E-Article

Adaptive Evolution Can Both Prevent Ecosystem Collapse and Delay Ecosystem Recovery

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abstract: There is growing concern about the dire socioecological consequences of abrupt transitions between alternative ecosystem states in response to environmental changes. At the same time, environmental change can trigger evolutionary responses that could stabilize or destabilize ecosystem dynamics. However, we know little about how coupled ecological and evolutionary processes affect the risk of transition between alternative ecosystem states. Using shallow lakes as a model ecosystem, we investigate how trait evolution of a key species affects ecosystem resilience under environmental stress. We find that adaptive evolution of macrophytes can increase ecosystem resilience by shifting the critical threshold, which marks the transition from a clear-water state to a turbid-water state to a higher level of environmental stress. However, following the transition, adaptation to the turbid-water state can delay the ecosystem recovery back to the clear-water state. This implies that restoration could be more effective when implemented early enough after a transition occurs and before organisms adapt to the alternative state. Our findings provide new insights into how to prevent and mitigate the occurrence of regime shifts in ecosystems and highlight the need to understand ecosystem responses to environmental change in the context of coupled ecological and evolutionary processes.

Keywords: ecosystem tipping points, ecosystem resilience, eco-evolutionary feedback, shallow lakes, alternative stable states.

Introduction

Ecosystem resilience is the ability of an ecosystem to absorb disturbances without shifting to an alternative, and often undesirable, state (May 1976; Scheffer et al. 2001; Folke et al. 2004). Ecological theory predicts that ecosystems can respond abruptly to gradual environmental change if they cross a critical threshold (i.e., tipping point) and shift to an alternative stable state (ASS; Scheffer and Carpenter 2003; Folke et al. 2004; Schroder et al. 2005). The presence of ASSs causes hysteresis, which is the lack of reversibility of an ecosystem, hindering the recovery of the ecosystem once it shifts to an alternative state. Such abrupt transitions, also known as regime shifts, can have large impacts on society by affecting the functioning of ecosystems and the services they provide (Levin and Lubchenco 2008; Carpenter et al. 2009). Existing theory has investigated the ecological processes involved in ecosystem tipping points and developed methods to predict regime shifts in response to environmental change (Guttal and Jayaprakash 2008; Scheffer et al. 2009; Carpenter et al. 2014). However, this theoretical framework still neglects evolutionary processes (Dakos et al. 2019).

Environmental change can trigger both ecological and evolutionary responses (Singer et al. 1993; Palumbi and Mu 2001; Olsen et al. 2004; Parmesan 2006; Allendorf and Hard 2009; Walther 2010). Evolutionary responses can rescue populations from extinction in degrading environmental conditions (Bell and Gonzalez 2009) and mediate both community and ecosystem responses to environmental change (Fussmann et al. 2007). Some progress has been made in integrating ecological and evolutionary processes into predictive models of ecosystems (Norberg et al. 2012; Palkovacs et al. 2012; Urban et al. 2012; Bolchoun et al. 2017). However, we know little about how coupled ecological and evolutionary processes can affect tipping point responses in natural ecosystems (Dakos

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et al. 2019), particularly those associated with population adaptation to gradual environmental change (Singer et al. 1993; Palumbi and Mu 2001; Olsen et al. 2004; Parmesan 2006; Allendorf and Hard 2009; Walther 2010).

Of the many examples of regime shifts in natural ecosystems (Biggs et al. 2018; Rocha et al. 2018), the regime shift in shallow lakes between clear-water and turbid-water states is the most studied (Scheffer et al. 1993; Scheffer 2009). The clear-water state dominated by macrophytes is typically preferred by society (Levin and Lubchenco 2008; Carpenter et al. 2009; Thomaz and Cunha 2010) but can shift to a turbid-water state dominated by algae when there is excessive nutrient loading (Scheffer 2009). In shallow lake ecosystems, the competitive interaction between macrophytes and algae—mediated through strong positive feedbacks—sets up the potential for ASSs (Scheffer 2009). Therefore, changes in traits underlying competition and affecting the positive feedbacks between macrophytes and algae have the potential to influence the occurrence of tipping points and the dynamics of shallow lake ecosystems under environmental stress.

Here, we extend an ecological model of the shallow lake system (Scheffer 2009; Dakos et al. 2019) to include evolutionary dynamics of macrophytes under environmental stress using quantitative genetics. Building on the framework proposed by Dakos et al. (2019), our eco-evolutionary model incorporates gradual evolution of a macrophyte trait, notably shading tolerance, which is a key trait affecting macrophyte competitive ability. This trait can therefore evolve in response to increased turbidity produced by the algae population. In short, we model how changes in turbidity can change the fitness landscape of macrophytes and thereby drive evolution in traits governing the competitive interactions between macrophytes and algae. As such, macrophyte evolution in this model ecosystem has the potential to alter the population dynamics of algae, which feeds back to affect selection pressures on macrophytes. Our modeling approach therefore enables exploring the feedback loops between ecological and evolutionary processes in the shallow lake ecosystem. We investigate the transient dynamics of the system besides its asymptotic behavior to understand the system responses to temporal changes in environmental stress. Since mechanisms analogous to those causing regime shifts in shallow lakes operate in other ecosystems (Scheffer 2009), our modeling approach is general enough for investigating the interaction between ecological and evolutionary processes in a wide range of ecosystems with tipping points under environmental stress.

Model Description and Analysis

Ecological Model

The basis of our eco-evolutionary model is a shallow lake ecological model that has been used to describe the ecological dynamics that cause transitions between the clear-water (macrophyte-dominated) and the turbid-water (algae-dominated) alternative states (Scheffer et al. 1993; Scheffer 2009). The main mechanism underlying the existence of ASSs in shallow lakes is that macrophytes reduce turbidity by limiting algae (i.e., phytoplankton) growth, whereas turbidity (mostly driven by algae density) decreases macrophyte growth because of shading. The densities of the algae A and the macrophyte M are given as follows (Scheffer 2004):

$$\frac{dM}{dt} = r_M M\left(1 - \frac{M}{K_M}\frac{h_A^P + A^P}{h_A^P}\right), \tag{1}$$

$$\frac{dA}{dt} = r_A A\left(1 - \frac{A}{T_0}\frac{h_M + M}{h_M}\right). \tag{2}$$

In this model, r_A and r_M are the maximum growth rates of the algae and macrophytes, respectively; T_0 is the nutrient loading and defines the carrying capacity of algae; and K_M is the carrying capacity of the macrophyte population. Algae limit macrophyte growth because of shading according to a Hill function whose steepness is defined by P and with half saturation h_A. The term h_A is the level of algae density where shading has half of its maximum effect on macrophyte growth. In turn, macrophytes negatively affect the growth of algae by limiting nutrient availability that defines algae carrying capacity following an inverse Monod function with half saturation h_M.

The half-saturation parameters, h_A and h_M, determine the effect of algae on macrophytes and vice versa; therefore, they can be influenced by traits affecting the interspecific competitive ability of algae and macrophytes. Here, we extend previous ecological models, which treat these parameters as fixed, to explore how the evolution of macrophytes affects the system dynamics.

Eco-Evolutionary Model

To model evolution in the macrophyte population, we assume a quantitative trait x that affects the response of macrophytes to algae h_A. The quantitative trait might correspond to, for example, photopigment synthesis that enhances shading tolerance (Henley and Ramus 1989). Following Dakos et al. (2019), we assume that

$$h_A(x) = h_{A0}e^{\lambda x},$$

where h_{A0} is the background half saturation and λ (>0) is an exponential factor that determines how h_A increases as function of the trait x.

We define x as a quantitative macrophyte trait that is normally distributed with mean $\bar{x}$ and phenotypic variance σ^2; therefore, its density function is $p(x, \bar{x}) = 1/(\sigma\sqrt{2\pi})\exp[-(x - \bar{x})^2/(2\sigma^2)]$. Following quantitative

genetics, the phenotypic variance σ^2 has genetic σ_G and environmental σ_E components, $\sigma^2 = \sigma_G^2 + \sigma_E^2$. Trait heritability is determined by the ratio of genetic variance to total trait variance (σ_G^2/σ^2).

As a result of resource allocation trade-offs, any trait change that increases competitive ability will be associated with a metabolic cost that affects macrophyte performance (Rien 1999). In our case, a resource trade-off between light harvesting (enhancing shade tolerance) and carboxylation capacities causes a reduction in growth (i.e., biomass yield per unit absorbed light) with increasing photopigment synthesis (Henley and Ramus 1989). To include this trade-off in the model, we consider an optimal trait value θ when turbidity is low, and thus the trait value (e.g., photopigment synthesis) is low. However, when the trait value increases, the increased cost of macrophyte competitive ability translates into a reduction in macrophyte carrying capacity K_M. Hence, K_M is maximal when $x = \theta$ and decreases in a Gaussian manner as x moves away from θ (similar to the trait-based approach of Lande 2009):

$$K_M(x) = K \exp\left(\frac{-(x-\theta)^2}{2\tau^2}\right)$$

In this expression, K is the macrophytes carrying capacity under low-turbidity conditions, and τ determines the width of the Gaussian function. Notice that no evolution is possible when the trait value x is fixed at the optimum ($x = \theta = 0$) and has no variance, such that $h_A = h_{A0}$ and $K_M = K$. Thus, this trait-based framework collapses into the classic shallow lake ecological model (eqq. [1], [2]).

The fitness W (i.e., per capita growth rate) of a macrophyte with trait x is given by

$$W(x, A, M) = r_M\left(1 - \frac{M}{K_M(x)}\frac{h_A(x)^P + A^P}{h_A(x)^P}\right),$$

and the average fitness $\bar{W}$ of the macrophyte population is

$$\bar{W}(\bar{x}, A, M) = \int_{-\infty}^{\infty} W(x, A, M)p(x, \bar{x})\,dx.$$

The ecological dynamics of the eco-evolutionary model are thus given by

$$\frac{dM}{dt} = M\bar{W}(\bar{x}, A, M), \tag{3}$$

and equation (2).

Following standard quantitative genetics techniques (Lande 1976), the phenotypic trait change depends on the fitness gradient and genetic variance such that

$$\frac{d\bar{x}}{dt} = \sigma_G^2\frac{\partial\bar{W}(\bar{x}, A, M)}{\partial\bar{x}}. \tag{4}$$

Asymptotic Stability

We use as a reference the asymptotic behavior of the ecological model (eqq. [1], [2], where $h_A = h_{A0}$, $K_M = K$) and compare this to the asymptotic behavior of the eco-evolutionary model (eqq. [2]–[4]). Specifically, we evaluate the equilibrium (steady state) and its stability using the MATLAB package MATCONT to numerically compute the continuation of equilibrium points as a function of the nutrient loading T_0 and their associated eigenvalues for the ecological and the eco-evolutionary model. This analysis enables us to determine how the eco-evolutionary feedback alters the stability of the ecological system. To do so, we evaluate the difference between the level of nutrient loading at which tipping points occur in the presence of eco-evolutionary feedback compared with the level of nutrient loading at which tipping points occur predicted by the ecological model alone (fig. 1). We test the robustness of our results by extending this analysis for the three parameters that affect the ecological equilibrium, namely, K, h_{A0} and h_M (fig. S1, available online). Note that r_M and r_A do not affect the ecological equilibrium (see the supplemental PDF, available online).

Transient Dynamics

To investigate the eco-evolutionary responses of the shallow lake ecosystem to environmental change, we simulate the system when ecological and evolutionary processes occur at comparable timescales. For this analysis, we assume phenotypic variance σ^2 to be equal to genetic variance σ_G^2 (i.e., high heritability) and use equations (2)–(4) when nutrient loading changes over time (i.e., $dT_0/dt = \varphi$). We examine the eco-evolutionary trajectories of the macrophyte density as lake conditions deteriorate as a result of nutrient loading increases ($\varphi > 0$) and as macrophytes recover when nutrient loading decreases ($\varphi < 0$). We compare the eco-evolutionary trajectories generated under various levels of genetic variance σ_G^2 and, thus, evolutionary rate. Specifically, we study eco-evolutionary trajectories under two main scenarios. The first is a scenario of increasing nutrient loading (T_0 increases from 0.01 to 7.5) at a slow rate ($\varphi = 0.001$ in fig. 2*A*, 2*B*) and a fast rate ($\varphi = 0.01$ in fig. 3*A*, 3*B*) in the absence and presence of genetic trait variance. In this scenario, we also test for the effects of the rate of environmental change and of the level of genetic variance on eco-evolutionary dynamics. Specifically, we simulate trajectories for increasing nutrient loading under a range of environmental rate change ($\varphi =$ 0.0001 to 0.1 in logarithmic steps of $100^{0.05}$) and a range of genetic trait variance ($\sigma_G^2 = 0.01$ to 0.15 in steps of 0.005; fig. 4). The second is a scenario of decreasing nutrient loading (T_0 decreases from 9 to 5 at a rate $\varphi = -0.001$) in

the absence and presence of genetic trait variance (fig. 5*A*, 5*B*). Last, we simulate different management intervention scenarios following a regime shift to the turbid-water state. Specifically, we simulate an early (10,000 time steps after the shift) and a late (50,000 time steps after the shift) intervention to reduce nutrient loading from 9 to 5 ($\varphi = -0.001$), and we calculate numerically the recovery time of macrophytes from the turbid-water to the clear-water state (fig. 6). We use standard MATLAB functions to numerically solve the differential equations of the system (the code is available on Zenodo at https://doi.org/10.5281/zenodo.5172193; Chaparro 2021).

Singular Perturbation Analysis

To investigate how feedbacks between ecology and evolution determine the eco-evolutionary dynamics observed in the numerical experiments, we use singular perturbation theory (figs. 2*C*, 3*C*, 3*D*, 5*C*). This theory enables studying dynamical systems with processes occurring in different timescales, such as ecological (fast) and evolutionary (slow) processes. The separation of timescales is the focus of this theory, which has been used previously to investigate eco-evolutionary dynamics (Cortez and Ellner 2010; Vasseur et al. 2011; Patel and Schreiber 2015). Using this theory, we approximate the ecological dynamics by assuming that they are always in a quasi-steady state determined by the mean trait value $\bar{x}^*$ of the macrophyte population. We can thus derive analytical expressions for macrophyte $M(\bar{x}^*)$ and algae $A(\bar{x}^*)$ density and calculate the fitness gradient $\partial \bar{W}(\bar{x}^*, A, M)/\partial \bar{x}^*$ using these quantities. Subsequently, we can investigate the transitions between these ecological states as evolution slowly drives phenotypic change. We use the MATLAB package MATCONT (Dhooge et al. 2008) to numerically compute the continuation of ecological equilibrium for different values of the mean trait.

All analysis were performed using parameter values following Dakos et al. (2019) for the ecological model and the macrophyte evolving trait (table 1).

Results

Can Evolution Affect the Resilience of the Shallow Lake Ecosystem? (Asymptotic Stability)

The asymptotic behavior of the system (fig. 1) shows that macrophyte trait evolution can increase the resilience of shallow lake ecosystems in two ways. First, trait evolution shifted the tipping point at which the lake shifts to the turbid-water state at a higher level of nutrient loading compared with the level predicted by the ecological model (e.g., tipping in the ecological model occurs at $T_0 = 7.3$, tipping in the eco-evolutionary model occurs at $T_0 = 8.5$; fig. 1). Second, trait evolution shifted the tipping point that marks the transition from the turbid-water back to the clear-water state at a higher level of nutrient loading compared with the level predicted by the ecological model (e.g., tipping in the ecological model occurs at $T_0 = 5.2$, tipping in the eco-evolutionary model occurs at $T_0 = 7.6$; fig. 1). Thus, the range of nutrient loading where bistability occurs was lower with evolution (blue vs. red region in fig. 1). In other words, evolution decreased the range of hysteresis over the nutrient loading gradient. These effects were robust to changes in parameters that affect ecological equilibria (fig. S1).

Can Evolution Prevent the Collapse of the Shallow Lake Ecosystem as the Environment Deteriorates over Time? (Transient Dynamics)

The increase in resilience predicted by the asymptotic behavior of the system (presented in the previous section) can prevent the collapse of the ecosystem when it is subjected to slow temporal increases in nutrient loading ($\varphi > 0$). In the absence of evolution, increasing nutrient loading from $T_0 = 0.01$ to $T_0 = 7.5$ beyond the tipping point (fig. 2*A*) caused the macrophyte population to collapse (green dashed line in fig. 2*B*). In contrast, when evolutionary trait change occurred, natural selection increased the mean trait of macrophytes (black solid line in fig. 2*B*), and macrophytes did not collapse (green solid line in fig. 2*B*) despite the fact that nutrient loading exceeded the value where the tipping point occurs in the ecological model (ecological tipping point $T_0 = 7.3$; fig. 2*A*). This is because as the trait value gradually evolved, the tipping point at which the macrophyte population collapses gradually shifted to a higher nutrient loading (fig. 2*C*). In this simulation scenario, evolution enabled the maintenance of the ecosystem in the clear-water state at nutrient loading levels that would otherwise cause the transition to the turbid-water state. However, this is not always the case. As we describe in the next section, if the increase in nutrient loading is too fast, evolution might not be fast enough to "push" the tipping point to higher, safer nutrient loading levels that can prevent the regime shift to the turbid-water state.

Can Evolution Influence the Recovery of the Macrophyte-Dominated State after Ecosystem Collapse?

When rates of environmental deterioration are fast—namely, when φ is high—the collapse of the macrophyte population cannot be prevented by phenotypic evolution (fig. 3*B*). In this simulation scenario, nutrient loading increases to $T_0 = 7.5$, ten times faster than that in figure 2*B*. Interestingly, the collapse to the turbid-water state still occurs even though

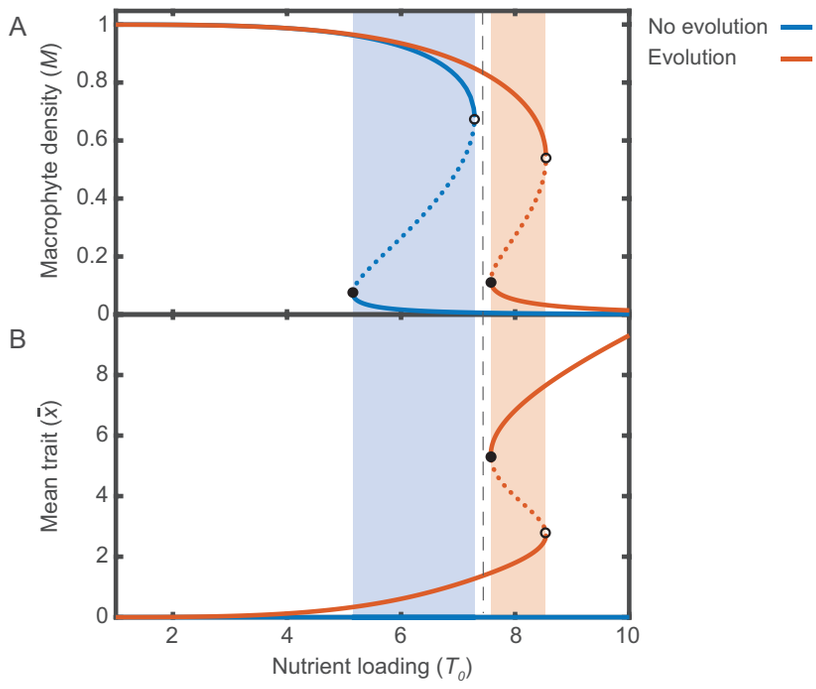

Figure 1: Asymptotic behavior of the shallow lake ecosystem. Shown are macrophyte density (*A*) and mean trait value (*B*) at the ecological (eqq. [1], [2]; blue lines) and eco-evolutionary (eqq. [2]–[4]; red lines) equilibrium as a function of nutrient loading. The ecological equilibrium is computed for a macrophyte population with mean trait value equal to zero (see "Model Description and Analysis" for further explanation) and no genetic trait variance ($\sigma_G^2 = 0$); therefore, natural selection cannot induce phenotypic changes. Solid lines represent stable equilibriums (states), and dotted lines represent unstable equilibriums (states). Bistability occurs in the shaded regions (blue in the ecological model, red in the eco-evolutionary model) delimited by tipping points that mark the transition between alternative stable states (open circles when the transition corresponds to the collapse of the macrophyte population, filled circles when it corresponds to recovery). The vertical dashed line indicates nutrient loading equal to 7.5. $\sigma_G^2 = 0.05$ in the eco-evolutionary model; other parameter values are as in table 1.

at $T_0 = 7.5$ the only eco-evolutionary stable state possible is the clear-water state (fig. 1). However, the collapse is temporary: macrophytes eventually recover (fig. 3*B*). When the macrophytes shift to low densities, the gradual increase in the trait value allows the macrophytes to slowly recover until their population abruptly shifts back to a high density (around time step 10,000 in fig. 3*B*). Gradual trait evolution therefore shifts the ecosystem back to the clear-water state, in which algae density and turbidity are low.

Such "evolutionary recovery" of the macrophyte population returns the ecosystem to a clear-water state without requiring reductions in nutrient loading. Before the increase in nutrient loading, the macrophyte population is well adapted to low nutrient loading conditions, and therefore its mean trait value is nearly zero. However, when nutrient loading quickly reaches 7.5, the fitness gradient becomes positive for trait values near zero (point i in fig. 3*D*). As a consequence, the mean trait gradually increases until a tipping point occurs ($\bar{x} = 5.35$, point ii in fig. 3*C*, 3*D*) where the macrophytes shift from low to high density. Gradual evolutionary trait change thus induces a transition from the turbid-water to the clear-water state, resulting in ecosystem recovery. Once the lake has recovered the fitness gradient turns negative, and therefore a smaller mean trait is selected for until the fitness gradient vanishes at the only (asymptotically) stable eco-evolutionary equilibrium when nutrient loading is 7.5 ($\bar{x} = 1.4$, point iii in fig. 3*C*, 3*D*). However, the transient ecosystem dynamics can include a "temporary" transition in the turbid-water state (fig. 3*B*) because the evolutionary dynamics occur more slowly than the ecological dynamics.

When Can Evolution Prevent Ecosystem Collapse?

From the two previous sections, it becomes obvious that whether evolution can prevent ecosystem collapse or drive its recovery after a transient collapse depends on the relative rates of environmental and heritable trait change (fig. 4). High genetic trait variance enabling fast evolutionary dynamics with respect to the ecological dynamics in combination with low rates of environmental change can prevent a regime shift from the clear-water to the turbid ecosystem

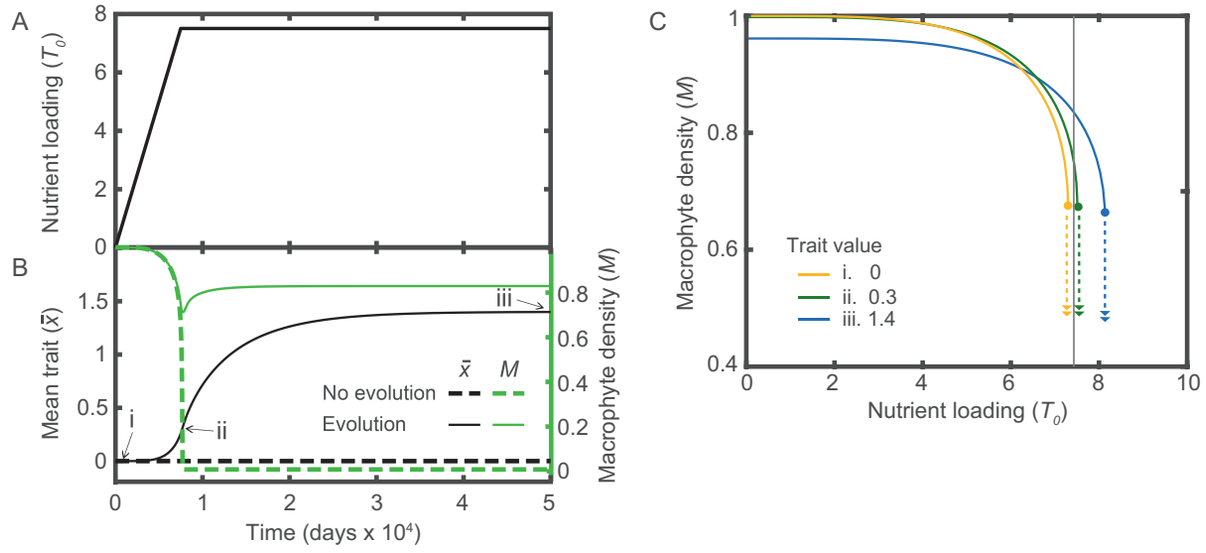

Figure 2: *A*, Eco-evolutionary dynamics when nutrient loading increases with a rate 0.001 per day from 0.01 until 7.5. *B*, Dynamics of the macrophyte density (green lines) and trait (black lines) when evolution does not take place (due to the absence of genetic trait variance; $\sigma_G^2 = 0$) and when it does occur ($\sigma_G^2 = 0.05$). When evolution occurs the macrophyte population initially has a trait value of zero (it is well adapted to the low nutrient loading), and as nutrient loading increases the trait value increases; when nutrient loading reaches its maximum (7.5) the trait value equals 0.3, and after nutrient load stabilizes the trait approaches a value of 1.4. We evaluate the equilibrium at these trait values (i, $x = 0$; ii, $x = 0.3$; iii, $x = 1.4$) in *C*. *C*, Macrophyte density at the equilibrium as a function of nutrient loading for three different trait values. Colored lines represent the clear-water stable state, and the circles correspond to the tipping points that mark the transition to the turbid-water state for the trait values indicated by points i, ii, and iii in *B*. The gray vertical solid line indicates nutrient loading equal to 7.5. Other parameter values are as in table 1.

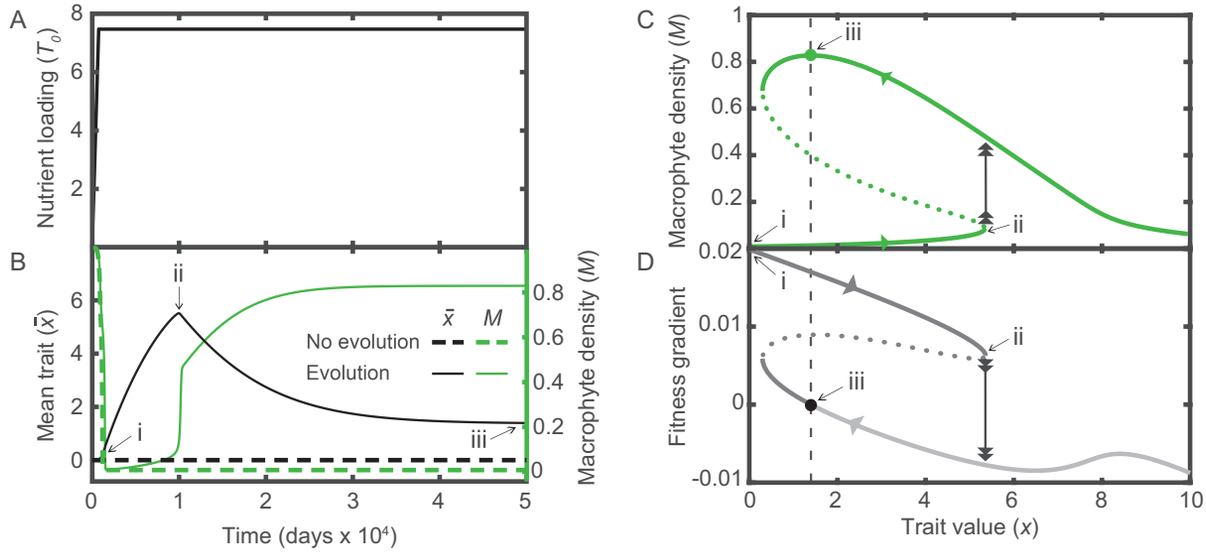

Figure 3: *A*, Eco-evolutionary dynamics when nutrient loading increases with a rate 0.01 per day from 0.01 until 7.5. *B*, Dynamics of the macrophyte density (green lines) and trait (black lines) when evolution does not take place (due to the absence of genetic trait variance; $\sigma_G^2 = 0$) and when it does occur ($\sigma_G^2 = 0.05$). *C*, *D*, Macrophyte density (*C*) and fitness gradient (*D*; dark gray when positive and light gray when negative) at the equilibrium as a function of trait value when nutrient loading is 7.5. At trait values near zero (point i), the only stable equilibrium (state) possible is the turbid-water state with low macrophyte density. At this trait value the fitness gradient is positive, and therefore larger values of the trait are selected for in the population (single dark gray arrow). As the trait value increases, the macrophyte density increases gradually until a trait value of 5.35 is reached, where a tipping point occurs (point ii). At this point, the system abruptly shifts to the clear-water state, with a higher density of macrophytes (black vertical double arrow). Following the regime shift the fitness gradient turns negative, and therefore a smaller trait value is selected for until the fitness gradient vanishes when the trait value equals 1.4 (point iii). Other parameter values are as in table 1.

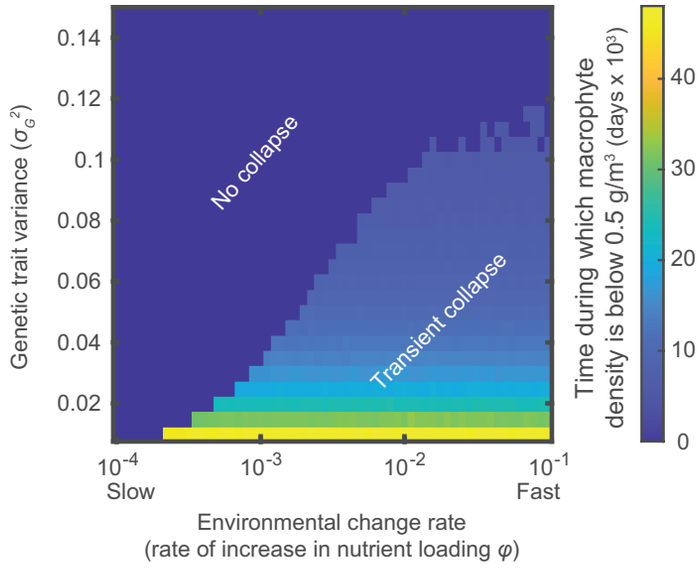

Figure 4: Time during which macrophyte density is below an arbitrary threshold of 0.5 g/m³ (color axis) when nutrient loading increases from 0.001 until 7.5 as a function of the rate of increase in nutrient loading (horizontal axis) and the genetic trait variance (vertical axis). The time during which the macrophyte density is below 0.5 equals zero when the combination of environmental and genetic trait variance enables evolution to prevent the collapse of the shallow lake ecosystem, whereas it is larger than zero when the ecosystem collapses and evolution drives the recovery. Other parameter values are as in table 1.

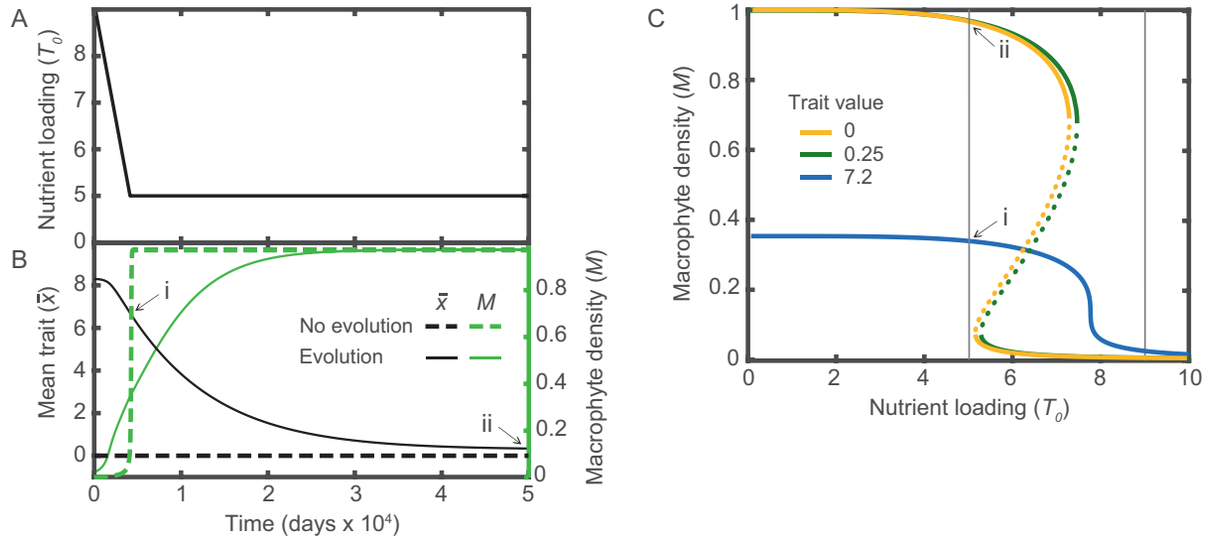

Figure 5: *A*, Eco-evolutionary dynamics when nutrient load decreases with a rate 0.001 per day from 9 until 5. *B*, Dynamics of the macrophyte density (green lines) and trait (black lines) for the nutrient loading trajectory in *A* when evolution does not take place (due to the absence of genetic trait variance; $\sigma_G^2 = 0$) and when it does occur ($\sigma_G^2 = 0.05$). When evolution occurs the macrophyte population initially has a trait value of 8.2 (it is well adapted for the nutrient loading level equal to 9), and as nutrient loading decreases the trait value decreases; when nutrient loading reaches its minimum (5) the trait value equals 7.2 (point i), and after nutrient loading stabilizes the trait approaches a value of 0.25 (point ii). We evaluate the ecological equilibrium at these trait values ($x = 0.25$, $x = 7.2$) in *C* besides the trait value when $x = 0$ (scenario without evolution). *C*, Macrophyte density in the equilibrium as a function of nutrient loading for three different trait values. Solid lines represent stable equilibriums (states), and dotted lines represent unstable equilibriums (states). The vertical gray lines indicate the nutrient loading levels equal to 5 and 9. Other parameter values are as in table 1.

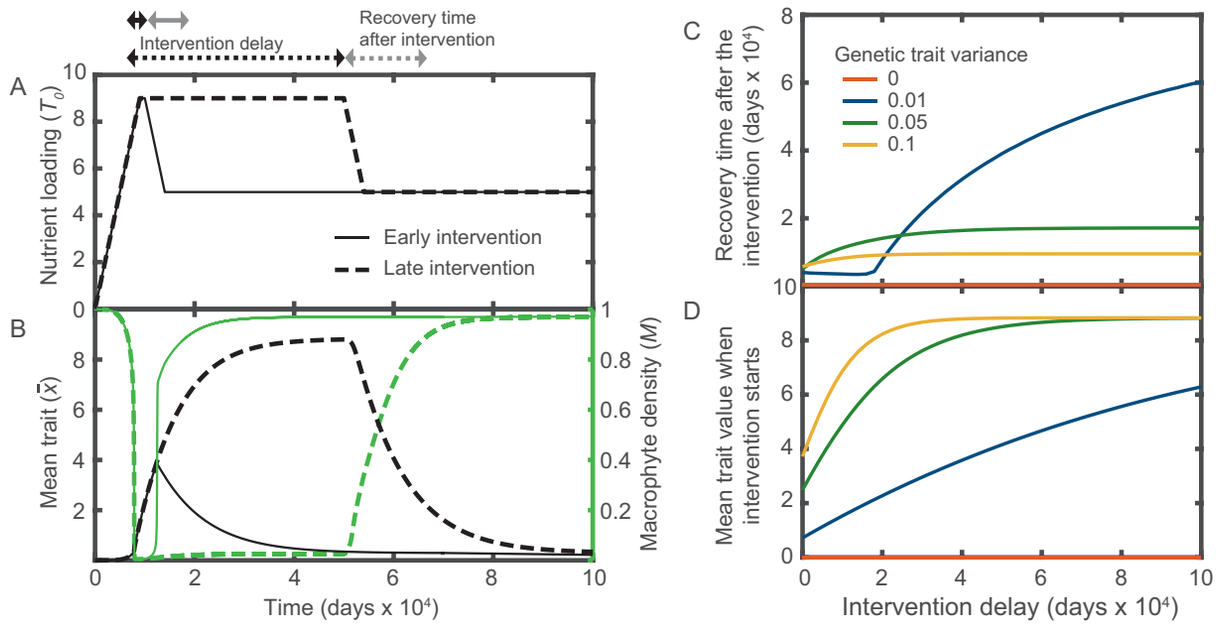

Figure 6: *A*, Nutrient loading of the shallow lake system when an increase in nutrient loading from 0.01 to 9 ($\phi = 0.001$ per day) is followed by an intervention to reduce nutrient loading from 9 to 5 ($\phi = -0.001$ per day) starting at time 10,000 days (solid line) and 50,000 days (dashed line). *B*, Dynamics of the macrophyte density (green lines) and trait (black lines) for the nutrient loading trajectories in *A*. The intervention delay (black arrows on top) corresponds to the time elapsed between the collapse (i.e., population density crosses 0.9 in the collapse trajectory) and the start of the intervention, whereas the recovery time (gray arrows on top) corresponds to the time elapsed between the start of the intervention and the time at which the macrophyte population recovers (i.e., population reaches a density of 0.9 in the recovery trajectory). *C*, *D*, Recovery time after the intervention (*C*) and average trait value of the macrophyte population at the start of the intervention (*D*) as a function of intervention delay. $\sigma_G^2 = 0.05$ in *A* and *B*; other parameter values are as in table 1.

state (top left corner in fig. 4). By comparison, low genetic trait variance and high rates of environmental change leads to ecosystem collapse (bottom right corner in fig. 4). Additionally, the lower the genetic trait variance, the longer the period of the transient collapse is (e.g., the period between ecosystem collapse and "recovery" is four times longer when $\sigma^2 = \sigma_G^2 = 0.01$ than when $\sigma^2 = \sigma_G^2 = 0.1$). Increasing genetic trait variance thus reduces both the range of environmental rates of change that causes ecosystem collapse and the duration of the transient collapse caused by fast environmental change.

Can Evolution Facilitate the Recovery of a Degraded Lake Ecosystem after Management Intervention?

When nutrient loading levels surpassed the tipping point predicted by the eco-evolutionary model ($T_0 = 8.5$), the only possible stable state for the shallow lake is the turbid-water state. In such situations, recovery of the ecosystem would require management interventions that substantially reduce nutrient loading levels due to hysteresis. However, the timing and extent of interventions needed to achieve ecosystem recovery will depend on the trait evolution of macrophytes.

Figure 5 illustrates this by simulating an engineered reduction in nutrient loading after the lake has shifted to the turbid-water state (from $T_0 = 9$ to $T_0 = 5$). The reduction in nutrient loading causes an immediate recovery in a lake with no evolving macrophytes when the nutrient loading crosses the tipping point that marks the transition from the turbid-water to the clear-water state ($T_0 = 5.2$; green line in fig. 5). However, in a lake with evolving macrophytes this intervention results in an almost one order of magnitude slower recovery (30,000 days [~83 years] with evolution instead of 4,300 days [~12 years] without evolution; fig. 5*B*). This is because macrophytes that are well adapted to high nutrient loading conditions ($T_0 = 9$) have low carrying capacity because of resource allocation trade-offs, and high carrying capacities are possible only when the trait value is small. Following the decrease in nutrient loading, natural selection selects for smaller trait values, but this response is slow. As a result, by the time the nutrient loading has reached the minimum (i.e., $T_0 = 5$, point i in fig. 5*B*), the mean trait is just $\bar{x} = 7.2$ and the macrophyte density at the stable equilibrium is limited to 0.34 (fig. 5*C*). The rise in macrophyte density occurs much later, only after the evolutionary process has driven the mean trait to low values (point ii in fig. 5*B*),

Table 1: State variables and model parameters, their units, and values

	Symbol	Unit	Value
State variables:			
Macrophyte density	M	g/m^3	…
Algae density	A	g/m^3	…
Trait affecting competitive ability of macrophytes (e.g., photopigment synthesis)	x	…	Evolving trait (nonnegative)
Parameters:			
Nutrient loading (measured as carrying capacity of algae)	T_0	g/m^3	Varied[a]
Growth rate of algae	r_A	day^{-1}	.1
Effect of macrophytes on algae	h_M	g/m^3	.2
Growth rate of macrophytes	r_M	day^{-1}	.05
Carrying capacity of macrophytes	K	g/m^3	1
Exponent in the Hill function	P	…	4
Genetic variance in the macrophyte population	$\sigma^2 = \sigma_G^2$	…	Varied[a]
Optimal trait value under low turbidity	θ	…	0
Width of Gaussian distribution for decreasing performance with x	τ	…	5
Background effect of algae on macrophytes	h_{A0}	g/m^3	2
Scaling exponent of the half-saturation parameter	λ	…	.1
Rate of environmental stress	φ	day^{-1}	Varied[a]

[a] Values of the varied parameters are specified in each figure legend.

and so evolution delays the recovery of the degraded lake ecosystem.

The delay to ecosystem recovery caused by evolution raises the question of how and when to perform an intervention. The time required to recover the ecosystem following an intervention depends on the mean trait of the macrophyte population at the time of intervention. Because phenotypic trait change through evolution takes time, an intervention soon after a transition to the turbid-water state may be more efficient because evolution otherwise would lead to adaptation to the turbid state (i.e., stabilizing the turbid state (fig. 6*B*). Indeed, as the time between the collapse and the intervention increases, the mean trait at the onset of the intervention increases, and therefore the time required for recovery following the intervention also increases (fig. 6*A*, 6*B*).

This delay in recovery depends on the rate of evolution and thus, in our model, on the amount of genetic variation (fig. 6*C*, 6*D*). As the amount of time before the intervention increases, the macrophytes adapt to the turbid-water state, but the degree to which they do so depends on genetic variation (fig. 6*C*). After the intervention, the delay in recovery then depends both on trait value at the moment of the intervention and the evolutionary rate determined by the amount of genetic variation. Overall, our simulations show that with increasing genetic variation the delay in recovery is reduced (fig. 6*D*), with one exception: if the intervention delay is short, then the setting with low genetic variation can show the fastest recovery time, because trait change during the intervention delay remained small.

Discussion

Evolutionary Effects on Tipping Points

We show that trait evolution can impact ecosystems with ASSs by changing the threshold of environmental stress at which tipping points occur (fig. 1). The possibility that evolution could shift ecosystem tipping points was proposed by Dakos et al. (2019). Here, we present theoretical support for this hypothesis using shallow lakes as a model system, demonstrating that macrophyte evolution can shift the tipping points to higher levels of environmental stress, increasing resilience of the shallow lake ecosystem. Our results, however, also point to a delay in ecosystem recovery if evolutionary trait change occurs before management interventions take place.

The ecosystem response to a deteriorating environment depends not only on the tipping points but also on the interaction between the rates of environmental change and evolution. Specifically, when environmental stress increases slowly and the evolutionary process is fast, adaptive evolution of macrophytes prevents ecosystem collapse (fig. 2). Conversely, a collapse to the turbid-water state occurs when there is a fast increase in environmental stress and the evolutionary process is comparatively slow (fig. 4). Genetic variance of fitness-related traits defines the "speed" of adaptive evolution; in wild populations, most estimates of genetic variance of fitness-related traits are typically below 0.1 (Hendry et al. 2018; Bonnet et al. 2019). In our simulations, both the transient collapse and the no-collapse scenarios occur for values of genetic variance below 0.1, suggesting that for the rates of evolution enabled by these values of genetic variance, ecosystem collapse may be avoided only if environmental stress increases slowly.

The introduction of evolutionary dynamics in the shallow lake ecological model makes the system sensitive to the rate of environmental change. While in the ecological model alone the ecosystem collapse occurs only when nutrient loading exceeds a certain magnitude, in the eco-evolutionary model such collapse can also be caused by the rate at which nutrient loading increases. This is the consequence of the different timescales at which ecological (fast) and evolutionary (slow) dynamics occur. In general, dynamical systems that have processes operating on different timescales are sensitive to both the magnitude and the rate of change of parameters (Ashwin et al. 2012). Similar dynamics have been described in other systems that have ecological processes occurring at different timescales (Vanselow et al. 2019; Gil et al. 2020).

Our results show that even when the collapse occurs, gradual evolutionary trait change can return the ecosystem to its precollapse state (fig. 3). Selection can drive the trait value beyond the tipping point that marks the transition to the clear-water state, resulting in evolutionary recovery of the ecosystem. Similar evolutionarily driven regime shifts, such as the one causing the evolutionary recovery in the shallow lake, have been documented in communities with intraguild predation (Patel and Schreiber 2015) and in communities connected through species with complex life cycles (Chaparro-Pedraza and de Roos 2020). However, if there are barriers to evolution, such as the absence of genetic variation or interference from trade-offs with responses to other selection pressures, the ecosystem can stay "trapped" in the turbid-water state. Although theoretically this evolutionarily driven regime shift enables the recovery of macrophytes from a state of very low density, demographic stochasticity could lead the population to extinction before the evolutionary process can drive the trait value beyond the tipping point that marks the transition to the clear-water state. Therefore, management measures should focus on maintaining large population sizes and genetic variability to prevent both demographic stochastic effects and genetic erosion. Such measures may include, for instance, introduction of genetic variants from diverse regional sites to increase genetic diversity of the macrophyte population at the time of the intervention.

Evolution can also have undesired effects in ecosystems with ASSs. We find that evolution can actually delay ecosystem recovery following a management intervention. Because ASSs correspond to qualitatively different ecological conditions (Scheffer 2009), selective pressures in the alternative states may greatly differ. We find that adaptation to the degraded state (i.e., the turbid-water state), although enabling the persistence of the macrophyte population in this state, delays the recovery of the ecosystem when conditions ameliorate (fig. 5). This is because of a trade-off between shading tolerance and performance. Similar negative effects caused by adaptation to degraded conditions have also been reported in response to pulse perturbations (Lyberger et al. 2020). Following an intervention to ameliorate environmental conditions, gradual evolutionary change drives the adaptation of the organisms present in the degraded ecosystem to the novel and improved conditions. Such an evolutionary process occurs slowly compared with the ecological dynamics, and as a consequence, ecosystem recovery may be slower than in systems without evolution. Tipping point theory predicts a regime shift back to the clear-water state to occur "fast" once the environmental conditions are restored to a level beyond the tipping point that marks the transition from the turbid-water state to the clear-water state (Scheffer et al. 2001; Scheffer and Carpenter 2003; Folke et al. 2004). In contrast, our results indicate that evolutionary change can transform such a regime shift in a more gradual response because the traits underlying ecosystem responses change slowly. Various mechanisms have been identified to underlie the slow unfolding of regime shifts after a tipping point has been exceeded (Hughes et al. 2013), including ecological processes that occur at different timescales. We here find that this transient behavior can also be caused by the interaction of ecological and evolutionary processes.

The delay in the recovery of a degraded ecosystem after an intervention has important implications for ecosystem management and policy. Our results show that once a bistable ecosystem shifts, recovery back to the desired state may be orders of magnitude slower if important organisms, such as macrophytes, have adapted to the undesired state prior to the management (fig. 6). Thus, rapid restoration after a regime shift might be crucial to increase the chances of a fast recovery. Alternatively, loss of trait variation during the collapse may delay adaptation to the undesired state, which would then prevent the delay in recovery after an intervention. In general, our results indicate that a long delay in the intervention after a regime shift may often be detrimental for the recovery time, and even more detrimental when trait variation is low. Measures aiming at restoring degraded ecosystems should therefore focus on a fast intervention to ameliorate conditions, in combination with conservation or introduction (e.g., through transplantations) of genetic variants that are well adapted to the desired state.

Limitations and Future Directions

The shallow lake model we use serves as a first step to understand how ecological, evolutionary, and stress dynamics interact in ecosystems with ASSs. Although macrophytes play a key role in the maintenance of the clear-water state, it is reasonable to speculate that evolution of competitive traits in algae may also shift ecosystem tipping points, probably reducing the increased resilience that only macrophyte evolution confers. Perhaps transient dynamics will be affected not only by such shifts in tipping points but also

by the very distinct generation times that algae and macrophytes have and how these differentially influence evolutionary rates. The effects of evolutionary processes of multiple interacting species on ecosystem tipping points and their associated dynamics need further investigation.

We adopt an ecological model that has been broadly used to describe the shallow lake ecosystem dynamics as the basis of our eco-evolutionary model. This model belongs to a group of models that assumes population size to be infinite, precluding the possibility of demographic stochasticity. On the one hand, this simplifying assumption facilitates an extensive mapping of qualitative system dynamics. On the other hand, effects of demographic stochasticity are neglected even though they may be consequential for populations at the brink of extinction (Lande 1993), for example, following a catastrophic collapse due to a regime shift. In addition, following standard modeling methods of quantitative genetics, we assume heritable trait variation to remain constant. Population size, however, may influence standing genetic variation. Heritable trait variation might therefore change with changes in population size, such as those caused by a collapse following a regime shift. Heritable trait variation mainly influences the evolutionary rate (Lande 1976) and has a small effect on the evolutionary end point that corresponds to the trait value where the fitness gradient vanishes (see eq. [4]). We therefore expect that variability in trait variance does not have a significant effect on the asymptotic behavior of the system and thus on the location of the tipping points. However, it likely alters the transient behavior of the system.

Our study focuses on the effects of evolutionary trait change in ecosystems with ASSs. However, adaptive trait changes that enable species to persist locally despite environmental change can also be mediated by phenotypic plasticity (Gienapp et al. 2008; Turcotte and Levine 2016). Evolutionary trait change is characterized by selection of existing heritable variants that are capable of coping with the novel conditions, whereas trait change due to phenotypic plasticity is mediated by the expression of different phenotypes in different environmental conditions by a single genotype. Evolutionary change can take generations, whereas trait changes mediated by phenotypic plasticity can occur within the life span of an organism. Hence, trait changes mediated by phenotypic plasticity occur on a timescale more similar to that of ecological processes than trait change mediated by evolutionary processes. However, even when phenotypic plasticity is the only mechanism underlying trait changes, adaptive changes might not be instantaneous, and thus tracking the environment is not possible when it changes quickly (Stomp et al. 2008). How fast trait changes mediated by phenotypic plasticity alter the short- and long-term dynamics of the system and the likelihood of regime shifts—and how this interacts with trait changes mediated by evolution, including evolution of phenotypic plasticity—needs further investigation. We expect a reduced legacy effect of trait changes, likely resulting in a reduced delay in recovery compared with the dynamics we modeled here.

Environmental change is occurring at an unprecedented rate (Steffen et al. 2004) and is likely to increase the frequency and severity of regime shifts in ecosystems (Drijfhout et al. 2015; Steffen et al. 2018). It is therefore of utmost importance to gain insight into the processes governing this phenomenon under environmental stress. By considering trait evolution of a key species in a shallow lake ecosystem, we demonstrate how evolutionary processes can be integrated into the study of regime shifts and resilience not only for shallow lakes but also for ecosystems in general. We have identified the balance between the rates of environmental change and evolution to be crucial factors triggering catastrophic regime shifts when environmental stress approaches a tipping point. Our findings suggest that ecosystem restoration measures may be more effective when implemented quickly after a regime shift and that high diversity of genetic variants can increase the chances of a fast recovery. This highlights the urgency to mitigate the effects of global change and loss of phenotypic diversity in ecosystems.

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Statement of Authorship

P.C.C.P., V.D., B.M., and L.d.M. conceived the ideas. V.D. and P.C.C.P. designed the methodology. P.C.C.P. analyzed the results and led the writing of the manuscript. V.D., B.M., and L.d.M. critically revised and contributed to later versions of the manuscript. All authors gave final approval of the manuscript to be published.

Data and Code Availability

No new data were collected and used for this study. The MATLAB code is provided on Zenodo at https://doi.org/10.5281/zenodo.5172193 (Chaparro 2021).

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