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3 **Ecosystem tipping points in an evolving world**

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28 **Abstract**

29 There is growing concern over tipping points arising in ecosystems due to the crossing of
30 environmental thresholds. Tipping points lead to abrupt and possibly irreversible shifts
31 between alternative ecosystem states potentially incurring high societal costs. Trait variation of
32 populations is central to the biotic feedbacks that maintain alternative ecosystem states, as
33 they govern the responses of populations to environmental change that could stabilize or
34 destabilize ecosystem states. However, we know little about how evolutionary changes in trait
35 distributions over time affect the occurrence of tipping points, and even less about how big
36 scale ecological shifts reciprocally interact with trait dynamics. We argue that interactions
37 between ecological and evolutionary processes should be taken into account for understanding
38 the balance of feedbacks governing tipping points in nature.

39

40 **keywords:** resilience, evo-to-eco, contemporary evolution, catastrophic shifts, eco-evolutionary
41 dynamics, traits

Tipping points in an evolving world

Tipping points mark the abrupt shift between contrasting ecosystem states (broadly termed regime shifts) when environmental conditions cross specific thresholds (Box 1). Prominent examples are the shift of shallow lakes from a clear to a turbid water state¹, or the collapse of vegetation to a desert state in drylands². Societal stakes associated with tipping points in natural ecosystems can be high and there is great emphasis on the mechanisms that trigger them³ and the possible ways to detect and avoid them⁴. Currently, however, tipping point theory largely lacks an evolutionary perspective, and this might limit our understanding of the occurrence, timing, and abruptness of shifts between states (Box 1, Figure I). Here we argue that both trait variation and evolution are important for understanding ecosystem dynamics in the vicinity of tipping points.

Developing a trait-based evolutionary perspective about tipping points in ecosystems is warranted by the growing evidence that changes in standing levels of trait variation and contemporary trait evolution are important drivers of ecological processes (e.g.^{5,6}), by influencing population dynamics (Yoshida et al. 2003), shaping the structure of species interactions in communities⁷, or affecting species composition at the metacommunity level⁸. Such ecological effects of evolution also extend to ecosystem functioning^{9–11}, by modifying material fluxes¹², primary production¹³, nutrient recycling¹⁴, and decomposition¹⁵. Changes in life-history traits caused by environmental stress (like fishing) have been shown to destabilise dynamics of populations¹⁶ or whole communities¹⁷, and even increase their risk of extinction¹⁸. Fitness-related traits (e.g. body size) can systematically change before populations collapse¹⁹

and can be used as indicators of biological transitions^{20,21}. Thus, it is reasonable to expect that changes in trait distributions might be important for understanding ecological tipping points as they might affect the variation in the sensitivity to environmental stress among species, populations, or individuals in an ecosystem^{22,23}. This sensitivity underlies the response capacity of communities to stress^{24,25} such that trait changes could affect the resilience of entire ecosystems²⁶ and their probability of tipping to a different state. It is the effect of evolutionary trait changes on tipping points at the ecosystem level that we are focusing on in this perspective.

Ecosystem resilience can be affected by variation in traits^{9,10} underlying the performance and fitness of organisms in a given environmental state (i.e. response traits), or those causing direct or indirect effects on the environmental state (i.e. effect traits) (Table 1). The distribution of such response and effect traits can vary due to phenotypic plasticity, species sorting, or evolutionary trait change, and distinguishing between these mechanisms can be important for understanding the ecological dynamics of trait change in general²⁷, and of tipping points in particular. Phenotypic plasticity, where genotypes exhibit different phenotypes in different environments, is a relevant source of trait variation, particularly when the phenotypic changes relate to the capacity of organisms to respond to stress. However evolutionary responses to stress depend on heritable trait variation in a population²⁸, which can originate from novel variants due to mutation²⁹, recombination³⁰, or gene flow among populations and species³¹. Below, we do not *a priori* distinguish between the genetic versus plastic sources of trait distributions (although we comment on their differences), but focus on how trait variation and

trait change over time can influence ecosystem tipping points in a generic way. We do this using a graphical approach where we illustrate how trait changes might modify the collapse and recovery trajectories of ecosystems along an environmental gradient.

Trait variation could affect the probability of tipping points

Differences in the amount of trait variation within or among populations could affect their response capacity to stress. In general, we predict that high trait variation may decrease the probability of tipping points turning ecosystem responses to non-catastrophic. A decrease in the probability of tipping events occurs because standing trait variation allows for portfolio effects that introduce strong heterogeneity in population processes, interactions, and responses³² buffering population dynamics³³. Such heterogeneity can be enhanced by Jensen's inequality³², where variation around the mean of a trait can affect the response of an ecological interaction or an ecological process in function of the nonlinear relationship between the trait and its effect³⁴. This effect can be clearly illustrated in a toy model describing shifts in the case of shallow lakes (Figure I in Box 1). Here, changing the amount of variation in the macrophytes' response trait to turbidity can increase or decrease the probability of a tipping point response. Under high levels of variation the transition from the clear to the turbid water state can even become non-catastrophic with no alternative states (Figure 1).

Trait change can delay a tipping point

As introduced in the previous paragraph, trait variation simply means that some resistant phenotypes are present. However, trait variation could also facilitate trait changes. On top of

that, trait changes might be fueled by *de novo* mutation and phenotypic plasticity. In ecosystems where stress gradients bring them closer to tipping points, trait changes could potentially delay tipping to the alternative state (Figure 2a). This resonates with the idea of evolutionary rescue^{35,36}, the difference being that there is no rescue, but rather only a delay in the collapse of the system by shifting the threshold at which the collapse occurs at a higher stress level (Figure 2b). For instance, in the case of a shallow lake turning turbid due to eutrophication (Box 1), aquatic macrophytes might delay the transition to a higher threshold level of nutrients because of contemporary changes in traits that convey tolerance to shading (Table 1).

Trait change can lead earlier to a tipping point

Trait change may not always buffer populations from environmental changes, but could also contribute to an increased risk of ecosystem collapse (Figure 2c, d). For example, environmental stress could impose directional selection on a trait in a given species or group of species that brings the system closer to tipping to an alternative ecological state^{37,38}. This is similar to evolutionary collapses or evolutionary suicide as defined in evolutionary biology^{39,40}, but here the collapse occurs at the scale of a whole ecosystem. Empirical examples of trait evolution leading to population collapse come mostly from fish populations under harvesting^{38,41}. For example, it has been shown how fishing pressure has led to the early maturation of Atlantic cod populations⁴² that is associated with lower reproductive output and irregular recruitment dynamics that could have increased the chance of stochastic extinction and the cod collapse in the 1990s. Evolutionary suicide might lead to an ecosystem-level collapse in the case of

drylands⁴³, where under increased aridity adaptive evolution can favor local facilitation among neighboring plants for resisting higher aridity. Whether evolution leads to a buffering effect depends on the seed dispersal strategy of the dominant vegetation type. In systems characterized by long-distance dispersal, evolution may actually enhance the collapse of the vegetation to a desert state due to the invasion of non-facilitating mutants. In our shallow lake example, macrophytes at intermediate turbidities might respond by growing longer stems with fewer leaves in order to reach well-lit surface waters and avoid shading. If this, however, results in less photosynthetic activity and less capacity to remove nutrients from the water column, it might reduce the capacity to outgrow the algae and maintain a clear water state.

Trait change can affect the path of recovery

Changes in trait distributions over time may also affect the recovery trajectory of an ecosystem back to its previous state and the range of hysteresis, i.e. the lag in the threshold of the environmental driver at which recovery to the pre-collapsed state occurs (see Box 1 and Box 3 (Glossary)). The most obvious example is the case where trait change delays a tipping point (Figure 3). In many cases, this delay will not necessarily result in an equally early recovery, which implies that hysteresis in the system will increase. This example illustrates that tipping points and hysteresis are the flip side of mechanisms buffering the stable states: if evolution or phenotypic plasticity buffers the system against environmental change, this can not only delay reaching a tipping point but it may also result in stronger hysteresis.

Another possibility is that evolutionary processes in the deteriorated state might cause the collapsed species to lose the genetic variation necessary for recovery to, and high fitness in, the alternate state⁴⁴. In a laboratory experiment, ref. ⁴¹ found that overharvested fish populations failed to recover even after reducing fishing pressure due to genetic changes in life history traits. This may result in a delay in recovery, or no recovery at all. The opposite scenario is also possible. Trait changes may accelerate recovery and reduce hysteresis (Figure 3). This may happen if, after the collapse, a highly adaptive phenotype is selected for facilitating recovery only at a small reduction of stress. For example, after the collapse of a phytoplankton population due to light stress in the laboratory, recovery took place earlier than expected due to a (probably plastic) adaptive photo-acclimation response⁴⁵. If after the collapse a different phenotype is selected for, or if there is recovery of the lost phenotypic variation (e.g. due to immigration), it may even be possible that the recovery pattern becomes non-catastrophic.

In all cases highlighted in the previous paragraphs, it is uncertain whether the ecosystem will actually recover to the exact same state as before the collapse (Figure 3). The degree to which complete recovery happens might probably depend on the trait that changes. It is a key open question whether trait changes that impact the probability of tipping also impact recovery trajectories.

Phenotypic plasticity, evolution and tipping points

There are more possibilities for the collapse and recovery paths of the ecosystem state than the ones we highlighted here. All will depend on the mechanisms of phenotypic change and it

requires both theoretical and empirical work to understand the most probable outcomes on tipping point responses that would result either from evolution, from phenotypic plasticity, or from their combined effect, including even the evolution of phenotypic plasticity. One reason why the distinction between phenotypic plasticity and evolutionary trait change is important is that the rates at which these processes operate tend to differ, with phenotypic plasticity being generally faster than evolutionary change. Conversely, phenotypic plasticity is often limited in amplitude, and evolutionary trait change might extend the range to which tipping points and hysteresis can be impacted. Importantly, trait change due to evolution also has an intrinsic impact on the population genetic structure that entails a legacy that may impact recovery (e.g. case of genetic erosion or a trait change that is adaptive in one stable state but maladaptive in the other state), whereas trait change mediated by phenotypic plasticity may impact tipping points without a legacy effect if the trait change is reversible.

Testing the effects of phenotypic change on tipping point responses

Integrating evolutionary dynamics in models of ecological tipping points

Coupling models on evolutionary dynamics with models of ecological bistability can offer a better understanding about when genetic trait change can affect tipping point responses. The adaptive dynamics framework - that assumes limited mutation and the separation of ecological and evolutionary timescales - has been used to study how evolution may incur evolutionary collapse and suicide³⁷. Under rapid environmental change, a quantitative genetics approach⁴⁶ is useful for studying how contemporary genetic trait change may lead to evolutionary rescue. Both modelling frameworks can be adapted for studying how trait changes might affect well-

understood models with ecological tipping points under changing environmental conditions. For instance, we could relax the assumption on the separation of timescales and the assumption of weak selection of each framework, respectively, and apply them to models with tipping points. Or one could develop hybrid models that can account simultaneously for selection gradients, while also accounting for genetic drift and demographic stochasticity that dominate the recovery trajectory of the collapsed state. We can then combine these models with recently developed methods that measure the relative impact of evolutionary vs ecological dynamics on stability (Patel et al. 2016) to understand when and how evolutionary dynamics can affect the probability of tipping responses.

Such modelling approaches can help to (i) compare how different mechanisms of trait change (genetic vs plastic) could affect tipping point responses, (ii) identify the conditions (e.g. rate and pattern of environmental stress, rate of trait evolution, costs and trade-offs) under which trait evolution will modify collapse and recovery trajectories, or even (iii) test when trait change itself could be so abrupt (due to disruptive selection) that it could cause ecosystem tipping points. In that way we could develop novel ways for detecting tipping points based on changes in ecological and trait dynamics (Box 2), and suggest new designs for experimental testing.

Adding evolutionary contrasts to experimental tests of ecological tipping points

There are two common approaches for experimentally testing tipping point theory. The first approach starts by establishing two alternative states of the system on either side of a tipping point, and then testing how the system responds to pulse perturbations of a state variable. For

example, if there is evidence for a positive feedback (Box 1) in two states with a different dominant species in each community, then the outcome of species dominance might strongly depend on the initial density of species (i.e. priority effects)⁴⁷. The second approach starts with the system in one state, and then applies a press perturbation of an environmental condition (e.g. increasing productivity, increasing mortality) to observe when the system transitions to a new state^{48–50}. To test for hysteresis in the system, the environmental condition can then be reversed while tracking system recovery to the initial state^{45,51}.

Independently manipulating evolutionary and ecological components of a system can provide new insights into how the dynamics of trait change can affect tipping points. Several experiments have been designed to study the interplay between ecological and evolutionary dynamics^{7,8,52,53}, and these could be usefully co-opted to experimentally test predictions from tipping point theory. A key challenge in these experiments will be to identify and be able to measure the variation of the relevant traits like the ones we highlight in Table 1. Clearly, the selection of traits to study and monitor should start by understanding the specifics of the study system and the mechanisms underlying the tipping points. Although it is challenging to quantify selection gradients in natural populations, useful estimates can be obtained from a wide range of traits (e.g. body size, condition) underlying individual performance⁵⁴. In one study of a tipping point induced in the laboratory with freshwater cyanobacteria⁴⁵, light level was manipulated to test for hysteresis associated with transitions between a high and low biomass state. Contrary to predictions from an ecological model, the population recovered to a higher light stress faster than expected. In the experiment, the recovering cells had lower pigment

concentrations, possibly reflecting adaptation to high irradiance conditions at a cost of photosynthetic efficiency at lower light irradiance. This suggests that the presence of trait variation (i.e. pigment production) in the population influenced the nature of the transition between the two states. A useful experimental test of this idea would be to manipulate standing levels of genetic variation in the stressed population and measure if tipping points change. Adding such evolutionary contrasts to ecological experiments would be a fruitful way to test how both trait variation and evolution may affect tipping points. In experimental systems it is possible to isolate the effects of density and diversity (ecological effects) from the effects of heritable trait change (evolutionary effects). Specifically, one might be able to differentiate between purely ecological effects, direct evolutionary effects linked to changes in functional effect traits, and density-mediated indirect evolutionary effects linked to changes in functional response traits⁵⁵.

Closing the loop: eco-evolutionary feedbacks and tipping point responses

Reciprocal interactions between ecological and evolutionary dynamics is an old idea (e.g.^{56,57}) that is increasingly being tested across a range of systems and study questions (e.g.^{11,58}). Here, we focused on the potential implications that heritable trait changes can have for ecological tipping points. The next step is to understand how reciprocal feedbacks between ecological tipping points and evolutionary dynamics might radically alter not only the dynamics of ecosystems close to tipping but also the evolution of populations and communities of these ecosystems. Tipping points between contrasting ecosystem states create different selection regimes that can shape the evolution of focal species (like keystone, or ecosystem engineers

species) and in their turn the dynamics of the ecosystem state they belong to⁵⁹. One possibility is that such selection regimes will be asymmetric, leading to evolutionary reversals, for example in body sizes in grazed populations⁶⁰, or could maintain the recurrence of harmful algal blooms in lakes⁶¹.

It remains an outstanding challenge to test these ideas. It will be important to identify under which conditions (e.g. type of environmental stress, type of response/effect trait, level of genetic variation, plasticity, spatial and temporal scales) trait change would modify tipping point responses. Under high rates of environmental change, trait changes may be too slow⁶² to have effects on ecological dynamics. Yet, traits of organisms with short generation times or with high levels of standing genetic polymorphism would be most likely best candidate traits to change, but it is unclear how the speed of evolutionary change will be affected by the level of selective pressure prior and past a tipping point. It might be that trait changes that may impact ecosystem collapse are very different to the ones that impact recovery trajectories. Figuring out such relationships will help us study the type of eco-evolutionary feedbacks that could develop along the collapse and recovery trajectories of ecosystems with tipping points. Ultimately one might even address the question about whether ecological bistability can lead to bistability in trait values that has relevant implications in the process of speciation and species divergence.

Perhaps the biggest challenge is how to experimentally study the effects of trait change in ecosystems with tipping points. Most theoretical work on eco-evolutionary dynamics has been experimentally corroborated in laboratory experiments using organisms with short generation

times⁶³. Similarly, ecological tipping points have been mostly studied in experimental microcosms at the population level with single species^{48,49} neglecting how synergistic effects across species can incur strong selection on trait changes⁶⁴. Ecosystem scale tipping points are harder to experimentally test (but see⁶⁵) and simultaneous information on trait variation of the organisms involved is rarely available. Yet, we can identify excellent candidate traits for study. For instance, light sensitivity of submerged macrophytes⁶⁶ is an important response trait in models of lake shifting to a turbid state⁶⁷, whereas the effect of macrophytes on nutrient concentrations⁶⁸ might be governed by rates of nutrient uptake⁶⁹. If we could start measuring such traits to get an idea of their variation, we could start unravelling how sustaining trait variation may be important not only for preventing collapse, but also for improving the success of ecological restoration. Despite the challenging task, the evolutionary perspective we advocate can improve our understanding and management of ecosystems under stress.

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Competing interests

We declare no competing interests.

Author contributions

305 VD and BM designed research and wrote the paper with contributions from all authors.

Table 1 Examples of ecosystem tipping points summarizing the organisms involved and the potential response and effect traits of these organisms. If these traits can experience phenotypic changes, they may affect the tipping point responses in any of the ways presented in the text . Response traits are defined as traits that respond to the environmental stressor(s) that can invoke a tipping point. Effect traits are defined as traits that may influence an ecosystem function that is linked to a tipping point. In the table we refer to the effect of such traits rather than the traits themselves. Representative references are also provided.

Ecosystem Tipping Point	Organism	Environmental driver	Response trait	Effects resulting from change in effect trait	Refs
lake shift to turbid state	macrophytes	nutrient loading	growth, morphology	nutrient retention, shading, allelopathy	1,70
	zooplankton	toxic algae linked to nutrient loading	detoxification	grazing on algae	
	phytoplankton	nutrient loading	growth, nutrient uptake, light requirement	shading, toxicity	
dryland desertification	shrubs	aridity	water retention	facilitation	71,72
		grazing	herbivory resistance	facilitation	
savanna forest/ bush encroachment	trees-shrubs-grasses	fire	fire resistance	facilitation	73,74
		grazing	herbivory resistance	facilitation	
		drought	drought resistance	facilitation	
coral reefs degradation	corals	temperature	temperature tolerance	habitat structure	75,76
		nutrient loading	growth, colonization rate	habitat structure	
		pathogen	resistance to	habitat structure	

		disease	pathogens		
salt-marsh mudflats erosion	marsh grasses	inundation	colonization rate, below sediment growth rate	habitat structure, sediment retention	77,78
intertidal bed degradation	seagrass	drought	drought resistance	habitat structure, sediment retention	79
		wave action	stem morphology	habitat structure, sediment retention, oxygenation	
		grazing	herbivory resistance	habitat structure, sediment retention	
plant-pollinator community collapse	pollinators	chemical stress	toxic resistance	pollination	80,81
		warming	phenology adaptation	pollination	
kelp forest overgrazing	kelp	grazing, wave erosion	herbivory resistance, morphology	habitat structure	82

Figure 1

Variation in a response trait (eg macrophyte shading tolerance) affects tipping points of shallow lake shifting to a eutrophic turbid state. a) The intersections of macrophyte and turbidity responses ($M'=0$, $T'=0$ nullclines) mark the equilibria of the system for two levels of trait variation in the shading tolerance of macrophytes. In the absence of variation ($\sigma^2=0$) there are two alternative equilibria (clear water and turbid water state at the crossing of solid green and brown lines). In the presence of variation ($\sigma^2=0.75$), there is only a single equilibrium of clear water state with no tipping points (at the crossing of dashed green and solid brown lines). b) Changing the level of trait variation in the response trait (eg shading tolerance) will affect the response of a shallow lake to environmental stress (turbidity). Under increasing trait variation hysteresis decreases, bistability disappears, and the tipping point turns into a gradual and non-catastrophic response. Extending similar models like the above along these directions will enable us to better understand the role of trait change and variation on ecological tipping points. Model details and parameters can be found in the Supplementary Information.

Figure 2

Hypothetical alterations of trajectories of ecosystem collapse (left panels, red solid lines) as a consequence of trait change (right panels, red dotted lines). (a, b) Contemporary adaptive mean trait change delays the threshold at which the tipping point occurs (ΔE), potentially associated with a cost that decreases the equilibrium ecosystem state. (c, d) Adaptive mean trait changes might in the short term increase the equilibrium ecosystem state while at the same time also induce an early collapse. [(a, c) Black and gray lines represent the two alternative states of the reference model with no phenotypic change, dashed lines mark the unstable boundary between the two states, circles denote tipping points. (b, d) Dashed black line is the reference scenario with no trait change]

Figure 3

Potential consequences of trait change on the recovery trajectories of an ecosystem after collapse (green dotted lines). Starting from a high value of environmental stress E , if stress is progressively reduced, the ecosystem recovers to the pre-collapse state at the tipping point following the black solid line (no phenotypic change trajectory). In the presence of phenotypic changes, recovery may be delayed or occur earlier (green dotted lines). This implies that phenotypic changes affect the range of hysteresis and the ease of recovery. In both cases, it is unclear whether the ecosystem shifts back to exactly the same state as before the collapse. It may even be possible that the collapse has allowed the emergence of a different (new) phenotype that could turn the recovery path non-catastrophic (smooth). [Solid lines represent the two alternative states of the reference model with no phenotypic change, dashed lines mark the unstable boundary between the two states, circles denote tipping points.]

Box 1: What is a tipping point?

Tipping points mark the shift between contrasting system states that occur when external conditions reach thresholds that trigger an accelerating transition to a contrasting new state⁸³. Mathematically, these transitions correspond to saddle-node or fold bifurcation points⁸⁴. They are also called catastrophic because they mark an unexpected and radical change in the equilibrium state of a system. Tipping points can occur at population level (e.g. due to Allee effects⁴⁸) and community level (e.g. due to priority effects and competition⁸⁵), but it is at the ecosystem scale that tipping points are most prominently studied because they can incur long-term disruption to vital ecosystem services⁸⁶. For example, clear lakes turn turbid dominated by algal blooms¹, coral reefs get overgrown by macroalgae⁸⁷, fisheries collapse due to overexploitation⁸⁸, and tropical forests shift to savanna-type ecosystems under high fire intensity⁷⁴.

Tipping points are typically observed in systems where strong positive feedbacks drive the establishment of alternative stable states⁸³. In the case of shallow lakes, dominance of aquatic macrophytes prevents the growth of algae by removing nutrients (phosphorus) from the water column that leads to the establishment of a stable clear water state (Fig I). When phosphorus loading exceeds a critical threshold macrophytes cannot successfully retain phosphorus, algae start to grow and lake turbidity increases. Rising turbidity kicks a vicious cycle: it hinders the growth of macrophytes but facilitates algae concentration in a self-enforced positive feedback loop (less macrophytes => more algae => more turbidity => less macrophytes and so on) that leads to the collapse of macrophytes and the establishment of a contrasting turbid lake state.

The same positive feedback loop can lead to the recovery of macrophytes, but this time at a lower critical level of phosphorus loading, where algae growth is limited to such an extent that turbidity decreases sufficiently for macrophyte to grow again, capture the phosphorus and reinforce a positive feedback loop leading back to the clear water state. Between these two tipping points, the system is bistable meaning that it can be found in one of the two alternative stable states. This difference in conditions that mark the forward and backward shift is called hysteresis. The stronger the hysteresis, the more difficult it is to recover an ecosystem back to its previous state.

Figure I

Tipping points mark discontinuous changes in the state of an ecosystem. Starting from the upper branch, the ecosystem follows the stable equilibrium line until conditions cross threshold

391 1 at which the upper stable equilibrium disappears (tipping point₁) and the ecosystem state
392 drops abruptly to the lower (alternative) stable state. In our example of the turbid and clear-
393 water states of shallow lakes, reducing nutrient conditions - but to a much lower level - leads to
394 the restoration of the previous state at the crossing of threshold 2 (tipping point₂). The
395 difference in the thresholds between the forward and backward tipping points marks the
396 hysteresis in the system. For this range of conditions the ecosystem can be found in either of
397 the two alternative stable states (bistability). Along the pathways depicted here, no change in
398 the traits of the organisms stabilizing the clear-water (macrophytes) or turbid (algae) state is
399 assumed. [Black lines represent the stable equilibria. Dotted line represents the border
400 between the basins of attraction of the two alternative stable states.]

Box 2: Detecting tipping points based on the dynamics of ecosystem-state and traits

Ecological tipping points are difficult to detect. However, theory suggests that subtle changes in the dynamics of an ecosystem state can provide early-warning information on the underlying stability and risk of a tipping response⁸⁹. This risk is typically quantified by indicators of resilience based on critical-slowness⁹⁰, and include an increase in recovery time back to equilibrium after a perturbation, a rise in variance as the state of the ecosystem fluctuates more widely around its equilibrium, and an increase in autocorrelation because the state of the ecosystem resembles more and more its previous state close to a tipping point. These indicators have been empirically tested in laboratory experiments^{48,49} and in the field^{65,77} focusing on the dynamics of the ecosystem state (species cover, biomass or abundance), while neglecting any trait changes. Accounting for trait change creates new challenges but also opportunities in the detection of tipping points. On one hand, although slowing down indicators should be expected - at least based on ecological dynamics - at the edge of tipping points⁴⁰, it is unclear whether trait changes would either weaken or nullify these signals. On the other hand, changes in traits themselves could be used as proxies for upcoming transitions²⁰. Early studies on fishing-induced evolutionary changes suggested that variation in maturation schedules of cod could have been used to detect its collapse⁴², or that shifts in the mean age-at-maturation of overfished populations could be indicator of their loss of stability (in terms of population variability)¹⁶. Recent work demonstrates how indicators based on both abundance and trait dynamics could complement each other to improve tipping point detection^{20,21}. For instance, measuring changes in mean and variance in body size in combination with resilience indicators based on species abundance improved the warning of collapse in an experimental system with

protists populations¹⁹. Theoretical work demonstrates that the promising possibility to use such fitness-related trait changes as indicators will depend on the rate of environmental change, the level of genetic variation, and the strength of plasticity⁹¹. Other work found no strong early-warnings in populations experiencing rapid environmental change leading them to extinction⁹². These works suggest that the dynamics of phenotypic changes will most likely be context-dependent. The next step is to test these predictions in more complex models of ecosystem-wide tipping points. Future work would need to assess whether changes in response and effect traits could be used as signals of impending transitions. The reported traits in Table 2 map potential traits that could be monitored to provide a proxy for the risk of a transition. Changes in traits like growth forms (density of leaves, length of stems) of macrophytes could be used as proxies of shading tolerance to indicate loss of resilience in shallow lakes. Alternatively, changes in the defense traits of vegetation to herbivores could be signals of vulnerability to overexploitation in dryland landscapes. Overall, the goal is to understand what pattern of trait changes to expect depending on the type of mechanism and stress involved.

438 **Box 3: Glossary**

439 **Alternative stable states:** contrasting states that a system may converge to under the same
440 external conditions

441 **Bistability:** the presence of two alternative stable states under the same conditions

442 **Catastrophic bifurcation:** a substantial change in the qualitative state of a system at a threshold
443 in a parameter or condition

444 **Contemporary (or rapid) evolution:** evolutionary changes that occurs sufficiently rapid that it
445 can have an impact on ecological dynamics at the same time-scale as other ecological factors

446 **Eco-evolutionary dynamics:** dynamics in which ecological processes influence evolutionary
447 processes and evolutionary processes influence ecological processes

448 **Effect trait:** a measurable feature of an organism that underlies an organism's direct effect on
449 an ecosystem function

450 **Genetic drift:** changes in allele frequencies due to random sampling during reproduction

451 **Hysteresis:** the lack of reversibility after a catastrophic bifurcation, meaning that when
452 conditions change in the opposite direction the system stays in the alternative state unless it
453 reaches another bifurcation point (different than the one that caused the first shift)

454 **Phenotypic plasticity:** non-heritable changes in the phenotype of an organism

455 **Response trait:** a measurable feature of an organism that underlies an organism's response to
456 environmental change

457 **Tipping point:** the point where following a perturbation a self-propagated change can
458 eventually cause a system to shift to a qualitatively different state

459 **Trait variation:** variability of any morphological, physiological, or behavioral feature

460 **Trait evolution:** genetic change in phenotype of a given trait

461

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655 **Supplementary Information - Shallow lake eutrophication model**

656 We used a minimal model that describes the dynamics of transition from a clear water state
657 dominated by macrophytes to a turbid water state where macrophytes are practically absent¹.
658 Such transition occurs at a crossing of a fold bifurcation (tipping point) due to changes in
659 nutrient loading (eutrophication). Below we explain how we analysed the model to highlight
660 the presence of alternative states as function of environmental stress (Box 1), and the effects of
661 standing phenotypic variation (Figure 1).
662 The model describes the interactions between macrophyte coverage and turbidity of a shallow
663 lake with the following two ordinary differential equations:

$$\frac{dT}{dt} = r_T T \left(1 - \frac{T}{T_o \frac{h_M}{h_M + M}}\right)$$
$$\frac{dM}{dt} = r_M M \left(1 - \frac{M}{K} \left(\frac{h_T^4 + T^4}{h_T^4}\right)\right)$$

664 where macrophyte cover M grows logistically with rate r_M ($= 0.05$) and carrying capacity K ($= 1$),
665 while it is limited by turbidity following a nonlinear decreasing Hill function defined by the half-
666 saturation h_T ($= 2$) and exponent p ($= 4$). Turbidity T grows with rate r_T ($= 0.1$) depending on the
667 level of background turbidity T_o ($= [2-8]$, used as proxy of nutrient loading acting as the
668 environmental stress in our analysis (nutrient loading, Fig I Box I)). Turbidity is negatively
669 affected by the level of macrophyte cover following an inverse Hill function with half-saturation
670 h_M ($= 0.2$).
671 Solving for steady state the nullclines of the system are:

$$M' = \frac{h_T^4}{h_T^4 + T^4}$$

$$T' = T_o \frac{h_M}{h_M + M}$$

672 Their intersections mark the two alternative stable states (clear and turbid state) and the
 673 unstable saddle depending on the value of background turbidity T_o (Fig. 1a). We hypothesize
 674 that the half-saturation h_T that affects the strength of nonlinear response of macrophytes to
 675 turbidity is defined by a response trait z (e.g. capacity to grow under low light
 676 conditionsshading). Different values of z will thus change the response of macrophytes to
 677 turbidity by changes in h_T (Supplementary Figure 1a). We assumed that trait z follows a *beta*
 678 distribution (closed limits) that we can parameterize in order to define a given mean μ ($=0$) and
 679 variance σ^2 . We further assumed that the half-saturation h_T depends on the trait z following
 680 $h_T = h_{T_o} e^{cz}$, where h_{T_o} is a background value ($= 2$) and c a factor ($=0.5$) (Supplementary Figure
 681 1b).
 682 Using this relationship and integrating for different limits of trait z and levels of variance of the
 683 *Beta* distribution, we can calculate the macrophyte equilibrium in the presence of standing
 684 phenotypic variation in z as:

$$M' = \int_{-z}^z \frac{h_T(z)^4}{h_T(z)^4 + T^4} p(z) dz$$

685
 686 where $p(z)$ is defined by the *Beta* distribution as explained above within a range of z ($= [-2,2]$).
 687 We repeat this for a range of turbidity T values ($= [0-8]$) to estimate the nullcline of

macrophytes M for this range of turbidity T , and we find the new equilibria states from the cross sections with the turbidity nullcline (Fig. 1a). We repeat this procedure to estimate all equilibria as a function of environmental conditions (T_o) and for different levels of standing phenotypic variation (σ^2) to construct the two dimensional bifurcation plot of Fig. 1b.

1 Scheffer, M. (1998) *Ecology of Shallow Lakes*, (1st edn) Chapman and Hall.

Supplementary Figure 1 a) Variation in a response trait z of macrophytes (e.g. shading tolerance) can affect the way macrophytes respond to water turbidity through parameter hT that determines the response of macrophytes to turbidity ($M' = \frac{h_T^4}{h_T^4 + T^4}$). b) Two scenarios of high (dashed) and low (solid) variation in the phenotype distribution of the response trait z ($\sim \text{Beta}(\mu, \sigma^2)$), where parameter h_T has a positive relationship with the trait (red line).