

Ecosystem tipping points in an evolving world

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25 **Abstract**

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

36

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

39

40 **Tipping points in an evolving world**

41 Tipping points mark the abrupt shift between contrasting ecosystem states (broadly termed
42 regime shifts) when environmental conditions cross specific thresholds (Box 1). Prominent
43 examples are the shift of shallow lakes from a clear to a turbid water state (Scheffer et al.
44 1993), or the collapse of vegetation to a desert state in drylands (Reynolds et al. 2007). Societal
45 stakes associated with tipping points in natural ecosystems can be high and there is great
46 emphasis on the mechanisms that trigger them (Oliver et al. 2015) and the possible ways to
47 detect and avoid them (Scheffer et al. 2009). Currently, however, tipping point theory lacks an
48 evolutionary perspective, and this might limit our understanding of the occurrence, timing, and
49 abruptness of shifts between states (Figure 1). Here we argue that both trait variation and
50 evolution are important for understanding ecosystem dynamics in the vicinity of tipping points.

51
52 Developing a trait-based evolutionary perspective about tipping points in ecosystems is
53 warranted by the growing evidence that changes in standing levels of trait variation and
54 contemporary trait evolution are important drivers of ecological dynamics (eg (Saccheri and
55 Hanski 2006; Kinnison and Hairston 2007)), influencing population dynamics (Yoshida et al.
56 2003), shaping the structure of species interactions and composition at the community (Pantel
57 et al. 2015), or at metacommunity level (Farkas et al. 2013). Such ecological effects of evolution
58 also extend to ecosystem functioning (Norberg et al. 2001; Matthews et al. 2011; Hendry 2017),
59 by modifying material fluxes (De Mazancourt et al. 1998), primary production (Gravel et al.
60 2011), nutrient recycling (Loeuille et al. 2002), and decomposition (Boudsocq et al. 2012). Thus,
61 it is reasonable to expect that trait distributions could be important for ecological tipping points
62 by affecting response diversity in an ecosystem; that is variation in the sensitivity among
63 species, populations, or individuals to environmental stress (Elmqvist et al. 2003). This
64 sensitivity underlies the response capacity of communities to stress (Vellend and Geber 2005),
65 such that trait change could affect the resilience of entire ecosystems to stress (Mori et al.
66 2013) and their probability of tipping to a different state.

67

68 Ecosystem resilience can be affected by variation in traits (Norberg et al. 2001; Matthews et al.
69 2011) underlying the performance and fitness of organisms in a given environmental state (i.e.
70 response traits), or those causing direct or indirect effects on the environmental state (i.e.
71 effect traits) (Table 1). The distribution of such response and effect traits can vary due to
72 phenotypic plasticity or evolutionary trait change, and distinguishing between these
73 mechanisms can be important for understanding the temporal dynamics of trait change in
74 general (Cortez 2011), and of tipping points in particular. Phenotypic plasticity, where
75 genotypes exhibit different phenotypes in different environments, is a relevant source of trait
76 variation, particularly when the phenotypic changes relate to the capacity of organisms to
77 respond to stress. However evolutionary responses to stress depend on heritable trait variation
78 in a population (Hansen et al. 2012), which can originate from novel variants due to mutation
79 (Nei 2007), recombination (Ortiz-Barrientos et al. 2016), or gene flow among populations and
80 species (Seehausen 2004). Below, we do not *a priori* distinguish between the genetic versus
81 plastic sources of trait distributions (although we comment on their differences), but focus on
82 how trait variation and trait change over time can influence ecosystem tipping points in a
83 generic way. We do this using a graphical approach where we illustrate how trait changes might
84 modify the collapse and recovery trajectories of ecosystems along an environmental gradient.

85

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

87 Differences in the amount of trait variation in populations could affect their response capacity
88 to stress. In general, we predict that high trait variation may decrease the probability of tipping
89 points turning ecosystem responses to non-catastrophic. A decrease in the probability of
90 tipping events occurs because standing trait variation allows for portfolio effects that introduce
91 strong heterogeneity in population processes, interactions, and responses (Bolnick et al. 2011)
92 buffering population dynamics (Schindler et al. 2010). Such heterogeneity can be enhanced by
93 Jensen's inequality (Bolnick et al. 2011), where variation around the mean of a trait can affect
94 the response of an ecological interaction or an ecological process in function of the nonlinear
95 relationship between the trait and its effect (Ruel and Ayres 1999). This effect can be clearly
96 illustrated in a toy model describing shifts in the case of shallow lakes (Figure I in Box 1). Here,

97 changing the amount of variation in the macrophytes' response trait to turbidity can increase or
98 decrease the probability of a tipping point response. Under high levels of variation the
99 transition from the clear to the turbid water state can even become non-catastrophic with no
100 alternative states (Figure 1).

101

102

103 ***Trait change could delay a tipping point***

104 As introduced in the previous paragraph, trait variation simply means that some resistant
105 phenotypes are present. However, trait variation could also facilitate trait changes. On top of
106 that, trait changes might be fueled by *denovo* mutation and phenotypic plasticity. In
107 ecosystems where stress gradients bring them closer to tipping points, trait changes could
108 potentially delay tipping to the alternative state (Figure 2a). This resonates with the idea of
109 evolutionary rescue (Gomulkiewicz and Holt 1995), the difference being that there is no rescue,
110 but rather only a delay in the collapse of the system by shifting the threshold at which the
111 collapse occurs at a higher stress level (Figure 2b). For instance, in the case of a shallow lake
112 turning turbid due to eutrophication (Box 1), aquatic macrophytes might delay the transition to
113 a higher threshold level of nutrients because of contemporary changes in traits that convey
114 tolerance to shading (Table 1).

115

116 ***Trait change could lead earlier to a tipping point***

117 Trait change may not always buffer populations from environmental changes, but could also
118 contribute to an increased risk of ecosystem collapse (Figure 2c, d). For example, environmental
119 stress could impose directional selection on a trait in a given species or group of species that
120 brings the system closer to tipping to an alternative ecological state (Dieckmann and Ferriere
121 2004; Rankin and Lopez-Sepulcre 2005). This is similar to evolutionary collapses or evolutionary
122 suicide as defined in evolutionary biology (Ferriere and Legendre 2013), but here the collapse
123 occurs at the scale of a whole ecosystem. Empirical examples of trait evolution leading to
124 population collapse come mostly from fish populations under harvesting (Rankin and Lopez-
125 Sepulcre 2005; Walsh et al. 2006). For example, it has been shown how fishing pressure has led

126 to the early maturation of Atlantic cod populations (Olsen et al. 2004) that is associated with
127 lower reproductive output and irregular recruitment dynamics that could have increased the
128 chance of stochastic extinction and the cod collapse in the 1990s. Evolutionary suicide might
129 lead to an ecosystem-level collapse in the case of drylands (Kéfi et al. 2008), where under
130 increased aridity adaptive evolution can favor local facilitation among neighboring plants for
131 resisting higher aridity. Whether evolution leads to a buffering effect depends on the seed
132 dispersal strategy of the dominant vegetation type. In systems characterized by long-distance
133 dispersal, evolution may actually enhance the collapse of the vegetation to a desert state due
134 to the invasion of non-facilitating mutants. In our shallow lake example, macrophytes at
135 intermediate turbidities might respond by growing longer stems with fewer leaves in order to
136 reach well-lit surface waters and avoid shading. If this, however, results in less photosynthetic
137 activity and less capacity to remove nutrients from the water column, it might reduce the
138 capacity to outgrow the algae and maintain a clear water state.

139

140 ***Trait change could 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 4
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 state (Murray et al. 2017). In a laboratory experiment, (Walsh et al. 2006) found that
154 overharvested fish populations failed to recover even after reducing fishing pressure due to

155 genetic changes in life history traits. This may result in a delay in recovery, or no recovery at all.
156 The opposite scenario is also possible. Trait changes may accelerate recovery and reduce
157 hysteresis (Figure 3). This may happen if, after the collapse, a highly adaptive phenotype is
158 selected for facilitating recovery only at a small reduction of stress. For example, after the
159 collapse of a phytoplankton population due to light stress in the laboratory, recovery took place
160 earlier than expected due to a (probably plastic) adaptive photo-acclimation response (Faassen
161 et al. 2015). If after the collapse a different phenotype is selected for, or if there is recovery of
162 the lost phenotypic variation (e.g. due to immigration), it may even be possible that the
163 recovery pattern becomes non-catastrophic.
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 one of the
167 outstanding questions whether trait changes that impact the probability of tipping also impact
168 recovery trajectories (Box 3).

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 suicide (Dieckmann and Ferriere 2004). Under rapid environmental change, a
193 quantitative genetics approach (Abrams 2005) is useful for studying how contemporary genetic
194 trait change may lead to evolutionary rescue. Both modelling frameworks can be adapted for
195 studying how trait changes might affect well-understood models with ecological tipping points
196 under changing environmental conditions. For instance, we could relax the assumption on the
197 separation of timescales and the assumption of weak selection of each framework,
198 respectively, and apply them to models with tipping points. Or one could develop hybrid
199 models that can account simultaneously for selection gradients, while also accounting for
200 genetic drift and demographic stochasticity that dominate the recovery trajectory of the
201 collapsed state. We can then combine these models with recently developed methods that
202 measure the relative impact of evolutionary vs ecological dynamics on stability (Patel et al.
203 2016) to understand when and how evolutionary dynamics can affect the probability of tipping
204 responses.

205

206 Such modelling approaches can help to (i) compare how different mechanisms of trait change
207 (genetic vs plastic) could affect tipping point responses, (ii) identify the conditions (e.g. rate and
208 pattern of environmental stress, rate of trait evolution, costs and trade-offs) under which trait
209 evolution will modify collapse and recovery trajectories, or even (iii) test when trait change
210 itself could be so abrupt (due to disruptive selection) that it could cause ecosystem tipping

211 points. In that way we could develop novel ways for detecting tipping points based on changes
212 in ecological and trait dynamics (Box 2), and suggest new designs for experimental testing.

213

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

215 There are two common approaches for experimentally testing tipping point theory. The first
216 approach starts by establishing two alternative states of the system on either side of a tipping
217 point, and then testing how the system responds to pulse perturbations of a state variable. For
218 example, if there is evidence for a positive feedback (Box 1) in two states with a different
219 dominant species in each community, then the outcome of species dominance might strongly
220 depend on the initial density of species (i.e. priority effects) (Fukami and Morin 2003). The
221 second approach starts with the system in one state, and then applies a press perturbation of
222 an environmental condition (e.g. increasing productivity, increasing mortality) to observe when
223 the system transitions to a new state (Dai et al. 2012; Veraart et al. 2012). To test for hysteresis
224 in the system, the environmental condition can then be reversed while tracking system
225 recovery to the initial state (Faassen et al. 2015).

226

227 Independently manipulating evolutionary and ecological components of a system can provide
228 new insights into how the dynamics of trait change can affect tipping points. Several
229 experiments have been designed to study the interplay between ecological and evolutionary
230 dynamics (Farkas et al. 2013; Pantel et al. 2015; Williams et al. 2016), and these could be
231 usefully co-opted to experimentally test predictions from tipping point theory. In an experiment
232 with freshwater cyanobacteria, light level was manipulated to test for hysteresis associated
233 with transitions between a high and low biomass state (Faassen et al. 2015). Contrary to
234 predictions from an ecological model, the population recovered to a higher light stress faster
235 than expected. In the experiment, the recovering cells had lower pigment concentrations,
236 possibly reflecting adaptation to high irradiance conditions at a cost of photosynthetic
237 efficiency at lower light irradiance. This suggests that the presence of trait variation in the
238 population influenced the nature of the transition between the two states. A useful
239 experimental test of this idea would be to manipulate standing levels of genetic variation in the

240 stressed population and measure if tipping points change. Adding such evolutionary contrasts
241 to ecological experiments would be a fruitful way to test how both trait variation and evolution
242 may affect tipping points. In experimental systems it is possible to isolate the effects of density
243 (ecological effects) from the effects of heritable trait change (evolutionary effects). Specifically,
244 one might be able to differentiate between purely ecological effects, direct evolutionary effects
245 linked to changes in functional effect traits, and density-mediated indirect evolutionary effects
246 linked to changes in functional response traits (Patel et al. 2016).

247

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

249 Reciprocal interactions between ecological and evolutionary dynamics is an old idea (e.g. (David
250 1968; Levins 1968)) that is increasingly being tested across a range of systems and study
251 questions (e.g. (Fussmann et al. 2007; Hendry 2017)). Here, we focused on the potential
252 implications that heritable trait changes can have for ecological tipping points. The next step is
253 to understand how reciprocal feedbacks between ecological tipping points and evolutionary
254 dynamics might radically alter not only the dynamics of ecosystems close to tipping but also the
255 evolution of populations and communities of these ecosystems. Tipping points between
256 contrasting ecosystem states create different selection regimes that can shape the evolution of
257 focal species (like keystone, or ecosystem engineers species) and in their turn the dynamics of
258 the ecosystem state they belong to (Matthews et al. 2015). One possibility is that such selection
259 regimes will be asymmetric, leading to evolutionary reversals, for example in body sizes in
260 grazed populations (Dercole et al. 2002), or could maintain the recurrence of harmful algal
261 blooms in lakes (Driscoll et al. 2016).

262

263 It remains an outstanding challenge to test these ideas along with several new questions (Box
264 3). Most theoretical work on eco-evolutionary dynamics has been experimentally corroborated
265 in laboratory experiments with short generation organisms (Yoshida et al. 2003). Similarly,
266 ecological tipping points have been mostly studied in experimental microcosms at the
267 population level with single species (Dai et al. 2012; Veraart et al. 2012). Ecosystem scale
268 tipping points are harder to experimentally test (but see (Carpenter et al. 2011)) and

269 simultaneous information on trait variation of the organisms involved is rarely available. Yet,
270 ecosystem collapses have evolutionary consequences that may trap an ecosystem in an
271 undesired state making recovery difficult. Thus, sustaining trait variation may be important not
272 only for preventing collapse, but also for improving the success of ecological restoration.
273 Despite the challenging task, the evolutionary perspective we advocate can improve our
274 understanding and management of ecosystems under stress.

275

276 **Acknowledgements**

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280 **Competing interests**

281 We declare no competing interests.

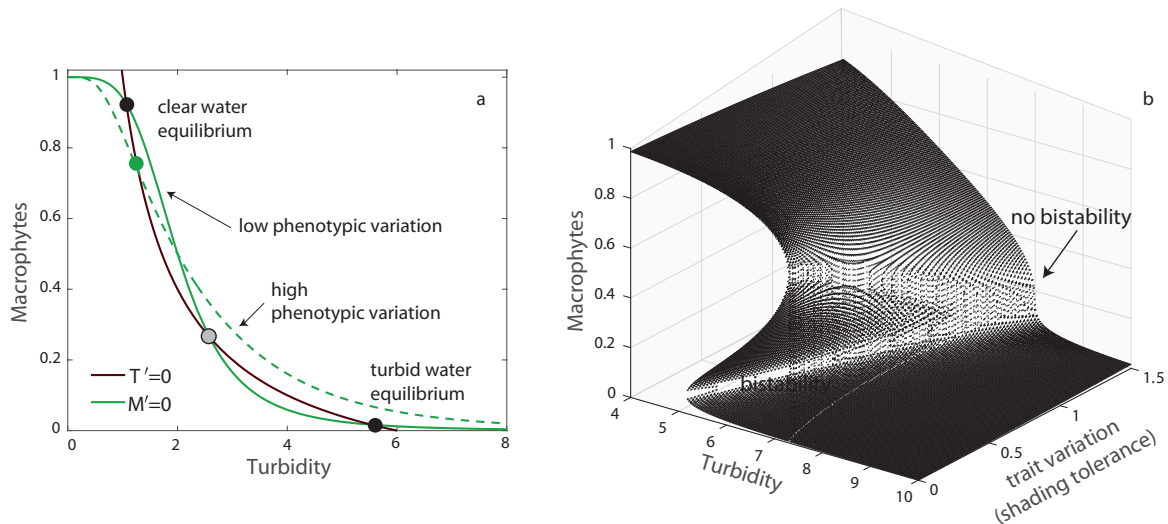
282 **Author contributions**

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

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

| Ecosystem Tipping Point | Organism | Environmental driver | Response trait | Effects resulting from change in effect trait |
|-----------------------------|---------------|--|---|--|
| lake shift to turbid state | 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 | shrubs | aridity | water retention | facilitation |
| | | fire | fire resistance, recruitment | facilitation |
| | | grazing | herbivory resistance | facilitation |
| coral reefs degradation | corals | temperature | temperature tolerance | habitat structure |
| | | nutrient loading | growth/ colonization rate | habitat structure |
| | | pathogen disease | resistance to pathogens | habitat structure |
| salt-marsh mudflats erosion | marsh grasses | inundation | colonization rate, below sediment growth rate | habitat structure, sediment retention |
| intertidal bed degradation | 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 | pollinators | chemical stress | toxic resistance | pollination |
| | | warming | phenology adaptation | pollination |
| kelp forest overgrazing | kelp | grazing, wave erosion | herbivory resistance, morphology | habitat structure |
| collapse due to Allee effect | yeast | salt stress | reproduction rate | growth |



292

293 **Figure 1**

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

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

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

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

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

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

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

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

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

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

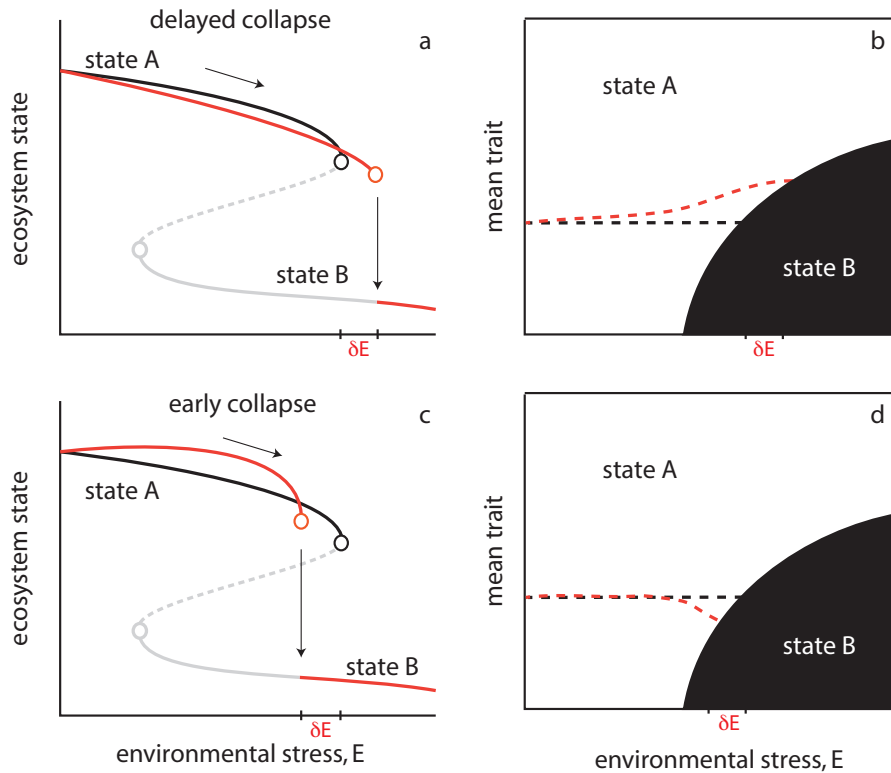
304 catastrophic response. Although not captured explicitly by this simple model, the effect of trait

305 variation on the ecosystem response could act through the existence of resistant individuals (or

306 subpopulations of macrophytes), but also on its potential to facilitate trait change. Model

307 details and parameters can be found in the Supplementary Information.

308



309

310 **Figure 2**

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

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

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

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

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

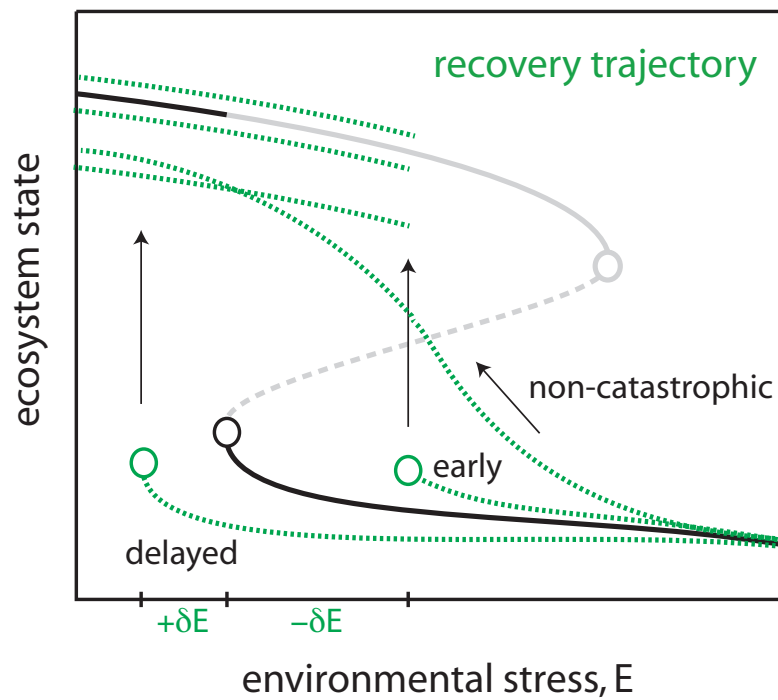
316 same time also induce an early collapse. [(a, c) Black and gray lines represent the two

317 alternative states of the reference model with no phenotypic change, dotted lines mark the

318 unstable boundary between the two states, dots denote tipping points. (b, d) Dotted black line

319 is the reference scenario with no trait change]

320



321

322 **Figure 3**

323 Potential consequences of trait change on the recovery trajectories of an ecosystem after
324 collapse (green dashed lines). Recovery may be delayed or occur earlier affecting the range of
325 hysteresis and the ease of recovery. In both cases, it is unclear whether the ecosystem shifts
326 back to exactly the same state as before the collapse. It may be possible that the collapse has
327 allowed the emergent of a different (new) phenotype that could even turn the recovery path
328 non-catastrophic. [Solid lines represent the two alternative states of the reference model with
329 no phenotypic change, dotted lines mark the unstable boundary between the two states, dots
330 denote tipping points.]

331

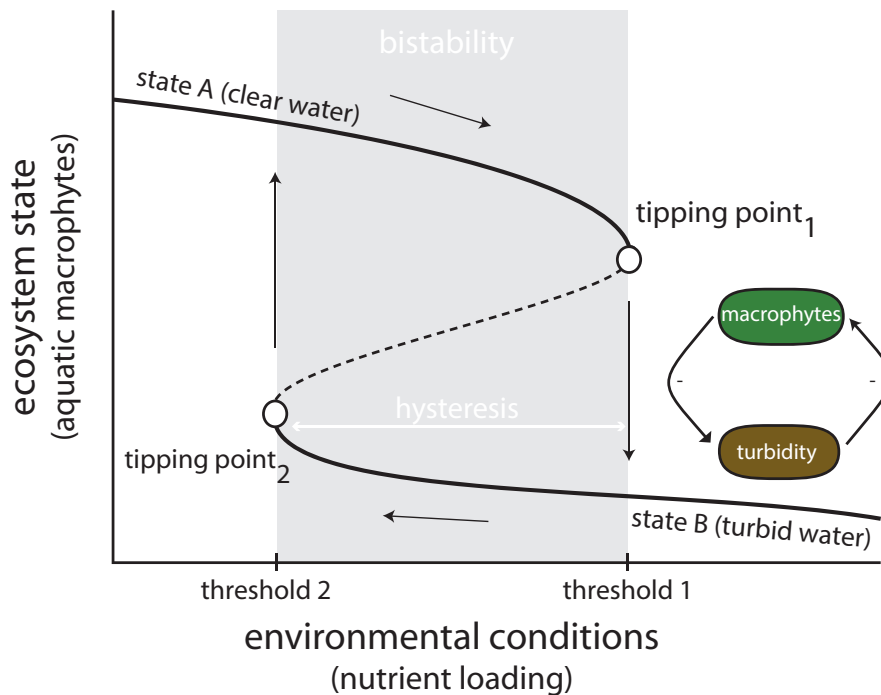
332 **Box 1: What is a tipping point?**

333 Tipping points mark the shift between contrasting system states that occur when external
334 conditions reach thresholds that trigger an accelerating transition to a contrasting new state
335 (Nes et al. 2016). Mathematically, these transitions correspond to saddle-node or fold
336 bifurcation points (Strogatz 1994). They are also called catastrophic because they mark an
337 unexpected and radical change in the equilibrium state of a system. Tipping points can occur at
338 population level (e.g. due to Allee effects (Dai et al. 2012)) and community level (e.g. due to
339 trophic cascades (Kitchell and Carpenter 1993)), but it is at the ecosystem scale that tipping
340 points are most prominently studied because they can incur long-term disruption to vital
341 ecosystem services (Barnosky et al. 2012) . For example, clear lakes turn turbid dominated by
342 algal blooms (Scheffer et al. 1993), coral reefs get overgrown by macroalgae (Knowlton 1992),
343 fisheries collapse due to overexploitation (Beddington and May 1977), and tropical forests shift
344 to savanna-type ecosystems under high fire intensity (Staver et al. 2011).

345

346 Tipping points are typically observed in systems where strong positive feedbacks drive the
347 establishment of alternative stable states (Nes et al. 2016). In the case of shallow lakes,
348 dominance of aquatic macrophytes prevents the growth of algae by removing nutrients
349 (phosphorus) from the water column that leads to the establishment of a stable clear water
350 state (Fig I). When phosphorus loading exceeds a critical threshold macrophytes cannot
351 successfully retain phosphorus, algae start to grow and lake turbidity increases. Rising turbidity
352 kicks a vicious cycle: it hinders the growth of macrophytes but facilitates algae concentration in
353 a self-enforced positive feedback loop (less macrophytes => more algae => more turbidity =>
354 less macrophytes and so on) that leads to the collapse of macrophytes and the establishment of
355 a contrasting turbid lake state. The same positive feedback loop can lead to the recovery of
356 macrophytes, but this time at a lower critical level of phosphorus loading, where algae growth
357 is limited to such an extent that turbidity decreases sufficiently for macrophyte to grow again,
358 capture the phosphorus and reinforce a positive feedback loop leading back to the clear water
359 state. Between these two tipping points, the system is bistable meaning that it can be found in
360 one of the two alternative stable states. This difference in conditions that mark the forward and

361 backward shift is called hysteresis. The stronger the hysteresis, the more difficult it is to recover
362 an ecosystem back to its previous state.
363



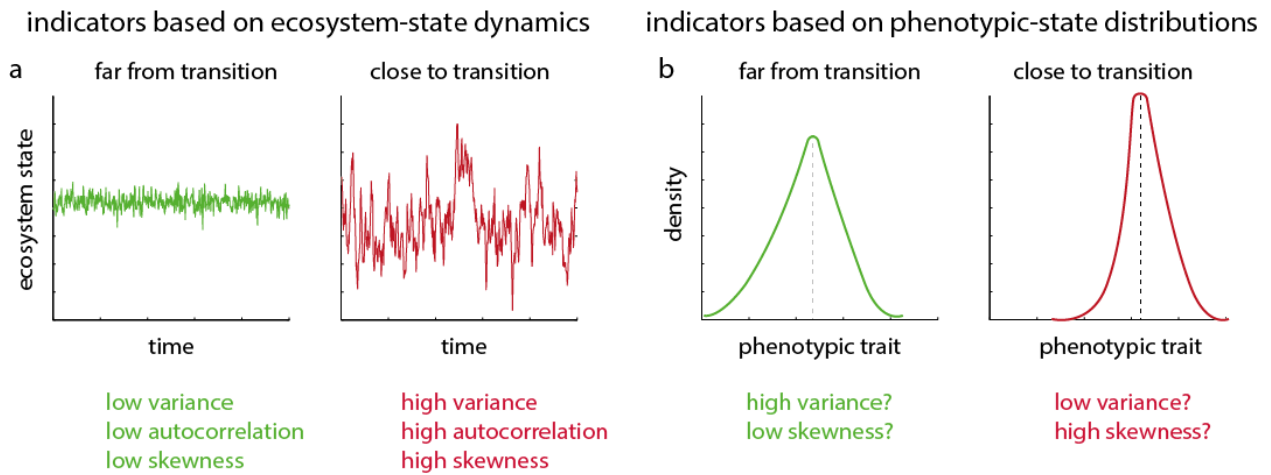
364
365

366 **Figure 1**

367 Tipping points mark discontinuous changes in the state of an ecosystem. Starting from the
368 upper branch, the ecosystem follows the stable equilibrium line until conditions cross threshold
369 1 at which the upper stable equilibrium disappears (tipping point₁) and the ecosystem state
370 drops abruptly to the lower (alternative) stable state. In our example of the turbid and clear-
371 water states of shallow lakes, reducing nutrient conditions - but to a much lower level - leads to
372 the restoration of the previous state at the crossing of threshold 2 (tipping point₂). The
373 difference in the thresholds between the forward and backward tipping points marks the
374 hysteresis in the system. For this range of conditions the ecosystem can be found in either of
375 the two alternative stable states (bistability). Along the pathways depicted here, no change in
376 the traits of the organisms stabilizing the clear-water (macrophytes) or turbid (algae) state is
377 assumed. [Black lines represent the stable equilibria. Dotted line represents the border
378 between the basins of attraction of the two alternative stable states.]

379 **Box 2: Detecting tipping points based on ecosystem-state and trait changes**

380 Ecological tipping points are difficult to detect. However, theory suggests that subtle changes in
381 the dynamics of an ecosystem state can provide early-warning information on the underlying
382 stability and risk of a tipping response (Scheffer et al. 2009). This risk is typically quantified by
383 indicators of resilience based on critical-slowing-down (Dakos et al. 2015), and include an
384 increase in recovery time back to equilibrium after a perturbation, a rise in variance as the state
385 of the ecosystem fluctuates more widely around its equilibrium, and an increase in
386 autocorrelation because the state of the ecosystem resembles more and more its previous
387 state close to a tipping point. These indicators have been empirically tested in laboratory
388 experiments (Dai et al. 2012; Veraart et al. 2012) and in the field (Carpenter et al. 2011; van
389 Belzen et al. 2017) focusing on ecosystem state, and neglecting any trait changes. Accounting
390 for trait change creates new challenges but also opportunities in the detection of tipping points
391 (Figure II). It is unclear whether trait change can affect the performance of resilience indicators,
392 or whether indicators based on both ecosystem state and trait state dynamics could
393 complement each other to improve tipping point detection. Changes in traits have been
394 suggested as a basis for predicting ecological responses (Enquist et al. 2015), and seeds of this
395 idea can be found in the suggestion that variation in maturation schedules of cod could have
396 been used to detect its collapse (Olsen et al. 2004). Recent work has shown that measuring
397 changes in mean or variance in body size in combination with resilience indicators based on
398 species abundance could improve warning of protists population collapse (Clements and Ozgul
399 2016). Nonetheless, slowing down indicators should be expected - at least based on ecological
400 dynamics - in ecosystems at the edge of tipping points (Ferriere and Legendre 2013). Although
401 changes in the dynamics of phenotypic adaptation will most likely be context-dependent, it
402 remains to be tested whether they could be used as signals of potential impending transitions.
403



404

405

406 **Figure II**

407 Deriving indicators of resilience for detecting the risk of tipping point responses from changes
408 in ecosystems dynamics and trait distributions. Close to tipping points, ecological dynamics
409 become slower in responding to disturbances. This slow recovery leads to a rise in variability
410 and memory in the dynamics of the monitored ecosystem state that can be used as indicator of
411 an increased risk of tipping (panel a). Alternatively to such ecosystem-state indicators, temporal
412 changes or changes along a gradient in trait values of focal species might be also informative for
413 quantifying the risk of approaching tipping points (panel b). Such trait based indicators may flag
414 changes even before signals from ecosystem state flare up.

415

416

417 **Box 3: Critical questions for understanding tipping points from an evolutionary perspective**

- 418 - Under which conditions (e.g. type and rate of environmental stress, type of
419 response/effect trait, level of genetic variation, plasticity, spatial and temporal scales)
420 does phenotypic change matter the most for ecological tipping points?
421 - In what ways do genetic vs plastic trait changes affect tipping point responses
422 differently?
423 - Do reciprocal interactions between species (e.g. in a network) that influence trait
424 changes (e.g. through coevolution) affect tipping point responses?
425 - Is there an intrinsic relationship between trait changes that impact collapse and
426 recovery, and to what extent can trait changes that impact collapse can be reversed so
427 as not to impact recovery?
428 - What type of eco-evolutionary feedbacks develop along the collapse and recovery
429 trajectories of ecosystems with tipping points?
430 - Can ecological bistability lead to bistability in trait values (or vice versa)?
431 - Can we use changes in trait variation as signals of approaching tipping points?
432 - How can we experimentally study the effects of trait change in ecosystems with tipping
433 points?
434 - Can we manage trait variation and evolution to reduce the risk of ecosystem tipping
435 points?

436

437 **Box 4: Glossary**

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

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

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

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

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

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

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

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

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

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

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

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

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

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Supplementary Information - Shallow lake eutrophication model

We used a minimal model that describes the dynamics of transition from a clear water state dominated by macrophytes to a turbid water state where macrophytes are practically absent¹. Such transition occurs at a crossing of a fold bifurcation (tipping point) due to changes in nutrient loading (eutrophication). Below we explain how we analysed the model to highlight the presence of alternative states as function of environmental stress (Box 1), and the effects of standing phenotypic variation (Figure 1).

The model describes the interactions between macrophyte coverage and turbidity of a shallow lake with the following two ordinary differential equations:

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

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

Solving for steady state the nullclines of the system are:

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

Their intersections mark the two alternative stable states (clear and turbid state) and the unstable saddle depending on the value of background turbidity T_o (Fig. 1a). We hypothesize that the half-saturation h_T that affects the strength of nonlinear response of macrophytes to turbidity is defined by a response trait z (e.g. capacity to grow under low light

conditionsshading). Different values of z will thus change the response of macrophytes to turbidity by changes in h_T (Supplementary Figure 1a). We assumed that trait z follows a *beta* distribution (closed limits) that we can parameterize in order to define a given mean μ ($=0$) and variance σ^2 . We further assumed that the half-saturation h_T depends on the trait z following $h_T = h_{T_0} e^{cz}$, where h_{T_0} is a background value ($= 2$) and c a factor ($=0.5$) (Supplementary Figure 1b).

Using this relationship and integrating for different limits of trait z and levels of variance of the *Beta* distribution, we can calculate the macrophyte equilibrium in the presence of standing phenotypic variation in z as:

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

where $p(z)$ is defined by the *Beta* distribution as explained above within a range of z ($= [-2,2]$).

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_0) 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 ($M' = \frac{hT^4}{hT^4 + T^4}$). 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).

