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1 *accepted as Perspective in NE&E*

2

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

4

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27

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

42 **Tipping points in an evolving world**

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

53

54 Developing a trait-based evolutionary perspective about tipping points in ecosystems is
55 warranted by the growing evidence that changes in standing levels of trait variation and
56 contemporary trait evolution are important drivers of ecological processes (e.g.^{5,6}), by
57 influencing population dynamics (Yoshida et al. 2003), shaping the structure of species
58 interactions in communities⁷, or affecting species composition at the metacommunity level⁸.
59 Such ecological effects of evolution also extend to ecosystem functioning⁹⁻¹¹, by modifying
60 material fluxes¹², primary production¹³, nutrient recycling¹⁴, and decomposition¹⁵. Changes in
61 life-history traits caused by environmental stress (like fishing) have been shown to destabilise
62 dynamics of populations¹⁶ or whole communities¹⁷, and even increase their risk of extinction¹⁸.
63 Fitness-related traits (e.g. body size) can systematically change before populations collapse¹⁹

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

72
73 Ecosystem resilience can be affected by variation in traits^{9,10} underlying the performance and
74 fitness of organisms in a given environmental state (i.e. response traits), or those causing direct
75 or indirect effects on the environmental state (i.e. effect traits) (Table 1). The distribution of
76 such response and effect traits can vary due to phenotypic plasticity, species sorting, or
77 evolutionary trait change, and distinguishing between these mechanisms can be important for
78 understanding the ecological dynamics of trait change in general²⁷, and of tipping points in
79 particular. Phenotypic plasticity, where genotypes exhibit different phenotypes in different
80 environments, is a relevant source of trait variation, particularly when the phenotypic changes
81 relate to the capacity of organisms to respond to stress. However evolutionary responses to
82 stress depend on heritable trait variation in a population²⁸, which can originate from novel
83 variants due to mutation²⁹, recombination³⁰, or gene flow among populations and species³¹.
84 Below, we do not *a priori* distinguish between the genetic versus plastic sources of trait
85 distributions (although we comment on their differences), but focus on how trait variation and

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

89

90 ***Trait variation could affect the probability of tipping points***

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

104

105 ***Trait change can delay a tipping point***

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

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

117

118 ***Trait change can lead earlier to a tipping point***

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

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

139

140 ***Trait change can affect the path of recovery***

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

150

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

163

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

169

170 ***Phenotypic plasticity, evolution and tipping points***

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

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

185

186 **Testing the effects of phenotypic change on tipping point responses**

187 ***Integrating evolutionary dynamics in models of ecological tipping points***

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

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

204

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

212

213 ***Adding evolutionary contrasts to experimental tests of ecological tipping points***

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

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

224

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

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

251

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

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

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

265

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

279

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

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

295

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301

302 **Competing interests**

303 We declare no competing interests.

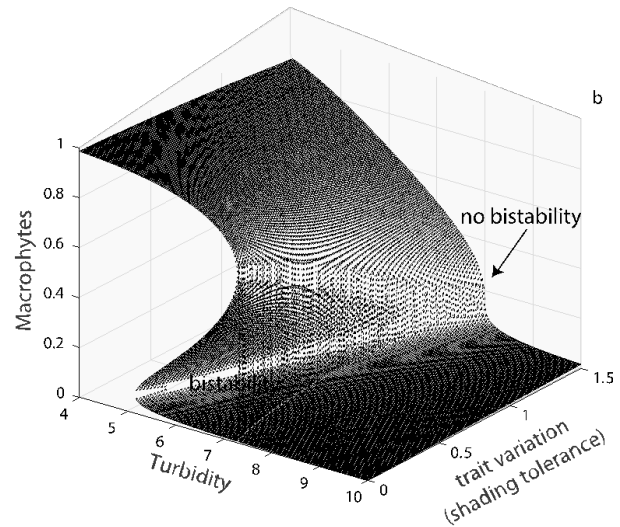
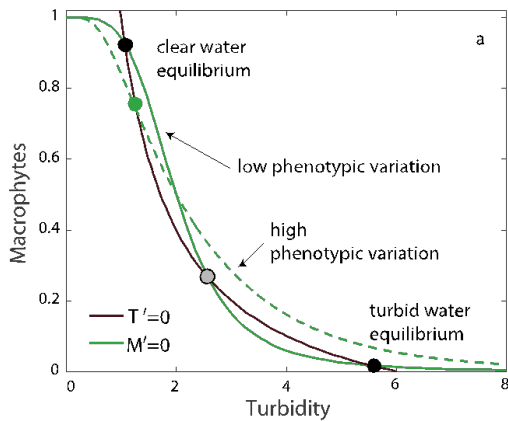
304 **Author contributions**

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

306 **Table 1** Examples of ecosystem tipping points summarizing the organisms involved and the
 307 potential response and effect traits of these organisms. If these traits can experience
 308 phenotypic changes, they may affect the tipping point responses in any of the ways presented
 309 in the text . Response traits are defined as traits that respond to the environmental stressor(s)
 310 that can invoke a tipping point. Effect traits are defined as traits that may influence an
 311 ecosystem function that is linked to a tipping point. In the table we refer to the effect of such
 312 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



314

315 **Figure 1**

316 Variation in a response trait (eg macrophyte shading tolerance) affects tipping points of shallow

317 lake shifting to a eutrophic turbid state. a) The intersections of macrophyte and turbidity

318 responses ($M'=0$, $T'=0$ nullclines) mark the equilibria of the system for two levels of trait

319 variation in the shading tolerance of macrophytes. In the absence of variation ($\sigma^2=0$) there

320 are two alternative equilibria (clear water and turbid water state at the crossing of solid green

321 and brown lines). In the presence of variation ($\sigma^2=0.75$), there is only a single equilibrium of

322 clear water state with no tipping points (at the crossing of dashed green and solid brown lines).

323 b) Changing the level of trait variation in the response trait (eg shading tolerance) will affect the

324 response of a shallow lake to environmental stress (turbidity). Under increasing trait variation

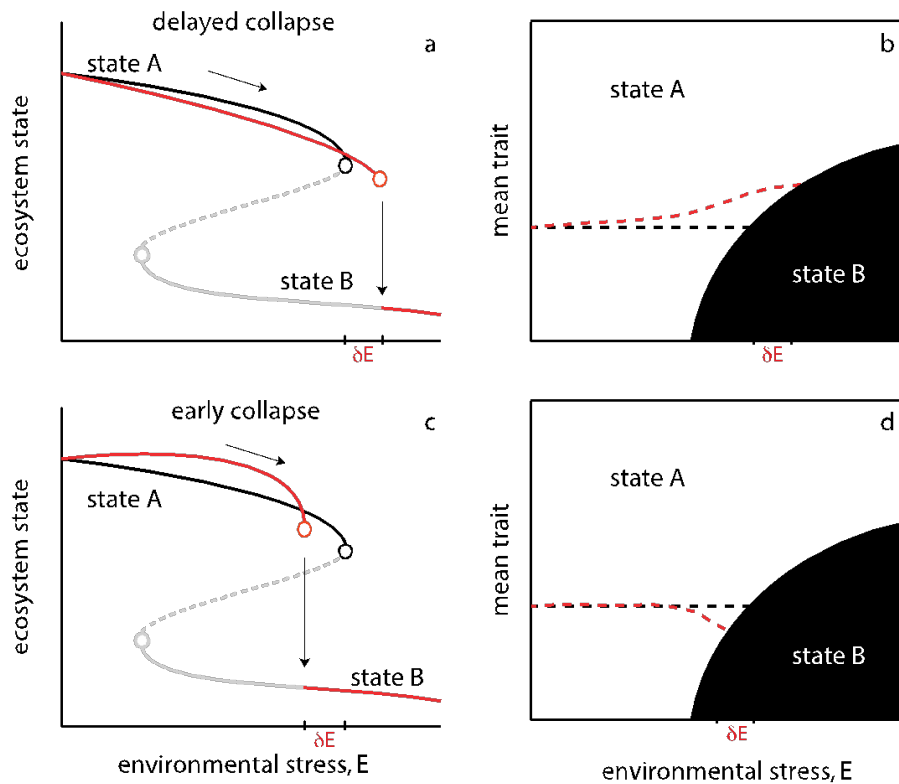
325 hysteresis decreases, bistability disappears, and the tipping point turns into a gradual and non-

326 catastrophic response. Extending similar models like the above along these directions will

327 enable us to better understand the role of trait change and variation on ecological tipping

328 points. Model details and parameters can be found in the Supplementary Information.

329



330

331 **Figure 2**

332 Hypothetical alterations of trajectories of ecosystem collapse (left panels, red solid lines) as a

333 consequence of trait change (right panels, red dotted lines). (a, b) Contemporary adaptive

334 mean trait change delays the threshold at which the tipping point occurs (δE), potentially

335 associated with a cost that decreases the equilibrium ecosystem state. (c, d) Adaptive mean

336 trait changes might in the short term increase the equilibrium ecosystem state while at the

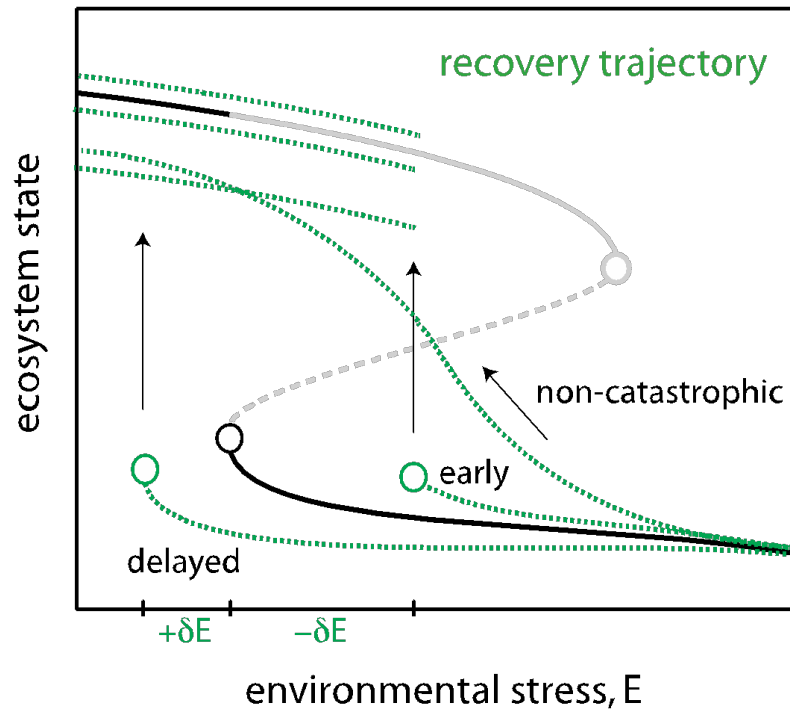
337 same time also induce an early collapse. [(a, c) Black and gray lines represent the two

338 alternative states of the reference model with no phenotypic change, dashed lines mark the

339 unstable boundary between the two states, circles denote tipping points. (b, d) Dashed black

340 line is the reference scenario with no trait change]

341



342

343 **Figure 3**

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

355 **Box 1: What is a tipping point?**

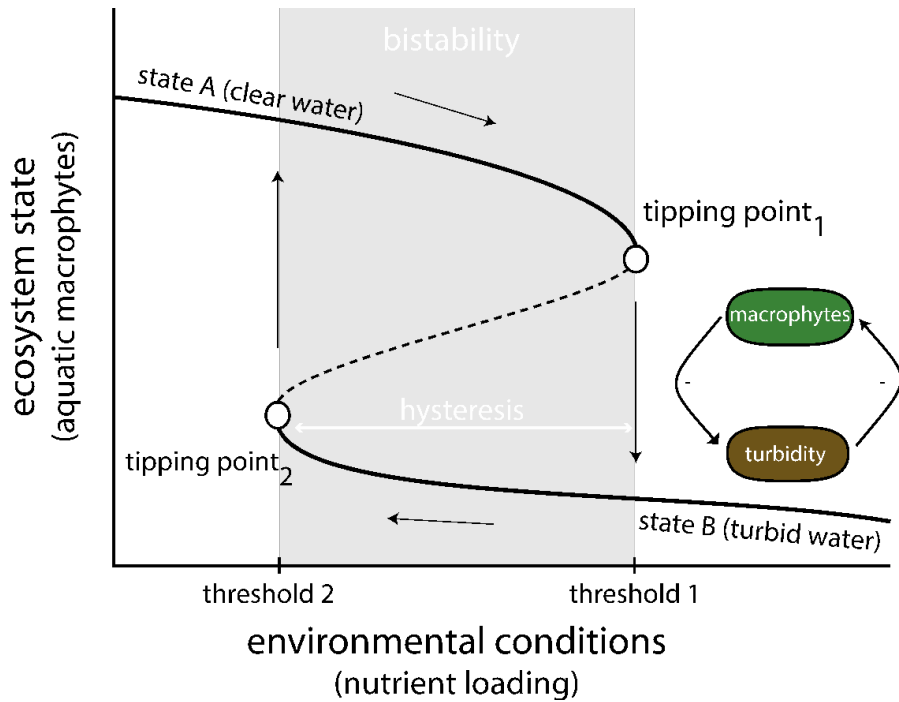
356 Tipping points mark the shift between contrasting system states that occur when external
357 conditions reach thresholds that trigger an accelerating transition to a contrasting new state⁸³.
358 Mathematically, these transitions correspond to saddle-node or fold bifurcation points⁸⁴. They
359 are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

367

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

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

385



386

387

388 **Figure 1**

389 Tipping points mark discontinuous changes in the state of an ecosystem. Starting from the
 390 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.]

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

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

423 protists populations¹⁹. Theoretical work demonstrates that the promising possibility to use such
424 fitness-related trait changes as indicators will depend on the rate of environmental change, the
425 level of genetic variation, and the strength of plasticity⁹¹. Other work found no strong early-
426 warnings in populations experiencing rapid environmental change leading them to extinction⁹².
427 These works suggest that the dynamics of phenotypic changes will most likely be context-
428 dependent. The next step is to test these predictions in more complex models of ecosystem-
429 wide tipping points. Future work would need to assess whether changes in response and effect
430 traits could be used as signals of impending transitions. The reported traits in Table 2 map
431 potential traits that could be monitored to provide a proxy for the risk of a transition. Changes
432 in traits like growth forms (density of leaves, length of stems) of macrophytes could be used as
433 proxies of shading tolerance to indicate loss of resilience in shallow lakes. Alternatively, changes
434 in the defense traits of vegetation to herbivores could be signals of vulnerability to
435 overexploitation in dryland landscapes. Overall, the goal is to understand what pattern of trait
436 changes to expect depending on the type of mechanism and stress involved.
437

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 conditions shading). 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

688 macrophytes M for this range of turbidity T , and we find the new equilibria states from the
 689 cross sections with the turbidity nullcline (Fig. 1a).
 690 We repeat this procedure to estimate all equilibria as a function of environmental conditions
 691 (T_0) and for different levels of standing phenotypic variation (σ^2) to construct the two
 692 dimensional bifurcation plot of Fig. 1b.

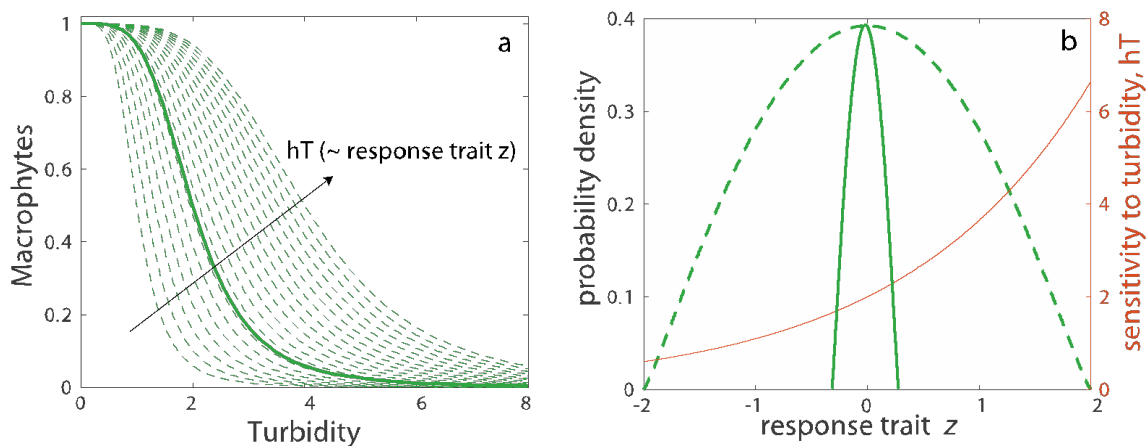
693

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695

696

697 **Supplementary Figure 1** a) Variation in a response trait z of macrophytes (e.g. shading
 698 tolerance) can affect the way macrophytes respond to water turbidity through parameter hT
 699 that determines the response of macrophytes to turbidity ($M' = \frac{h_T^4}{h_T^4 + T^4}$). b) Two scenarios of
 700 high (dashed) and low (solid) variation in the phenotype distribution of the response trait z (\sim
 701 $Beta(\mu, \sigma^2)$), where parameter h_T has a positive relationship with the trait (red line).



702