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Ecosystem tipping points in an evolving world

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

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 turbid water state[1] and the collapse of vegetation leading to a desert state in drylands[2]. Societal stakes associated with tipping points in natural ecosystems can be high, and there is a large emphasis on uncovering the mechanisms that trigger them[3] and possible methods to detect and avoid them[4]. Currently, however, tipping point theory largely lacks an evolutionary perspective, and this might limit the understanding of the occurrence, timing, and abruptness of shifts between states (see figure in Box 1). Here we argue that both trait variation and evolution are important for understanding how ecosystem dynamics affect tipping points.

Developing a trait-based evolutionary perspective on tipping points in ecosystems is warranted by the growing amount of evidence that changes in standing levels of trait variation and contemporary trait evolution are important drivers of ecological processes (for example, refs. [5,6]) by influencing population dynamics[7], shaping the structure of species interactions in communities[8], or affecting species composition at the metacommunity level[9]. Such ecological effects of evolution also extend to ecosystem functioning[10–12] by modifying material fluxes[13], primary production[14], nutrient recycling[15], and decomposition[16]. Changes in life-history traits of organisms caused by environmental stress (like fishing) have been shown to destabilize dynamics of populations[17] or whole communities[18], and even to increase the risk of extinction[19]. Fitness-related traits (for example, body size) can systematically change before populations collapse[20] and can be used as indicators of biological transitions[21,22]. 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 sensitivity to environmental stress among species, populations, or individuals in an ecosystem[23,24]. This sensitivity underlies the response capacity of communities to stress[25,26] such that trait changes could affect the resilience of entire ecosystems[27] 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[10,11] that underlie the performance and fitness of organisms that exist in a given environmental state (that is, response traits), or those traits through which organisms have direct or indirect effects on the environmental state (that is, effect traits) (Table 1). The distribution of such response and effect traits can vary because of phenotypic plasticity, species sorting, and evolutionary trait change, and distinguishing between these mechanisms can be important for understanding the ecological dynamics of trait change in general[28] and of tipping points in particular. Phenotypic plasticity, whereby a genotype exhibits 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 population[29], which can originate from novel variants due to mutation[30], recombination[31], and gene flow among populations and species[32]. Below, we do not a priori distinguish between the genetic versus plastic sources of trait distributions (although we comment on their differences), but instead 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 and 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 a high level of trait variation may decrease the probability of catastrophic ecosystem responses. A decrease in the probability of tipping events occurs because standing trait variation allows for portfolio effects that introduce strong heterogeneity in

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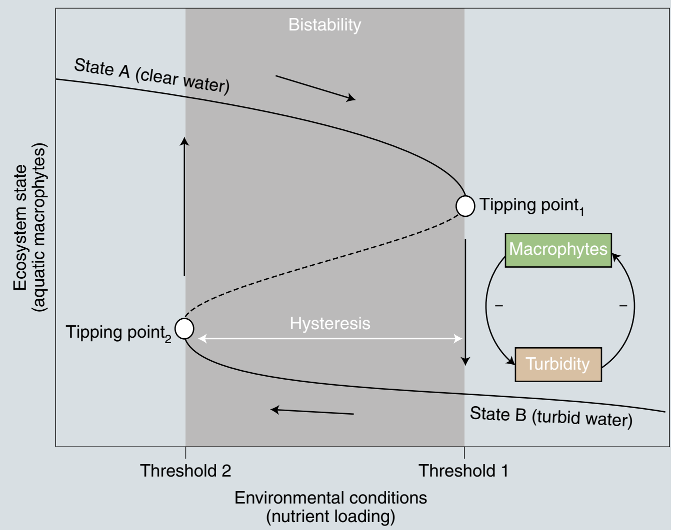
Box 1 | What is a tipping point?

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 state[83]. Mathematically, these transitions correspond to saddle-node or fold bifurcation points[84]. 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 the population level (for example, because of Allee effects[50]) and the community level (for example, because of priority effects and competition[85]), but it is at the ecosystem scale that tipping points are most prominently studied because they can incur long-term disruption to vital ecosystem services[86]. For example, clear lakes become turbid and dominated by algal blooms[1], coral reefs are overgrown by macroalgae[87], fisheries collapse owing to overexploitation[88], and tropical forests shift to savannah-type ecosystems under high fire intensity[74].

Tipping points are typically observed in systems where strong positive feedbacks drive the establishment of alternative stable states[83]. 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 (see the figure in this box). When phosphorus loading exceeds a critical threshold, macrophytes cannot successfully retain phosphorus, algae starts to grow, and lake turbidity increases. Rising turbidity kicks off a vicious cycle: it hinders the growth of macrophytes but facilitates algae growth in a self-enforced positive feedback loop (fewer macrophytes → more algae → more turbidity → fewer 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 at a lower critical level of phosphorus loading, where algae growth is limited to such an extent that turbidity decreases sufficiently for macrophytes 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.



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 1, at which the upper stable equilibrium disappears (tipping point$_1$) and the ecosystem state drops abruptly to the lower (alternative) stable state. In our example of the turbid and clear-water states of shallow lakes, reducing nutrient conditions—but to a much lower level—leads to the restoration of the previous state at the crossing of threshold 2 (tipping point$_2$). The difference in the thresholds between the forward and backward tipping points marks the hysteresis in the system. For this range of conditions, the ecosystem can be found in either of the two alternative stable states (bistability). Along the pathways depicted here, no change in the traits of the organisms stabilizing the clear-water (macrophytes) or turbid (algae) state is assumed. Black lines represent the stable equilibria. The dashed line represents the border between the basins of attraction of the two alternative stable states.

population processes, interactions, and responses[33] buffering population dynamics[34]. Such heterogeneity can be enhanced by Jensen's inequality[33], whereby variation around the mean of a trait can affect the response of an ecological interaction or an ecological process as a function of the nonlinear relationship between the trait and its effect[35]. This effect is clearly illustrated in a model of water clarity shifts in shallow lakes (see figure in Box 1). Here, changing the amount of variation in the macrophyte response trait to turbidity can increase or decrease the probability of the ecosystem reaching a tipping point. Under high levels of variation in the macrophyte response traits, the transition from the clear to the turbid water state can even become non-catastrophic and the lake no longer exhibits bistability (Fig. 1).

Trait change can delay a tipping point

Trait variation simply means that some resistant phenotypes are present in a population. However, trait variation could also facilitate trait changes. On top of that, trait changes might be fuelled by de novo mutation and phenotypic plasticity. In ecosystems that are brought closer to tipping points by stress gradients, trait changes could potentially delay tipping to the alternative state (Fig. 2a). This resonates with the idea of evolutionary rescue[36,37], the difference being that there is no rescue, but rather only a delay in the collapse of the system by shifting the threshold of stress at which the collapse occurs to a higher level (Fig. 2b). For instance, in the case of a shallow lake becoming turbid because of eutrophication (Box 1), aquatic macrophytes might delay the transition by increasing the threshold of nutrients at which the tipping occurs because of contemporary trait changes that convey tolerance to shading (Table 1).

Trait change can lead to an earlier tipping point

Trait change may not always buffer populations from environmental changes. It can also contribute to an increased risk of ecosystem collapse (Fig. 2c,d). For example, environmental stress could impose directional selection on a trait in a given species or a group of species that brings the system closer to tipping to an alternative state[38,39]. This is similar to evolutionary collapses or evolutionary suicide as defined in evolutionary biology[40,41], 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 subjected to harvesting[39,42]. For example, researchers have shown how fishing pressure has led to early maturation of Atlantic cod populations[43], which is associated with lower reproductive output and irregular recruitment dynamics that may have increased the chance of stochastic extinction and contributed to the cod collapse in the 1990s. Evolutionary suicide might lead to an ecosystem-level

Table 1 | Examples of ecosystem tipping points and potential evolving response and effect traits

Ecosystem Tipping Point	Organism	Environmental driver	Response trait	Ecosystem effects of trait change
Lake shift to turbid state[1,70]	Macrophytes	Nutrient loading	Growth, morphology	Nutrient retention, shading, allelopathy
	Zooplankton	Toxic algae linked to nutrient loading	Detoxification	Grazing on algae
	Phytoplankton	Nutrient loading	Growth, nutrient uptake, light requirement	Shading, toxicity
Dryland desertification[71,72]	Shrubs	Aridity	Water retention	Facilitation
		Grazing	Herbivory resistance	Facilitation
Savannah forest/ bush encroachment[73,74]	Trees, shrubs, and grasses	Fire	Fire resistance	Facilitation
		Grazing	Herbivory resistance	Facilitation
		Drought	Drought resistance	Facilitation
Coral reef degradation[75,76]	Corals	Temperature	Temperature tolerance	Habitat structure
		Nutrient loading	Growth, colonization rate	Habitat structure
		Pathogen disease	Resistance to pathogens	Habitat structure
Salt-marsh mudflat erosion[77,78]	Marsh grasses	Inundation	Colonization rate, below sediment growth rate	Habitat structure, sediment retention
Intertidal bed degradation[79]	Seagrass	Drought	Drought resistance	Habitat structure, sediment retention
		Wave action	Stem morphology	Habitat structure, sediment retention, oxygenation
		Grazing	Herbivory resistance	Habitat structure, sediment retention
Plant–pollinator community collapse[80,81]	Pollinators	Chemical stress	Toxic resistance	Pollination
		Warming	Phenology adaptation	Pollination
Kelp forest overgrazing[82]	Kelp	Grazing, wave erosion	Herbivory resistance, morphology	Habitat structure

If these traits can experience phenotypic changes, then 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 effects of trait change in general, inclusive of both response and effect traits. Representative references are also provided.

collapse in the case of drylands[44], where, under increased aridity, adaptive evolution can favour local facilitation among neighbouring 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 vegetation, resulting in a desert state due to the invasion of plant genotypes that do not facilitate resistance to aridity in neighbouring plants. In our shallow lake example, macrophytes in lakes 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 lessened photosynthetic activity and a lowered capacity to remove nutrients from the water column, it might reduce the macrophytes' capacity to outgrow 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 trajectory of an ecosystem's recovery to its previous state and the range of hysteresis, which is the lag in reaching the threshold of an environmental driver at which recovery to the pre-collapsed state occurs (Box 1 and Box 2). The most obvious example is the case where trait change delays the occurrence of a tipping point (Fig. 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 how tipping points and hysteresis can be affected in opposite ways: if evolution or phenotypic plasticity buffers the system against environmental change, this can not only delay the reaching of a tipping point but also may 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 alternative state[45]. In a laboratory experiment[42], scientists found that overharvested fish populations failed to recover even after fishing pressure was reduced owing to genetic changes in their 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 (Fig. 3). This may happen if, after the collapse, a highly adaptive phenotype is selected for, facilitating recovery after only 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 because of a (probably plastic) adaptive photo-acclimation response[46]. If a different phenotype is selected for after the collapse, or if there is recovery of lost phenotypic variation (due to immigration, for example), it may even be possible that the recovery pattern becomes non-catastrophic (Fig. 3).

In all cases highlighted in the previous paragraphs, it is uncertain whether the ecosystem will actually recover to a state exactly the same as that before the collapse (Fig. 3). The degree to which complete recovery happens likely depends on the trait that changes. Whether trait changes that impact the probability of tipping also impact recovery trajectory is an open key question.

Phenotypic plasticity, evolution and tipping points

There are more possibilities for the collapse and recovery paths of the ecosystem state than those highlighted here. All depend on the mechanisms of phenotypic change, and both theoretical and

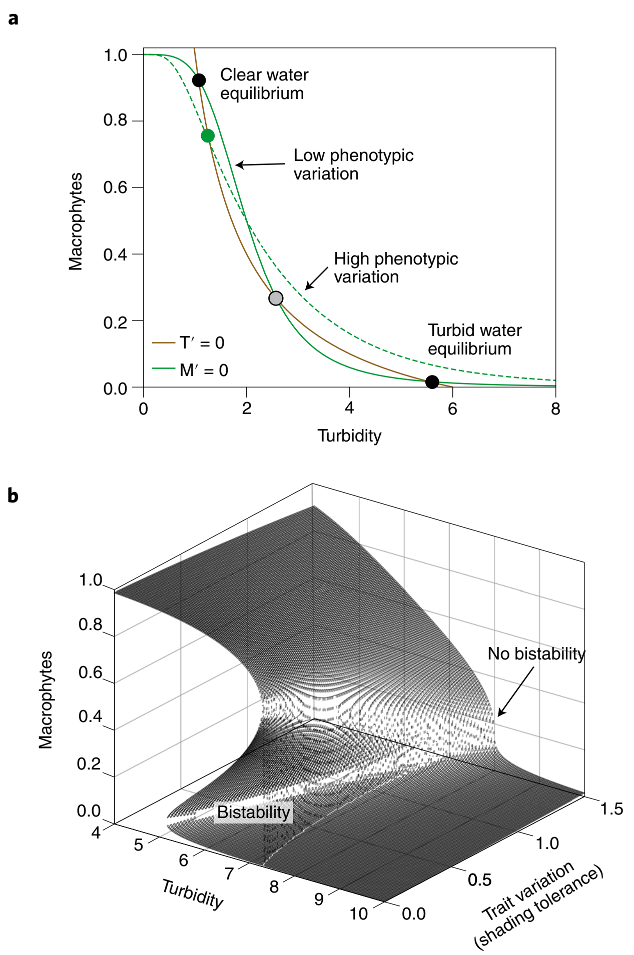


Fig. 1 | Variation in a response trait (such as macrophyte shading tolerance) affects the tipping point at which a shallow lake shifts to a eutrophic turbid state. a, The intersections of macrophyte and turbidity responses ($M' = 0$, $T' = 0$ nullclines) mark the equilibria of the system for two levels 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 states, located at the crossings of the solid green and brown lines). In the presence of variation ($\sigma^2 = 0.75$), there is only a single equilibrium (clear water state) with no tipping points (at the crossing of the dashed green and solid brown lines). **b**, Changing the level of trait variation in 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 response becomes a gradual and non-catastrophic response. Although not captured explicitly by this simple model, the effect of trait variation on ecosystem response could act not only through the existence of resistant individuals (or subpopulations of macrophytes), but also on its potential to facilitate trait change. Extending similar models like the above along these directions will enable scientists 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.

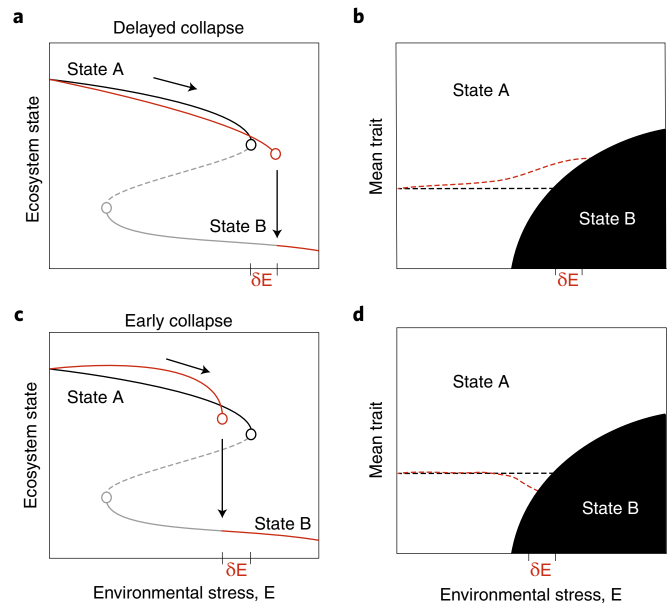


Fig. 2 | Hypothetical alterations of trajectories of ecosystem collapse (left panels, red solid lines) as a consequence of trait change (right panels, red dashed lines). a,**b**, Contemporary adaptive mean trait change delays the threshold at which the tipping point occurs (δE), which is potentially 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. In **a** and **c**, black and grey lines represent the two alternative states of the reference model with no phenotypic change, and grey dashed lines mark the unstable boundary between the two states. Circles denote tipping points. In **b** and **d**, the dashed black line is the reference scenario with no trait change.

empirical work are required to understand the most probable outcomes of tipping point responses that result either from evolution or phenotypic plasticity, or from their combined effects, including 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 generally being 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, entailing a legacy that may impact recovery (for example, a case of genetic erosion or a trait change that is adaptive in one stable state but maladaptive in the alternative state), whereas trait change mediated by phenotypic plasticity may impact tipping points without a legacy effect if that trait change is reversible.

Testing how phenotypic change affects tipping point response

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—which assumes limited mutation and the separation of ecological and evolutionary timescales—has been used to study how evolution may incur evolutionary collapse and suicide[38]. Under rapid environmental change, a quantitative genetics framework[47] 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 of ecological tipping points under changing environmental conditions. For instance, one could relax the assumption on the separation of ecological and evolutionary timescales and the assumption of weak selection of each respective framework mentioned previously and apply them to models with tipping points. Or one could develop hybrid models that can

Box 2 | Glossary

- Alternative stable states: contrasting states that a system may converge to under the same external conditions
- Bistability: the presence of two alternative stable states under the same conditions
- Catastrophic bifurcation: a substantial change in the qualitative state of a system at a threshold in a parameter or condition
- Contemporary (or rapid) evolution: evolutionary changes that occur rapidly enough to have an impact on ecological dynamics at the same timescale as other ecological factors
- Eco-evolutionary dynamics: dynamics in which ecological processes influence evolutionary processes and evolutionary processes influence ecological processes
- Effect trait: a measurable feature of an organism that underlies that organism's direct effect on an ecosystem function
- Genetic drift: changes in allele frequencies due to random sampling during reproduction
- Hysteresis: the lack of reversibility after a catastrophic bifurcation, meaning that when conditions change in the opposite direction, the system stays in the alternative state unless it reaches another bifurcation point (different than the one that caused the first shift)
- Phenotypic plasticity: the ability of individual genotypes to produce different phenotypes in different environmental conditions
- Response trait: a measurable feature of an organism that underlies an organism's response to environmental change
- Tipping point: the point following a perturbation at which a self-propagated change can eventually cause a system to shift to a qualitatively different state
- Trait variation: variability of any morphological, physiological, or behavioural feature
- Trait evolution: genetic change in phenotype of a given trait

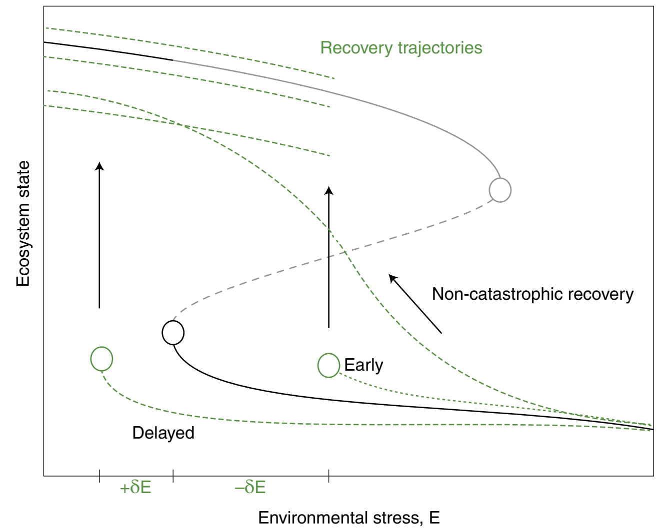


Fig. 3 | Potential consequences of trait change on the recovery trajectories of an ecosystem after collapse. Starting from a high value of environmental stress (E), if stress is progressively reduced, the ecosystem recovers to the pre-collapse state at the tipping point following the black solid line (no phenotypic change trajectory). In the presence of phenotypic changes, recovery may be delayed or occur earlier (green dashed 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 (continous smooth green dashed line). Solid lines represent the two alternative states of the reference model with no phenotypic change, and grey dashed lines mark the unstable boundary between the two states. Circles denote tipping points.

simultaneously account for selection gradients and the 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 versus ecological dynamics on stability[48] to understand when and how evolutionary dynamics can affect the probability of tipping responses.

Such modelling approaches can help to (1) compare how different mechanisms of trait change (genetic versus plastic) could affect tipping point responses, (2) identify the conditions (for example, rate and pattern of environmental stress, rate of trait evolution, and costs and trade-offs) under which trait evolution will modify collapse and recovery trajectories, and even (3) test when trait change itself could be so abrupt (owing to disruptive selection) that it could cause an ecosystem tipping point to occur. In this manner, researchers could develop novel methods to detect tipping points based on changes in ecological and trait dynamics (Box 3) 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 all species in the community (that is, priority effects)[49]. The second approach starts with the system in one state and then applies a change in environmental conditions (for example, increasing productivity, increasing mortality) to observe when the system transitions to a new state[50–52]. To test for hysteresis in the system, the environmental condition can then be reversed while system recovery to the initial state is tracked[46,53].

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[8,9,54,55], 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 measure the variation of relevant traits, like the ones that we highlight in Table 1. Clearly, selection of traits to study and monitor should start with an understanding of 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 (for example, body size and condition) underlying individual performance[56]. In one study of a tipping point induced in the laboratory with freshwater cyanobacteria[46], 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 from 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

Box 3 | | 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 response[89]. This risk is typically quantified by indicators of resilience based on critical slowing down[90] 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 more closely resembles its previous state near a tipping point. These indicators have been empirically tested in laboratory experiments[50,51] and in the field[65,77], with a focus 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 on the basis of ecological dynamics—at the edge of tipping points[41], 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 transitions[21]. Early studies on fishing-induced evolutionary changes suggested that variation in maturation schedules of cod could have been used to detect collapse of the population[43], or that shifts in the mean age-at-maturation of overfished populations could be an indicator of their loss of stability (in terms of population variability)[17]. Recent work demonstrates how indicators based on both abundance and trait dynamics could complement each other to improve tipping point detection[21,22]. 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 protist populations[20]. Theoretical work demonstrates that the possibility of being able to use fitness-related trait changes as indicators will depend on the rate of environmental change, the level of genetic variation, and the strength of plasticity[91]. Other work found no strong early-warnings in populations experiencing rapid environmental change leading to extinction[92]. 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 1 map potential traits that could be monitored to provide a proxy for the risk of a transition. Changes in traits like growth forms of macrophytes (density of leaves and length of stems) could be used as proxies of shading tolerance to indicate loss of resilience in shallow lakes. Alternatively, changes in the defence 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.

suggests that the presence of trait variation (that is, pigment production) in the population influenced the nature of the transition between the two states. A useful experimental test of this idea would be manipulating standing levels of genetic variation in the stressed population and assessing how a tipping response changes. 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 among 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 traits[48].

Closing the loop

Reciprocal interactions between ecological and evolutionary dynamics is an old idea (for example, refs. [57,58]) that is increasingly being tested across a range of systems and study questions (for example, refs. [12,59]). 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 in these ecosystems. Tipping points between contrasting ecosystem states create different selection regimes that can shape the evolution of focal species (like keystone or ecosystem-engineer species) and, in turn, the dynamics of the ecosystem state they belong to[60]. One possibility is that such selection regimes will be asymmetric, leading to evolutionary reversals, for example in body sizes in grazed populations[61], or they could maintain the recurrence of harmful algal blooms in lakes[62].

Testing these ideas remains an unsolved challenge. It will be important to identify under which conditions (for example, the type of environmental stress, the type of response/effect trait, the level of genetic variation, plasticity, and spatial and temporal scales) trait change would modify tipping point responses. Under high rates of environmental change, trait changes may be too slow[63] to have effects on ecological dynamics. Yet traits of organisms with short generation times or with high levels of standing genetic polymorphism would most likely be the 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 to and past a tipping point. It might be that trait changes that may impact ecosystem collapse are very different compared with the ones that impact recovery trajectories. Figuring out such relationships will help researchers 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 of 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 times[7]. Similarly, ecological tipping points have been mostly studied in experimental microcosms at the population level with single species[50,51], neglecting how synergistic effects across species can incur strong selection on trait changes[64]. Ecosystem-scale tipping points are harder to experimentally test (but see ref. [65]), 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 macrophytes[66] is an important response trait in models of shifts to a turbid state in lakes[67], whereas the effect of macrophytes on nutrient concentrations[68] might be governed by rates of nutrient uptake[69]. If scientists could start measuring such traits to get an idea of their variation, then they 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

The authors declare no competing interests.

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