Eco-evolutionary dynamics of ecosystems resilience

1. Summary of the research plan

Anthropogenic changes impose stress upon ecosystems at an unprecedented rate, therefore understanding how ecosystems will respond to perturbations is an urgent matter. Previous works have demonstrated that ecosystems do not always respond to gradual environmental change in a smooth manner but that abrupt regime shifts between alternative stable states occur when environmental conditions cross certain thresholds[1–3]. Despite environmental change trigger both ecological and evolutionary responses[4–9], the theoretical framework used to predict stress responses of ecosystems with alternative stable states lacks the evolutionary component. This project proposes to develop a novel eco-evolutionary theory that serves as a foundation to generate accurate predictions regarding environmental stress responses in ecosystems with alternative stable states. Using the shallow lake system as a model system, *this project aims at unraveling how trait (co)evolution affects the resilience of ecosystems under environmental stress focusing on the interaction between ecological, evolutionary, and stress dynamics.* To do so, this project will integrate insights derived from quantitative population models and individual-based simulations (IBM). While quantitative population models will allow for more extensive mapping of qualitative dynamics, the IBM will allow testing the robustness of the results by relaxing assumptions that are inherent to the quantitative population model approach. The results of this research project will produce a first generation eco-evolutionary framework to study resilience in ecosystems with alternative stable states. This framework will contribute to improve our ability to predict, and potentially prevent and/or mitigate, the occurrence and severity of regime shifts in natural ecosystems.

2. Research plan

2.1 Current state of research in the field

Ecosystem resilience is the ability of an ecosystem to absorb disturbances without shifting to an alternative, and often undesirable, state[1,10,11]. Ecological theory predicts that ecosystems respond to environmental change either gradually or abruptly, the latter occurring when ecosystems cross a tipping point and shift to an alternative stable state (ASS)[1–3]. Such abrupt transitions affect the composition, species diversity and functioning of ecosystems that often alter the availability of the services they generate[12,13], incurring potentially large impacts on society. Hence, large body of research has focused on the ecological mechanisms that trigger regime shifts and on methods to predict them[14–16].

Growing evidence shows that environmental changes do not only trigger ecological but also evolutionary responses[4–9]. These evolutionary responses can rescue populations from extinction in degrading environmental conditions[17], and mediate ecosystem responses to environmental changes[18]. However, the theoretical framework used to predict the responses of ecosystems with ASS still lacks an evolutionary component[19]. Here, we propose to develop an eco-evolutionary theory of ecosystem resilience to help improve our ability to predict, and potentially prevent, the occurrence and severity of regime shifts in natural ecosystems. Specifically, we will explore how trait evolution affects the resilience of ecosystems under environmental stress. There are more than 30 different examples of regime shifts in natural ecosystems[20], but the regime shift between a turbid and a clear state of shallow lakes is arguably the most studied[21,22]. This model system will be used to test how trait (co)evolution of key species, namely macrophytes and algae, can affect ecosystem dynamics over a range of environmental conditions in general, and in the vicinity of tipping points in particular. This question will be investigated by integrating evolutionary dynamics into the ecological model of shallow lake ecosystems (Fig. 1).

2.2 Project description

Goal and research questions - This research project aims at developing a theoretical framework for understanding how ecological and evolutionary processes interact and influence the resilience of ecosystems under environmental stress. To do so, the research project will address the following questions:

Research question RQ1: How do ecological dynamics and trait evolution interact to affect the resilience of an ecosystem under environmental stress?

Research question RQ2: How does coevolution of interacting species affect its resilience?

These questions will be investigated by integrating evolutionary dynamics into existing ecological models of shallow lake ecosystems (Fig. 1).

The existing ecological model - Shallow lake ecosystems can be either clear dominated by aquatic vegetation (i.e. macrophytes) or turbid dominated by phytoplankton (i.e. algae). The clear state with abundant macrophytes is usually desired because the structural complexity provided by macrophytes increases the diversity of the ecosystem and the availability of ecosystem services[12,13,23]. Nutrient load can shift these ecosystems from the clear-water state to the turbid state. When nutrient loading is low the lake is clear while when nutrient loading is high it is turbid. At an intermediate range of nutrient level, both the clear and the turbid state exist[22].

The competitive interaction between macrophytes and algae is key in the existence of ASSs. Hence, changes in distribution of competitive traits (i.e., resource efficiency) are likely to alter this interaction and thus the possibility to shift between ASSs. This project will explicitly account for the evolution of traits that affect the interspecific competitive ability only in the macrophyte population (*RQ1*) and in the macrophyte and the algae population (*RQ2*).

Methodology for the eco-evolutionary model - The essence of the mechanism causing the existence of ASSs in shallow lakes is that macrophytes reduce turbidity, of which a large fraction is caused by algae growth, whereas turbidity lessens vegetation growth.

A model describing the biomass of the algae A and the macrophyte M has been typically used to describe the ecological dynamics that cause transitions between ASSs[21,22]:

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

(Eq. 1)

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

(Eq. 2)

In this model, r_A and r_M are the maximum growth rates of the algae and the macrophyte, respectively. T_0 is nutrient loading. K_M is the carrying capacity of the macrophyte population in the absence of algae. Algae limits macrophyte growth according to a nonlinear decreasing Hill function with half saturation h_A and exponent P; whereas it is negatively affected by macrophytes following an inverse Monod function with half saturation h_M. h_A and h_M determine the effect of algae on macrophytes and vice versa, respectively, therefore they are influenced by traits affecting the interspecific competitive ability of algae and macrophytes. h_A and h_M have been traditionally considered fixed parameters, however, since they are influenced by traits they can vary as a result of trait evolution. We therefore propose to incorporate the evolutionary dynamics of trait change directly influencing h_A and h_M into the ecological model described above.

This project will investigate the eco-evolutionary responses to nutrient load T_0 as driver of environmental stress in the shallow lake ecosystem. The model will be parameterized with existing data from wild populations of macrophytes and algae.

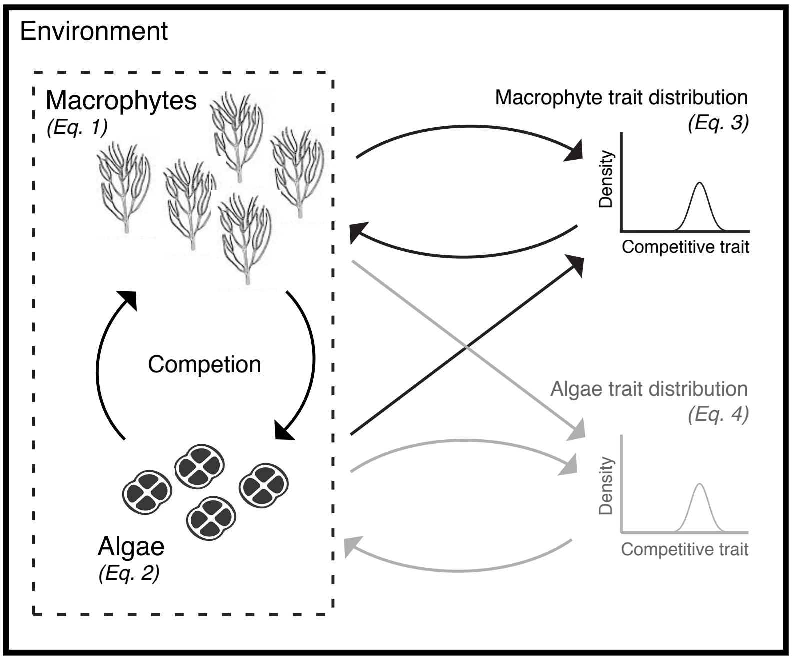

Figure 1. Eco-evolutionary model of shallow lake ecosytems. The existing ecological model (framed by a dashed line) in which macrophytes and algae compete will be extended to include the evolutionary process. The fitness of alternate phenotypes depends on the competitive interaction between macrophytes and algae. This leads to changes in trait (or allele) distribution via trait inheritance and the emergence of new phenotypes driven by mutation and recombination. Reciprocally, changes in trait distribution influence competitive interactions and the size of the macrophyte and algae populations. The environment (solid line frame), for instance nutrient load, affects the eco-evolutionary dynamics. *RQ1* will be investigated in the model represented only by black arrows, while *RQ2* (coevolution) will be investigated in the full model (including grey arrows). The dynamics of macrophyte and algae

densities as well as of trait distributions are described by the differential equations 1, 2, 3 and 4 in the following sections.

RQ1: How do the interplay between ecological dynamics and trait evolution affect the resilience of an ecosystem under environmental stress?

To answer this question we will investigate the interaction between ecological dynamics (changes in population size of macrophytes and algae) and the evolution of a phenotypic trait x that enhances the competitive ability of macrophytes h_A, i.e. high tolerance to turbidity. Due to resource allocation tradeoffs any trait change that increases competitive ability will be associated with a metabolic cost that affects macrophyte performance i.e. reduced carrying capacity K_M[24]. The trait enhancing interspecific competitive ability will be modeled as a normally distributed trait with population mean $\bar{x}$ and variance σ_x^2 [25]

$$\frac{d\bar{x}}{dt} = \varepsilon_x \frac{\partial \overline{W_M}(\bar{x}, A, M)}{\partial \bar{x}}$$

(Eq. 3)

The mean trait value of the population changes depending on the mean fitness gradient $\overline{W_M}$, and the parameter ε_x ($\varepsilon_x = h_x^2\ \sigma_x^2$, where h_x^2 is heritability and σ_x^2 the variance of the trait) determines the timescale separation between the ecological and evolutionary dynamics[26]. When ε_x is small (large), the evolutionary processes occur slowly (quickly) relative to the ecological processes.

The effect of the interaction between ecological and evolutionary dynamics on the resilience of the shallow lake ecosystem will be examined by addressing the following research questions:

A. *How does the trait value influence the stability of the ecological equilibrium (asymptotic behavior of the system)?*

The integration of the evolutionary process may cause the tipping points to shift them to different levels of environmental stress. These changes that can alter the resilience of ecosystems will be analyzed through the following procedure. 1) Determining the trait value at the evolutionary equilibrium (where fitness gradient $\overline{W_M} = 0$) for different levels of environmental stress. 2) Performing a stability analysis of the ecological equilibrium (asymptotic behavior) for different degrees of environmental stress when the mean trait value of the macrophyte population equals the trait values found in step 1. This will allow comparing the stress levels at which the tipping points, if they exist, occur for different trait values. This analysis will enable understanding how trait change influences the resilience of the clear and the turbid state, by shifting the tipping points to higher or lower levels of stress. A reasonable expectation is that macrophytes evolving to increase competitive ability might shift the tipping point where the collapse occurs to higher stress levels; therefore evolution may increase the resilience of the clear state. The evolutionary process may also change the range of hysteresis and therefore the trajectories of collapse (regime shift from the clear to the turbid state) and recovery (regime shift from the turbid to the clear state). This change is the consequence of trait changes that alter the stability of the ecological equilibrium under certain levels of environmental stress that are stable in the absence of evolution, in the more extreme case causing the bistability to disappear.

B. How *do the rates of environmental and evolutionary change affect the transient dynamics of regime shifts?*

If the expectation above is true, rapid evolutionary process might delay the collapse when environmental stress increases slowly ($dT_0/dt = \omega > 0$, where ω is small). Conversely, if the evolutionary process is slow (relative to the ecological process) and the environmental stress increases rapidly (ω is large) the collapse might occur at lower levels of stress. Therefore, we will simulate eco-evolutionary dynamics using equations 1, 2 and 3 for different rates of increasing environmental stress ω when the evolutionary process is slow (small ε_x). This analysis will be repeated for increasing rates of evolutionary trait change ε_x, and in each simulation, the level of stress at which the regime shift occurs will be recorded. Analogously, this analysis will be performed once the ecosystem is in the turbid state and the environmental stress is gradually reduced ($\omega < 0$). This analysis will enable understanding how timescale differences in evolutionary and environmental change influence the risk of regime shift from the desired clear state to the undesired turbid state and the potential to recover.

RQ2: Does coevolution of interacting species alter ecosystem resilience?

The expectation from *RQ1* that macrophytes evolving to increase competitive ability might increase the resilience of the clear-water state might be counterbalanced by evolution of competitive abilities by the competitor. Therefore, we would need to understand the effect of the coevolving process of competing species on ecosystem resilience. The model presented above will be extended to add a phenotypic trait y that enhances the competitive ability of algae h_M, i.e. high nutrient uptake. As in the macrophyte phenotype, there is a tradeoff between competitive ability and performance. The same theoretical framework will describe the evolutionary dynamics of the algae trait. Therefore,

$$\frac{d\bar{y}}{dt} = \varepsilon_y \frac{\partial \overline{W_A}(\bar{y}, A, M)}{\partial \bar{y}}$$

(Eq. 4)

the mean trait value of the population $\bar{y}$ changes depending on the mean fitness gradient $\overline{W_A}$, and the parameter ε_y as explained above, determines the timescale separation between the ecological and the evolutionary dynamics.

In this extended model, we will investigate how the eco-evolutionary dynamics of coevolving populations affect the resilience of the shallow lake ecosystem. To do so, the following research questions will be addressed:

A. *How is the stability of the system affected by coevolving populations?*

To answer this question, we will follow the same approach used to perform the stability analysis in *RQ1*. The difference is that in the first step is necessary to determine the values of both traits at the evolutionary equilibrium (where fitness gradient $\overline{W_M} = 0$ and $\overline{W_A} = 0$) for different levels of environmental stress. The stability analysis of the ecological equilibrium for different degrees of environmental stress is performed for each pair of traits calculated in the previous step. With these and the results of the stability analysis in *RQ1*, it will be possible to compare the stress level at which the tipping points occur when interacting populations coevolve relative to the evolution of only one of the populations. In addition, it will be possible to assess whether coevolution reduces, increases or does not affect the range of stress levels at which bistability occurs. This enables testing the hypothesis that coevolution may counterbalance the increase in resilience expected by evolutionary processes only in the macrophyte population.

B. *How do different evolutionary rates in coevolving populations influence the transient eco-evolutionary dynamics of the shallow lake ecosystem?*

Algae and macrophytes have very distinct generation times and turnover rates. Because generations are shorter in algae, the evolutionary rate in the algae population is higher than in the macrophyte population. We will simulate eco-evolutionary dynamics using equations 1, 2, 3 and 4 for different combinations of evolutionary rates of the two populations. These simulations will be performed for various rates of increasing environmental stress until the regime shift to the turbid state occurs and of decreasing environmental stress until the ecosystem recovers to the clear state. The results of this analysis enable understanding whether the effects of eco-evolutionary processes on ecosystem resilience observed in *RQ1* are altered by coevolving populations.

Robustness of results: Individual-based model - The insights from the quantitative genetics model will be contrasted with individual-based simulations (IBM) to assess whether the results are robust against different assumptions regarding the genetic basis, reproduction modes and demographic stochasticity (population size). Algae (phytoplankton) reproduce clonally whereas macrophytes reproduce sexually. The IBM will allow simulating eco-evolutionary dynamics while incorporating these different modes of reproduction in the two populations. In addition, we will investigate the effects of single or multiple loci with additive and non-additive effects contrasting the effects of the different reproduction modes and generation length of the two populations. Because recombination can speed up evolution in organisms with sexual reproduction[27], this reproduction mode may counterbalance to a certain extent the fast evolutionary rate of algae due to shorter generation time. Therefore, by explicitly modeling the genetic architecture of functional traits and reproduction modes, the IBM will enable to assess the effects that different mutation and recombination rates in the macrophyte population have on the evolutionary rate and regime shifts. These results will be contrasted with data on mutation and recombination rates of macrophytes species, and mutation rate and generation time of phytoplankton groups to determine realistic ranges of evolutionary rate for macrophytes ε_x and algae ε_y. In addition, this will be combined with data on shallow lake sizes that constrain population size and therefore may affect the rate of evolution.

Expected outcomes - The results of this research project will produce a first generation eco-evolutionary framework to study resilience in ecosystems with ASSs. These results are a single unity that will be presented in an international conference (i.e. European Society for Evolutionary Biology) and published in a top peer-reviewed journal with high long-term impact factor (i.e. American Naturalist, Evolution).

2.3 Risks, gains and potential impact

This project is mostly theoretical and given the expertise of the team in mathematical and computational tools the risk of failure is low. It is possible that some of the expected results change and that unexpected dynamical behavior arises; but the first generation eco-evolutionary model to study resilience in ecosystems with ASSs is a highly probable outcome.

Mechanisms analogous to those causing regime shifts in shallow lakes operate in other ecosystems[22]. The generalization of the results to those ecosystems will advance the theory of eco-evolutionary dynamics of ecosystems under anthropogenic stress. Therefore, the eco-evolutionary theoretical framework developed in this research will serve as a foundation to generate accurate predictions regarding environmental change responses in ecosystems with ASSs. Such predictions are necessary for the prospects of management and recovery for any ecosystem. Furthermore, this proposal will open the scope for future research to reveal how eco-evolutionary dynamics and coevolution influence resilience. For instance, following this research, I am interested in investigating the role of eco-evolutionary dynamics in regime shifts caused by predator-prey interactions[28] that have caused dramatic trophic-cascades in aquatic ecosystems[29,30].

2.4 Budget, implementation and resources

This project will be developed by a postdoc, hence the budget requested for this proposal includes a one-year salary of a postdoc, as well as costs associated with the dissemination of the results in an international conference.

The project will progress in a step-wise fashion. The model to respond *RQ1* will be first implemented and investigated, and subsequently, it will be extended to respond *RQ2*.

Month	1	2	3	4	5	6	7	8	9	10	11	12
Implementation model for *RQ1*	■	■										
Analysis model *RQ1*		■	■	■								
Extension model for *RQ2*					■							
Analysis model *RQ2*					■	■	■					
Implementation and analysis of the IBM						■	■	■	■	■		
Writing manuscript									■	■	■	■

Resources: The resources required will be produced developing the prototypes in MATLAB/Octave and Julia and all the codes will be deposited in open access repositories. The host institute provides a license to MATLAB; the other programs are open source.

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