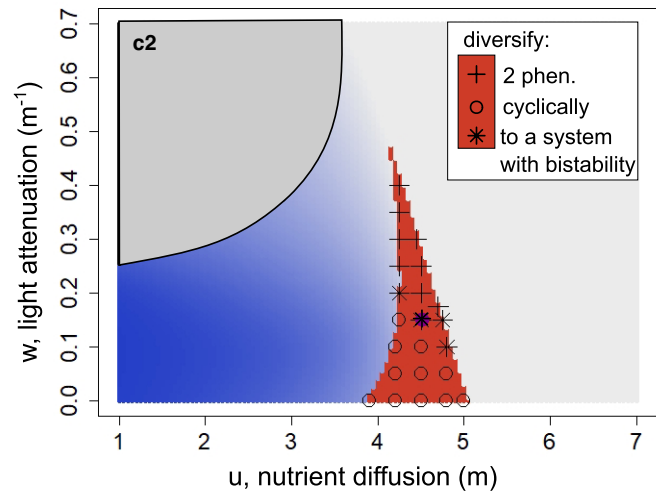
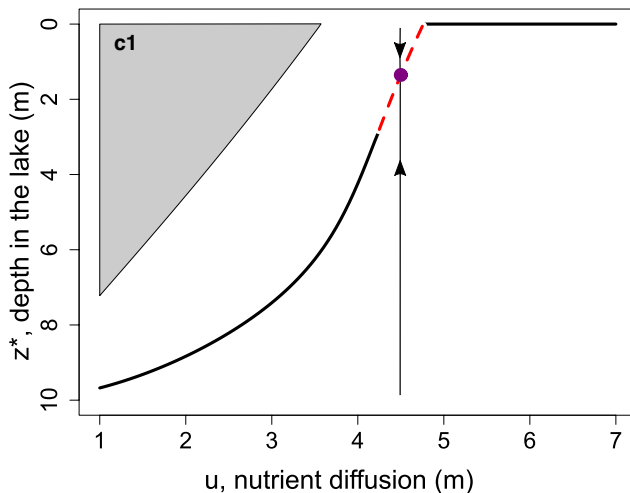


FIGURE 4 (Left panels) E^3 -diagram showing the evolutionary singularity according to the strength of nutrient diffusion u . The population converges to a selected strategy and settles there (solid black line a1), or converges towards the line and then diversifies (Branching point, dashed red, b1, c1). Arrows show the direction of evolution for phenotypes above or below the singularity. (Right panels) Joint effect of nutrient diffusion and light attenuation on the singularity. In the blue region of the plot, the population converges towards a selected depth. Diversification is possible in the red region. Symbols are placed where we ran simulations. Purple dots correspond to simulations of Figure 3. (a) Evolutionary scenario 1: The population always converges to a selected depth. (b) Evolutionary scenario 2: In most cases, the population converges to a selected depth, but some combinations of nutrient diffusion and light attenuation enable the emergence of polymorphism (b2). (c) Evolutionary scenario 3: Ecological perturbations after diversification can lead to tipping points (star in c2).

multiple phenotypes; it does not exhibit abrupt transitions between alternative stable states (Appendix d Figure d2).

In conclusion, scenario 2 enables the diversification of the population, which satisfies a necessary condition for the emergence of alternative stable states (existence of multiple phenotypes). However, the combination of the two mechanisms alone is not sufficient for evolution to lead to bistability.

Evolutionary scenario 3: Unequal exploitation efficiencies kick off a positive feedback

In the third scenario, we consider a third mechanism, that of better efficiency in nutrient exploitation when a macrophyte grows close to the bottom of the lake. Under such conditions, evolution can lead to a system that diversifies and exhibits bistability.

As in scenario 2, diversification occurs in a restricted set of nutrient diffusion and light limitation

(Figures 3c1,c2, 4c1, c2). However, this set is smaller in scenario 3 compared to scenario 2 and spans different limits. In some cases, after diversification, one of the phenotypes goes extinct, and the remaining monomorphic population returns to the convergent singularity where disruptive selection started again, leading to a cyclical diversification behaviour (Figure 5c).

In four out of the 12 simulated cases (marked by black stars in Figure 4c2), we found bistability (Figure 5e). In the case of cyclic branching (Figure 5c), we find that the emergence of bistability depends on the trait values during the evolutionary cycle. During the late stage of the cycle and before the population becomes monomorphic again, bistability exists (Figure 5g), while at the early part of the cycle, bistability is not possible (Figure 5f). During the evolution of macrophytes, the lake can, or not, experience tipping point responses. For the rest of the cases, only smooth transitions (Figure 5a,d), just like in scenario 2 (Appendix d Figure d2), occur.

In sum, the third scenario shows a full range of possible eco-evolutionary dynamics, from cases in which

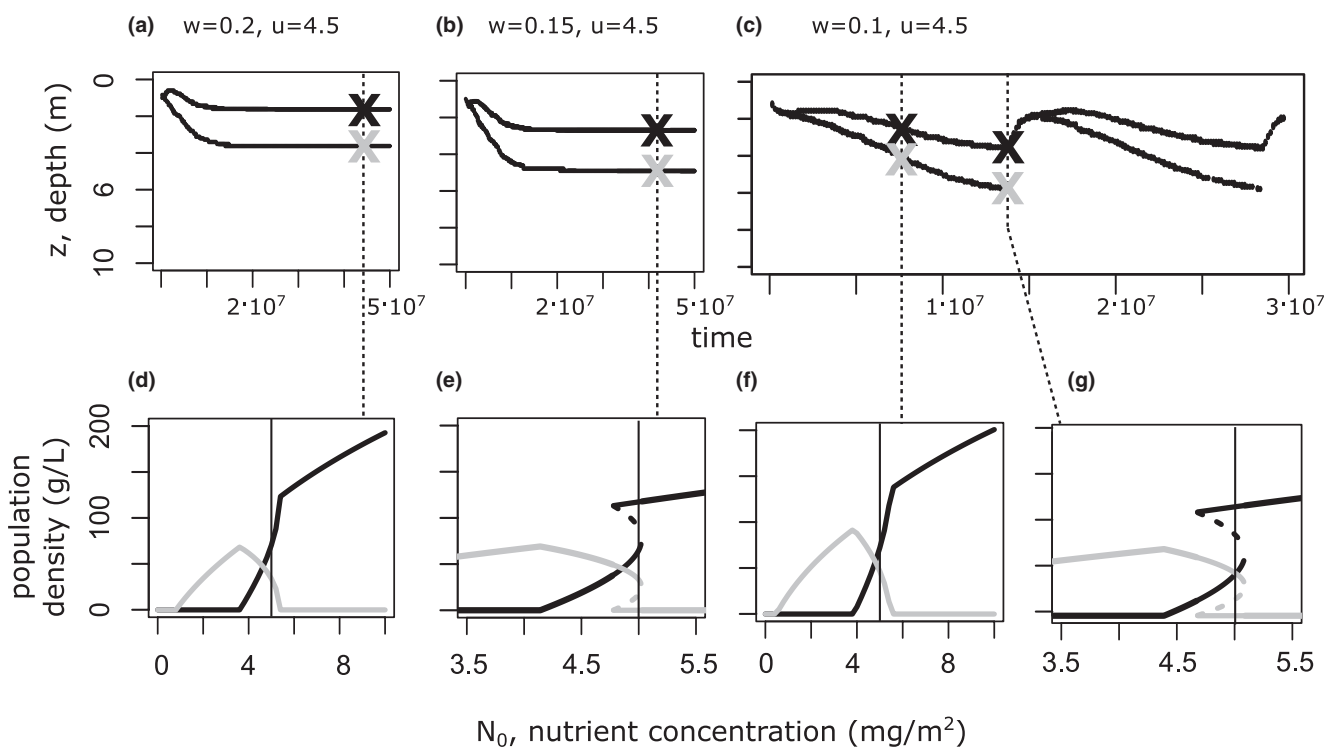


FIGURE 5 Ecological dynamics with and without alternative states following evolution. (a–c) Eco-evolutionary simulations of the third evolutionary scenario for different light attenuation conditions. Each line represents the evolution of a phenotype with a specific growth depth z . In most cases, evolution leads to two dominant phenotypes (a, b), whereas in some cases to cyclical diversification events where after branching one phenotype goes extinct abruptly and diversification repeats itself (c). Crosses mark trait values of w and u used for the bifurcation analysis of panels (d–g). (d–g) Bifurcation analysis of an ecological perturbation of the two evolved macrophyte populations (black and grey lines) from panels (a–c). Thin vertical lines recall N_0 at which evolution took place. Solid lines are stable equilibria, dashed lines are unstable equilibria of population density as a function of increasing nutrient concentration in the lake N_0 . In some cases, the two populations evolve to a depth where they do not respond with tipping points to nutrient enrichment, but with smooth transitions (transcritical bifurcations) from the dominance of the deeper macrophyte (grey line) to coexistence and outcompetition by the shallower macrophyte at high nutrient levels (a, d). In other cases, populations evolve at a depth where nutrient enrichment leads to coexistence followed by the deeper macrophyte collapsing through a tipping point (fold bifurcation) when outcompeted by the shallower phenotype (b, e). In the case of cyclical diversification, the response to nutrient enrichment depends on the timing of disturbance: smooth early in the evolutionary cycle (f), or abrupt (through a tipping point) closer to the end of the cycle (g).

a monomorphic population settles at a given depth, to cases in which disruptive selection leads to stable or cyclic diversification. In the latter two cases, for a specific range of conditions and depending on the depth of the two diversified phenotypes, bistability can emerge.

DISCUSSION

Tipping point responses are increasingly considered a major risk to ecosystems under global change (Barnosky et al., 2012), but the question of when evolution could lead to their emergence has been neglected. We explored whether the evolution of a photosynthetic organism in a shallow lake can lead to an ecosystem with bistability. Using adaptive dynamics, we studied the evolution of vertical position in a lake to find conditions yielding the emergence of alternative states. We show that, in addition to a light–nutrient trade-off gradient, two other mechanisms are necessary. First, asymmetric competition for light (or nutrient, Appendix e) is necessary to induce diversification. Second, unequal exploitation efficiency ensures – but only under some conditions – that evolution leads to an ecosystem with alternative stable states (Table 1). In general, our findings corroborate the ecological mechanisms inducing alternative states between floating and submersed macrophytes (Scheffer et al., 2003). Our results shed light on how each mechanism affects the eco-evolutionary dynamics of macrophytes and their ability to display tipping points.

Diversification: The necessary condition for the emergence of alternative states

Bistability in shallow lakes is characterised by the dominance of competing organisms occupying different depths in the water column (i.e. submersed and floating macrophytes, layers of phytoplankton). We first studied the conditions that allowed macrophytes to diversify into at least two distinct phenotypes. Since the shape of trade-offs between traits can determine possibilities of diversification (de Mazancourt & Dieckmann, 2004; Kisdi, 2015), we expected that changing the trade-off with the parameters controlling nutrient diffusion and light attenuation (u and w) would be sufficient to induce

diversification. In the case of a weak trade-off (no light attenuation and low nutrient diffusion, or strong light attenuation and strong nutrient diffusion), we expected the population to converge to extreme strategies, that is, the surface or the bottom of the lake. In the case of phytoplankton evolving in a poorly mixed water column, Klausmeier and Litchman (2001) and Wickman et al. (2017) found contrasting results (evolution to an optimal depth in the former and diversification in the latter) using different growth functions. We found that by only modifying the nutrient diffusion and light attenuation parameters, regardless of the resulting trade-off, the population never diversifies (Evolutionary scenario 1). Instead, the population evolves to a single optimal depth, as found in Klausmeier and Litchman (2001).

The mere existence of a trade-off is, thus, insufficient to lead to diversification. Instead, we found that asymmetric competition for light (or nutrient, Appendix e) through shading enabled diversification (evolutionary scenario 2). This finding resonates with Kisdi (1999) who showed that the evolutionary dynamics of a continuous trait in a simple asymmetric Lotka–Volterra competition model led to diversification. In terrestrial communities, a forest model in which competition for light is asymmetric also leads to diversified communities (Falster et al., 2017). Nonetheless, asymmetric competition does not always lead to diversification. We found combinations of asymmetric competition, nutrient diffusion and light attenuation that lead to a single selected depth. Such convergence occurs for strong nutrient diffusion or strong light attenuation when the incentive to go to the surface overpowers the effects of asymmetric competition. In other cases, convergence to a single depth occurs when environmental conditions are limiting, that is, close to the “Unfeasible” area. In limiting conditions, macrophyte biomass is not sufficient for asymmetric competition between the resident and the mutant populations to induce disruptive selection (Doebeli & Dieckmann, 2000; Kisdi, 1999).

While our results show that diversification may lead, in some instances, to alternative stable states, we do not mean that sympatric speciation is needed for these to occur. In particular, branching events could represent other phenomena ranging from the emergence of (within species) polymorphism to the sorting of phenotypes through assembly processes based on pre-existing

TABLE 1 Summary of the mechanisms of each scenario and their result.

Scenario	Mechanism			Outcome	
	Trade-off between nutrient and light	Asymmetric competition for light	Unequal exploitation efficiency	Diversification	Alternative stable states
1	Yes	No	No	No	No
2	Yes	Yes	No	Yes	No
3	Yes	No	Yes	No	No
4	Yes	Yes	Yes	Yes	Yes

variability (both intra-specific variability and inter-specific variability). For deeper discussions on how eco-evolutionary dynamics relate to ecological community assembly, see (Brännström et al., 2012; Edwards et al., 2018; Leibold et al., 2022).

Evolution allows for alternative states only for a limited range of conditions

Our main objective was to see under which conditions the shallow lake would evolve to bistability. Only in the presence of the third mechanism, higher nutrient exploitation efficiency of the deepest phenotype, alternative states emerge, and only in a certain range of nutrient and light availability. This result concurs with Scheffer et al. (2003) where the presence of three competitive asymmetries is necessary for alternative states and Huisman and Weissing (1995) who showed that two phytoplankton populations can exhibit alternative stable states on a water column with a light and nutrient trade-off. These asymmetries, though necessary, are not sufficient since only some parameter conditions enable the emergence of bistability.

Although bistability may emerge in our eco-evolutionary model, we do not find that the macrophytes diversify to two distinct phenotypes, that is, “floating” ($z = 0$) and “submersed” ($z = z_b$) typically observed in ponds as modelled by Scheffer et al. (Scheffer et al., 2003). The intermediate depth phenotypes could resemble pondweeds (*Potamogeton spp.*) and stoneworts (*Charophytes spp.*), which are both submersed macrophytes and have been shown to asymmetrically compete for light and carbon (Van Den Berg et al., 1999). Theoretical work on the evolution of phytoplankton predicts diversification between light specialists and nutrient specialists (Troost et al., 2005), and studies have shown that alternative stable states are possible in models of competition for light and nutrients in aquatic ecosystems (Huisman & Weissing, 1995; Yoshiyama & Nakajima, 2006), under the condition that competitors are well differentiated in their ability to uptake light and nutrients. In our case, evolved phenotypes are not very different but only separated by approximately 2 meters (Figure 3b2, c2). This relatively small difference between the diversified phenotypes is explained by the trade-off for light and nutrients that allows diversification only within a range of (intermediate) depths. Out of this range, diversification is not possible because shallow phenotypes lack nutrients, whereas deep phenotypes lack light. Consequently, we find a specific range of conditions where light and nutrient availability allow the existence of diversified phenotypes (red area in Figure 4b2, c2) and an even more limited range where the phenotypes constitute alternative states (stars in Figure 4c2). Cyclic branching events and further work on the depth difference between the two phenotypes (Appendix f) support

the idea that sufficient differentiation is required between the two phenotypes.

Small phenotypic differences can lead to strong positive feedbacks

It might seem odd that alternative states arise for rather small phenotypic difference between the two phenotypes. The strength of the positive feedback depends not only on the difference in depth (which sets the effect of competition) but also on the relative position of the two macrophytes in the lake (that sets the effect of the light–nutrient opposing gradient). For two phenotypes growing in similar but shallow depths, outcompetition occurs gradually (Figure 5a,d), whereas when the two macrophytes become less similar and grow in deeper depths the resulting asymmetries are strong enough to create positive feedbacks and tipping point responses. This is important to note, as our finding contrasts the results of other eco-evolutionary models (e.g. Kéfi et al., 2007), where variation in the trait that directly controls the strength of the positive feedback determines the extent of alternative states. In our case, it is the interaction between direct competition and the environmental conditions under which competition acts that determines whether alternative states emerge.

Note that alternative stable states between the dominance of phenotypes that are not very differentiated may not be as spectacular as the documented cases of bistability, since the two phenotypes here have functional traits that do not vastly differ.

Limitations

Our model is a simplistic representation of lake ecology and macrophyte evolution. We assumed that total available nutrient content is fixed, meaning that basal nutrient content does not vary with macrophyte biomass. Nutrient storage in the sediment is high, such that nutrient recycling from macrophyte biomass has a negligible effect on the nutrient stock. It would be worthwhile to explore if the feedback between macrophyte nutrient uptake, decay and mineralisation could affect our conclusions. Furthermore, macrophytes have complex life cycles (Bakker et al., 2013), reproducing by rhizomes and acquiring nutrients not just by their roots but also by their stems and leaves. Here, by using the evolving trait, z , as the depth at which a macrophyte lives, we simplistically assume that this depth determines the average availability of nutrients and light as well as the average shading and nutrient access of a macrophyte. A more realistic formulation would integrate along the whole depth that a macrophyte lives, as floating macrophytes have roots that can grow deep in the water column, and submersed macrophytes absorb

nutrients not just from their roots. Alternatively, our evolving depth could also represent diversified phytoplankton layers. Our results complement previous theoretical studies on the evolution of a single or multiple depth phytoplankton layers (Huisman & Weissing, 1995; Klausmeier & Litchman, 2001; Mellard et al., 2011) by showing that two layers of phytoplankton may also represent alternative states.

CONCLUSION

Our work can help better understand how evolution works in the context of opposing resource gradients and multiple feedbacks. The opposing gradients of nutrient and light availability creating a trade-off between two resources are not unique to lakes. Such trade-offs can be found in seagrass beds (Williams, 1987), or in grasslands selecting for deep roots or higher stems in terrestrial plants (Olff et al., 1990). In wetlands, opposing stress gradients of anoxic to oxygenated soils coexist with a low to high salinity gradient (Sanderson et al., 2008), and in hilly drylands, water availability follows an opposite gradient to erosion stress (Bautista et al., 2007). Studying coexistence in opposing gradients of resources has been done extensively in aquatic systems (Huisman & Weissing, 1995) as well as in terrestrial systems (Falster et al., 2017; Reynolds & Pacala, 1993). While evolution is expected to predominantly lead to a single best-adapted phenotype or coexistence, we suggest that considering competitive asymmetries that can be caused by the opposing gradient itself could allow alternative stable states to emerge by natural selection. Whether such competitive asymmetries are present and could explain the occurrence of alternative stable states in ecosystems around us is a worthy question to ask.

AUTHOR CONTRIBUTIONS

All authors conceived the model and contributed to the interpretation of results. AA performed the analysis and wrote the first draft. All authors made corrections and modifications, and approve the submitted version.

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DATA AVAILABILITY STATEMENT

Scripts used to perform analysis, simulations, and produce Figures 3–5 and supplementary figures are available online: <https://doi.org/10.5281/zenodo.6606311>

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