Title: The rate of environmental change as an important driver across scales in ecology

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Abstract

Global change has been predominantly studied from the prism of ‘how much’ rather than ‘how fast’ change occurs. The paradigm underlying the former assumes that a smooth change in an environmental driver can force a regime shift between alternative states (Bifurcation-tipping). This presupposes that environmental conditions change at a rate which allows the ecological entity to track them and thus reach equilibrium. However, current rates of environmental change are often too fast for this paradigm to apply, necessitating a shift in approach to improve predictions on the impacts of rapid environmental change. The theory of rate-induced tipping (Rate-tipping) demonstrates how rates of environmental change can cause tipping phenomena even in the absence of alternative states. We illustrate how Rate-tipping can apply to a range of ecological scenarios and explore the literature for properties which increase the sensitivity to rates of change. Further, we discuss how targeted empirical studies can investigate the ecological and evolutionary mechanisms through which rate-induced phenomena can propagate across levels of organisation. Finally, we argue for the inclusion of Rate-tipping in the study of global change as the first step towards the theoretical synthesis necessary to account for multiple stressors impacting ecological entities simultaneously.

Introduction

Understanding how ecosystems will respond to ongoing anthropogenic changes (e.g., increasing mean temperatures, atmospheric CO_2 and nitrogen enrichment, habitat loss and fragmentation) is a formidable challenge in ecology (Steffen *et al.* 2005; Rillig *et al.* 2019; Sage 2020). Related theory has focused on so-called tipping phenomena, where the (eco)system undergoes a significant, and sometimes catastrophic, change. Three types of tipping have been identified: Bifurcation-, Noise- and Rate-tipping (Ashwin *et al.* 2012) (Box 1, Fig. 1). Bifurcation-tipping or B-tipping presupposes the existence of *stable states*, with transitions occurring due to change in the magnitude of a parameter exceeding a threshold (Fig. 1, green lines). B-tipping has formed the dominant paradigm in ecology and beyond; the notion of tipping points and catastrophic transitions between *alternative states* guides policy in the fight against the global ecological crisis (Rockström *et al.* 2009; Steffen *et al.* 2015). Noise-tipping or N-tipping is related to noise driven *regime shifts*, where noisy fluctuations in a driving factor can lead the system dynamics to switch from one stable state to an alternate one (Fig. 1, yellow lines). Rate-tipping or R-tipping occurs when the rate of change of a forcing parameter exceeds a critical threshold (Fig. 1, red lines). R-tipping leads to a situation where the system dynamics are unable to track the corresponding changes in the dynamical attractor, thereby departing from the stable state. R-tipping does not require the existence of alternative states.

In this work, we emphasise the ecological relevance of R-tipping to the ongoing ecological crisis, which is partially driven by unprecedented rates of environmental change (Waters *et al.* 2016; Pattyn *et al.* 2018; Ceballos *et al.* 2020). Significantly, B- and R-tipping occur due to different causal factors; exceeding a critical magnitude versus exceeding a critical rate of change in an external parameter, respectively. Therefore, R-tipping can be triggered by continuously increasing rates of change in an external factor like temperature, atmospheric CO_2

concentrations or habitat loss (which are known drivers of the current ecological crisis). Hence, we argue for the application of R-tipping theory to improve our understanding of ecological dynamics under the current ecological crisis.

BOX 1: Tipping

B-tipping: Bifurcation-induced tipping occurs when the system shifts to an alternate state once a critical threshold in magnitude of an external driver is passed.

N-tipping: Noise-induced tipping occurs when a stochastic noisy event in the external forcing parameter can lead to a departure from the current state to an alternate state.

R-tipping: Rate-induced tipping occurs when the dynamics of the system are unable to track the changes in the attractor due to an increased rate of change in the external driver/forcing parameter. The system exhibits a tipping response when the rate of change exceeds a critical threshold.

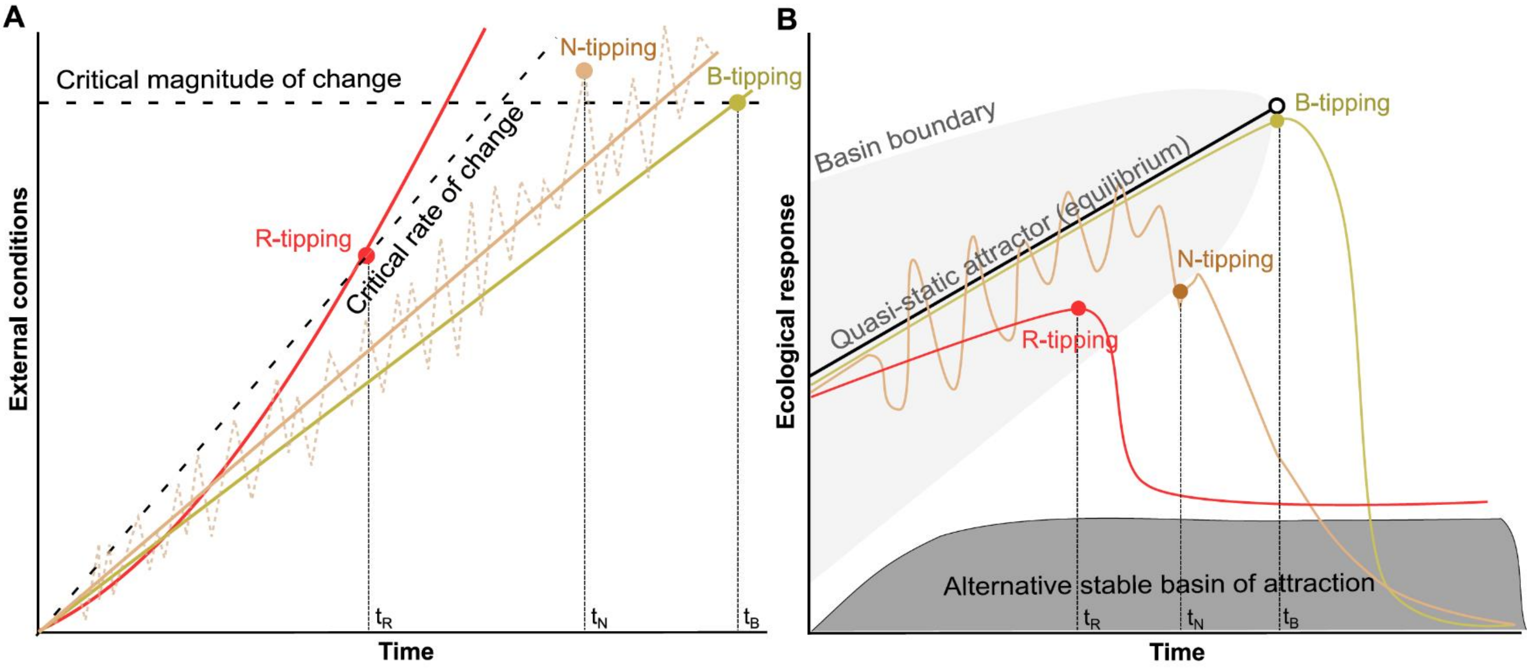


Figure 1. *Illustration of how a change in an external driver can induce tipping in the state of an ecological entity: Bifurcation-induced tipping (B-tipping), noise-induced tipping (N-tipping), and rate-induced tipping (R-tipping). A) Different ways in which the external driver can change; B) the three corresponding types of tipping (the colours of the curves in panel A correspond to the same-colour responses in panel B). An equilibrium state changes over time due to a continuous directional change in an external condition. Even if the change is slow so that the ecological entity can track the moving equilibrium, it can tip into an alternative basin of attraction if the change exceeds a critical magnitude (B-tipping, green curves) or if consecutive stochastic perturbations force it beyond the current attractor's basin boundary (N-tipping, brown curves). If the change is too fast, the ecological entity cannot keep track of the equilibrium trajectory, and the gap eventually causes tipping behaviour (R-tipping, red curves). Note that R-tipping can happen without necessarily*

Bifurcation theory in ecology

The occurrence of drastic regime shifts in response to an *external driver* crossing a critical threshold has drawn a lot of attention in ecology. Prominent examples are shallow lake systems exhibiting shifts between a clear water state dominated by submerged plants and a turbid state dominated by algae caused by eutrophication (Scheffer *et al.* 1993; Scheffer & Carpenter 2003). Other examples are the shift of coastal systems to an alternative depauperate state caused by the over-exploitation of top predators (sea otters) (Estes & Palmisano 1974; Jackson *et al.* 2001; Estes *et al.* 2011), the occurrence of cyanobacterial blooms in lakes with climate warming and eutrophication causing drastic shifts in the community composition of aquatic systems (Wilkinson *et al.* 2018), or the woody encroachment of grasslands (Ratajczak *et al.* 2014; Sala & Maestre 2014).

These transitions correspond to catastrophic regime shifts mediated by a bifurcation in the underlying system, referred to as B-tipping (Scheffer 2009; Ashwin *et al.* 2012). While such a regime shift in principle can also be smooth - the system state changing smoothly with a continuous shift in the forcing parameter (Kéfi *et al.* 2013) - when talking about tipping, we refer to abrupt or catastrophic regime shifts. These lead to a drastic functional and structural re-organisation of the ecological entity. Additionally, once a critical threshold in the magnitude of the forcing parameter is crossed, the transition might not be easily reversed (Scheffer & Carpenter 2003; Hughes *et al.* 2013), leading to hysteresis (Scheffer *et al.* 2009).

The necessity of a “bifurcation” between alternate states in the underlying dynamics limits the general applicability of the B-tipping formalism. This is emphasized by a lack of evidence for well-defined alternate states and corresponding regime shifts (Capon *et al.* 2015; Montoya *et al.* 2018; Hillebrand *et al.* 2020). Moreover, there is a pressing need to further develop an understanding on how ecosystems will respond to temporal changes in critical drivers. Consequently, an important question is how the rate of environmental change will impact populations, communities and ecosystems (Joos & Spahni 2008; Trusel *et al.* 2018; Pinek *et al.* 2020). Therefore, we require a paradigm shift to consider this aspect of change in ecological predictions (Williams *et al.* 2021).

Glossary

Alternative stable state: When more than one dynamical attractor coexist for a fixed set of system parameters. This parameter range is called hysteresis area.

Bifurcation: When small, smooth changes to the parameter values of the system cause a sudden, qualitative change in its dynamics due to changes in the stability properties of an attractor.

Dynamical system: A differential/difference (time continuous/discrete) equation system, defining the dynamical rules of the changes of all state variables over time. State variables can, for example, be the biomass of an individual, of populations or of multiple species representing a functional group or a community. Dynamical systems provide predictions on the immediate future values of all state space variables on the basis of their present values.

Ecological entity: The object of study which can range from an individual organism to a whole ecosystem.

External driver: The general environment where the system is located. Typically, there exists no feedback between the ecological entity and the abiotic conditions. Hence, factors describing the abiotic conditions which influence system dynamics are considered as external.

Regime shift: A qualitative change in the system state. Regime shifts can be smooth, i.e., the quantitative behaviour changes smoothly with respect to the parameter, or abrupt/catastrophic, i.e., the behaviour changes abruptly, so even a small change in the environmental parameter can result in a large change in the dynamic behaviour.

Stable state/attractor: The dynamical regime/state a dynamical system settles on in the long term, after the transient dynamics phase. Examples of such attractors are a fixed point equilibrium, a limit cycle (periodic oscillations), or a strange attractor.

Significance of rates of change

The theory of R-tipping describes how high rates of parameter change cause the departure of the dynamical system from the stable state, when this rate exceeds a critical value (Ashwin *et al.* 2012). It is important to note that the occurrence of R-tipping does not necessitate the presence of an alternate state. This makes R-tipping even more concerning: it can lead to a catastrophic loss of the current system state, in the absence of an alternative state that the system can settle onto. A complete loss of any equilibrium state (or the ability to reach any equilibrium state) would have drastic consequences for the underlying ecosystem, possibly triggering a cascade of species extinctions. Below we present studies which have explored the potential ramifications of R-tipping in simple ecological settings.

In consumer-resource models, the coupling of fast and slow processes can lead to a collapse in the community (Siteur *et al.* 2016; Vanselow *et al.* 2019). In one case, the reduction in the growth rate of the resource over time caused a lag in the response of the consumers (Siteur *et al.* 2016). When the rate of reduction was too high, the depleted resources were overconsumed by the slow-responding consumers, causing the community to eventually crash. A similar approach identified a critical threshold in the rate of reduction in the resource carrying capacity (Vanselow *et al.* 2019). Below this threshold, dynamics tracked the equilibrium with a temporal lag; once the reduction rate threshold was crossed, the community collapsed to extremely low densities. Significantly, the R-tipping occurred in a parameter space of stable consumer-resource coexistence under the assumption of static parameters. This implied that no regime shift in the classical sense was possible, i.e., the response was caused by the rate of change in the carrying capacity rather than by passing a critical threshold in the magnitude of carrying capacity. The prey population abruptly collapsed (fast dynamics) and remained at extremely low densities (slow dynamics), before eventually recovering and converging to the equilibrium. In a natural setting, this long phase of extremely low resource densities would make the community vulnerable to stochastic extinctions; hence the significance of such a collapse should not be underestimated, and its irreversibility not excluded.

In a different system, it has been described how the rate of increasing soil temperature can cause an explosive release of soil carbon into the atmosphere (Luke & Cox 2011; Wieczorek *et al.* 2011). Increasing soil temperatures (e.g. through climate change) increase microbial soil respiration, and vice versa in a self-reinforcing cycle (positive feedback). Meanwhile, soil carbon and soil respiration are regulated by a negative feedback; increasing soil carbon increases respiration, which in turn limits soil carbon, keeping both quantities in check. The so-called ‘compost-bomb instability’ arises when the rate of increasing atmospheric temperature causes the positive feedback to overpower the negative feedback, forcing the release of soil carbon into the atmosphere in large amounts.

Though simplified in their ecological conception, these studies seem both relevant and alarming. Therefore, it is necessary to apply this theory more broadly within ecology, where it currently remains largely understudied (Pinek *et al.* 2020), with some exceptions. The framework of climate velocity has helped to quantify the impacts of the rate of temperature increases relative to the rate of species range shifts on ecosystem dynamics (Loarie *et al.* 2009; Burrows *et al.* 2011; Garciá Molinos *et al.* 2016). Recently the potential for R-tipping in a marine food-web was demonstrated (Gil *et al.* 2020); a rapid increase in top predator density causing the collapse of herbivores and the proliferation of algae. In a broader application, a framework for ecological conservation based on rates of environmental change identified three potential outcomes (Williams *et al.* 2021): (1) ecological change tracks climate change, (2) ecological change lags behind, creating an extinction or evolutionary debt, or (3) ecological change fails to track the rate of climate change leading to abrupt or catastrophic regime shifts. The authors found that the realised outcome will depend on specific traits, such as body size, topographic heterogeneity or the number of interspecific interactions and their effects on ecosystem dynamics.

Here, we bring together the mathematical theory of R-tipping (Ashwin *et al.* 2012) and a broad ecological perspective (Williams *et al.* 2021) to help fill the gap in the study of rate-induced phenomena in ecology (Pinek *et al.* 2020), while preserving the rigour of the original theory. R-tipping takes place when a directional change in external conditions occurs at a rate which induces an ecological or evolutionary response even though the magnitude of change alone would not (Fig. 1). When conditions occur slower than a critical rate (Fig. 1A, red curve for $t < t_R$), the ecological entity will "track" the equilibrium - the deviations from the equilibrium are bounded (Fig. 1B, red curve for $t < t_R$). However, when external or environmental change exceeds the critical rate (Fig. 1A, red curve for $t \geq t_R$), the deviation is unbounded, and the ecological entity moves rapidly away from the equilibrium (Fig. 1B, red curve for $t \geq t_R$).

Manifestations of R-tipping may already exist. For example, increasing atmospheric CO_2 concentrations cause the acidification of the oceans (Cao & Caldeira 2008), adversely affecting coral reefs (Anthony *et al.* 2008; Kiessling & Simpson 2011; Pandolfi *et al.* 2011; Albright *et al.* 2016). Besides the increase in the amount of CO_2 (magnitude of change), the rate of increase presents a threat in itself (Connell 1997): coral reefs may not be able to adapt to the rate of increasing CO_2 (Hoegh-Guldberg *et al.* 2007) and as a result suffer damage even at pH levels which would not otherwise be considered harmful (Fabricius *et al.* 2011). In a further example, species will have to shift their ranges in order to follow climatic changes (Burrows *et al.* 2011; Sunday *et al.* 2015). Both marine and terrestrial species have been shifting their ranges towards higher elevations or latitudes as they fail to adapt to the rapidly changing conditions (Parmesan & Yohe 2003; Chen *et al.* 2011; Pecl *et al.* 2017). However, this only works if species can physically move at a rate which tracks the climatic shifts (Thomas *et al.* 2004); many species such as certain tropical Andean trees (Feeley *et al.* 2011; Fadrique *et al.* 2018), European butterflies (Parmesan *et al.* 1999) or French birds (Devictor *et al.* 2008) cannot. The mismatch between optimal conditions and those experienced by slower-moving species lead to a loss of fitness and a so-called extinction debt or result in direct extinction (Williams *et al.* 2021). Mismatches in range shifts of migrating species can also generate new interactions (Ordonez & Williams 2013) and alter the functioning of ecosystems (Garciá Molinos *et al.* 2016), which can be considered a shift to a novel regime.

What increases sensitivity to rates of change?

To seek the properties that make ecological entities sensitive to rates of change, we conducted a narrative literature review (based on keywords), selecting only studies which explicitly investigated the impact of the rate of change on a target variable. We found 22 studies met our selection criteria (see the Supplementary Information for a list of these studies and a description of the review process). Within certain studies multiple target organisms or target variables were investigated; we treated these as independent data points which increased the total number of data points to 30. This low number of studies explicitly aimed at sensitivities to rates of change is congruent with the findings of a recent review (Pinek *et al.* 2020) and highlights the knowledge gap that needs to be addressed. From our review, we created the following categorical predictive variables with sufficient repetition between the studies to allow for an indicative statistical analysis: level of ecological organisation (organism, population, community, ecosystem/biome), kingdom (bacteria, fungi, plants, animals), ecosystem type (terrestrial, aquatic) and study type (experimental, observation, model). We defined the response variable as 'no tipping' (dynamics track the equilibrium – linear response) or 'tipping' (dynamics cannot track the equilibrium – nonlinear response), and used the conditional inference tree algorithm of machine learning (Hothorn *et al.* 2006; Ryo & Rillig 2017), which classified the studies into subgroups based on the categorical variables (Fig. 2).

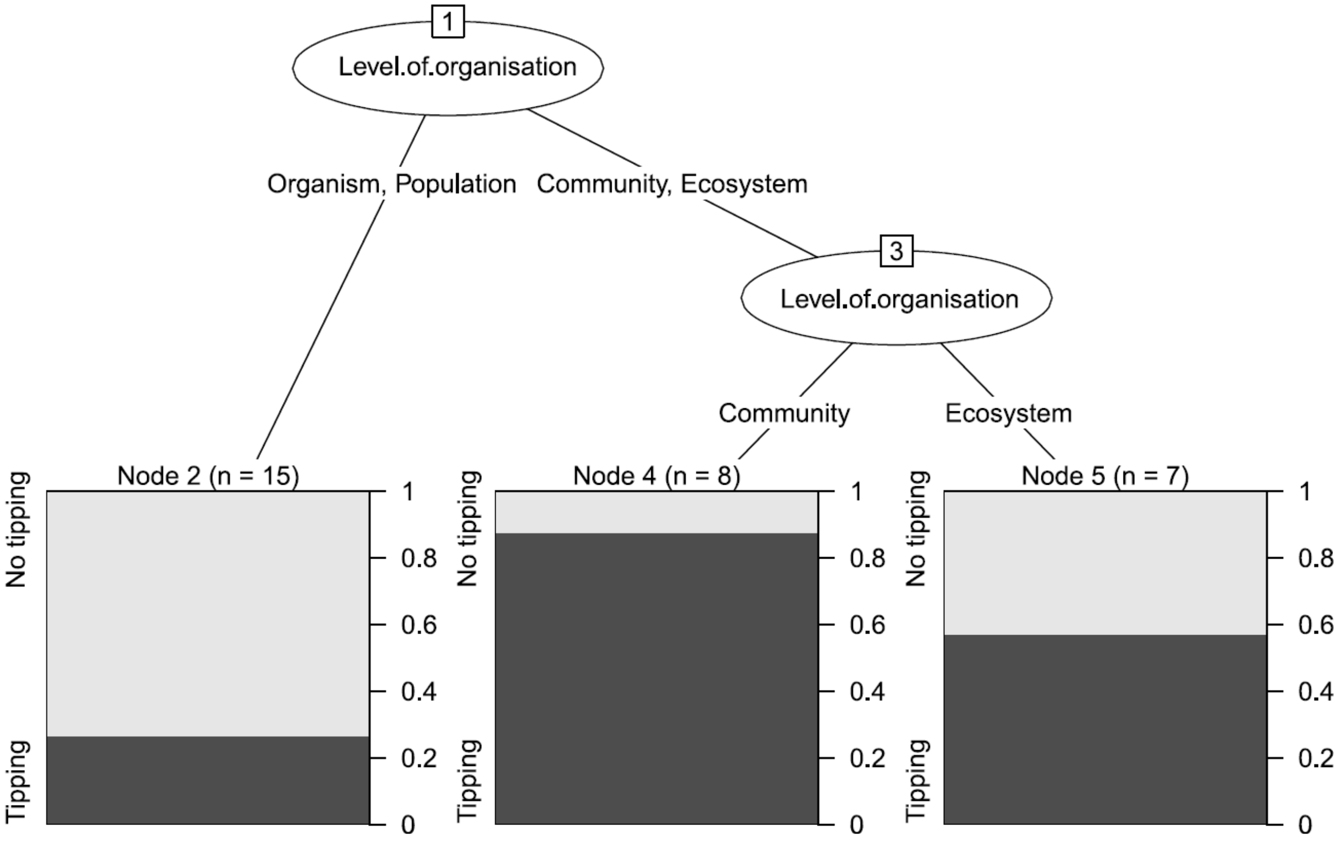


Figure 2. *Conditional inference tree algorithm of machine learning for 22 studies analysing rate-induced changes, leading to 30 data points due to multiple experiments in certain studies. Level of organisation was the strongest predictor to split distinguish 'tipping (nonlinear)'*

(community, ecosystem/biome) from 'no tipping (linear)' (organism, population) outcomes. At a secondary level of prediction, 'tipping' occurred at 85% of the cases at the community and 55% of the cases at the ecosystem/biome level.

Level of ecological organisation was the only predictor, among the other variables, to explain the consequence (tipping or no tipping) of the rate of environmental change: higher levels (community, ecosystem/biome) were most likely to undergo 'tipping', while at lower levels (organism and population) 'no tipping' dominated the outcomes. It is intuitive that higher levels of ecological organisation are sensitive to tipping, since these will contain a higher number of interactions (Williams *et al.* 2021) and more likely include fast-slow processes, which increase the likelihood of R-tipping (Ashwin *et al.* 2012; Siteur *et al.* 2016). Within the first group, community had a higher prevalence of 'tipping' (85% of cases) than ecosystem/biome (55% of cases). We should note that the very limited sample size (n=30) does not allow for generalisations based on these results, and therefore, we do not consider the relatively high p-value (e.g., p=0.25) as a lack of evidence. Rather, we regard this emergent pattern as an important perspective that needs further investigation.

Testing rate-sensitivity across levels of organisation

To this point, we have elucidated how R-tipping can manifest itself in a broad ecological context (Fig. 1) and demonstrated the potential significance of different levels of organisation (Fig. 2). Here we discuss how empirical studies can help advance the theory on R-tipping phenomena.

Study design

It is vital that empirical approaches share a common definition of what constitutes rapid environmental change, by seeking thresholds along a continuum rather than by picking extreme scenarios of slow and rapid change (Pinek *et al.* 2020). It is also critical to disentangle transitions driven by the magnitude of change from rate-sensitive responses, as transitions that have been attributed to the former could have been induced by the rapidity of change (Vanselow *et al.* 2019). Since the rate of change equals the magnitude of change divided by time (i.e., the duration of the treatment), one could seek existing studies where both a treatment's magnitude and its duration have been recorded. Alternatively, new experiments could investigate rates of change by varying both the magnitude and the duration of a treatment, essentially producing a full factorial design (Fig. 3). Statistical analyses can then help to reveal whether it is the magnitude or the rate of change, the latter modelled as the interaction of magnitude with duration, driving the response.

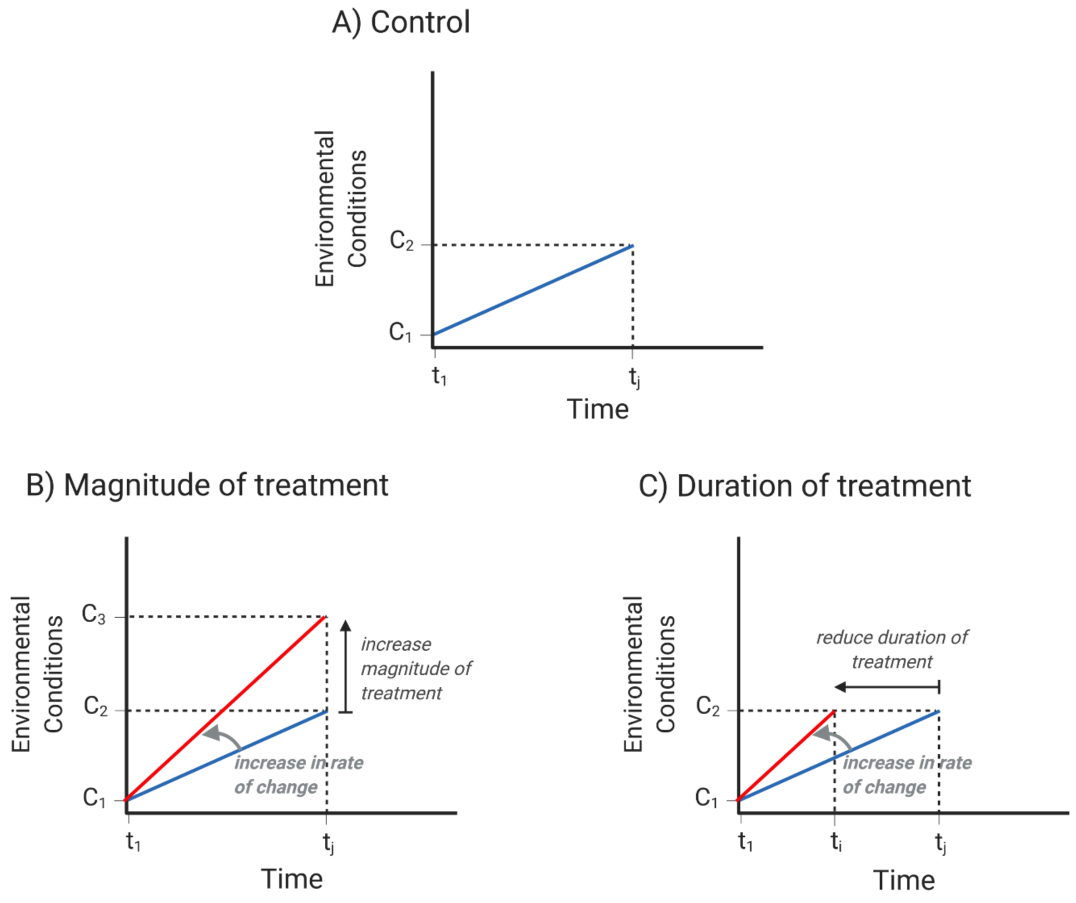


Figure 3. *A visualisation of how to investigate increasing rates of change in environmental conditions. The rate of change in the treatment (i.e., environmental conditions) equals the change in magnitude over the duration of the treatment. One can investigate the same increase in the rate of change by either increasing the magnitude of change (B) or by reducing the treatment duration (C). A) The control: the change in conditions is* $\delta C = C_2 - C_1$ *within a time of* $\delta t = t_j - t_i$. *B) Increasing the rate of change by increasing the magnitude of the treatment,* $\delta C = C_3 - C_1$, *while keeping the duration* δt *constant. C) Increasing the rate of change by reducing the treatment duration* $\delta t = t_j - t_1$ *and preserving the magnitude of* δC. *Direct comparison of the effect of the different approaches to increasing the rate of change over a range of different rates of change can help disentangle the effect of the magnitude of change from the rate of change*.

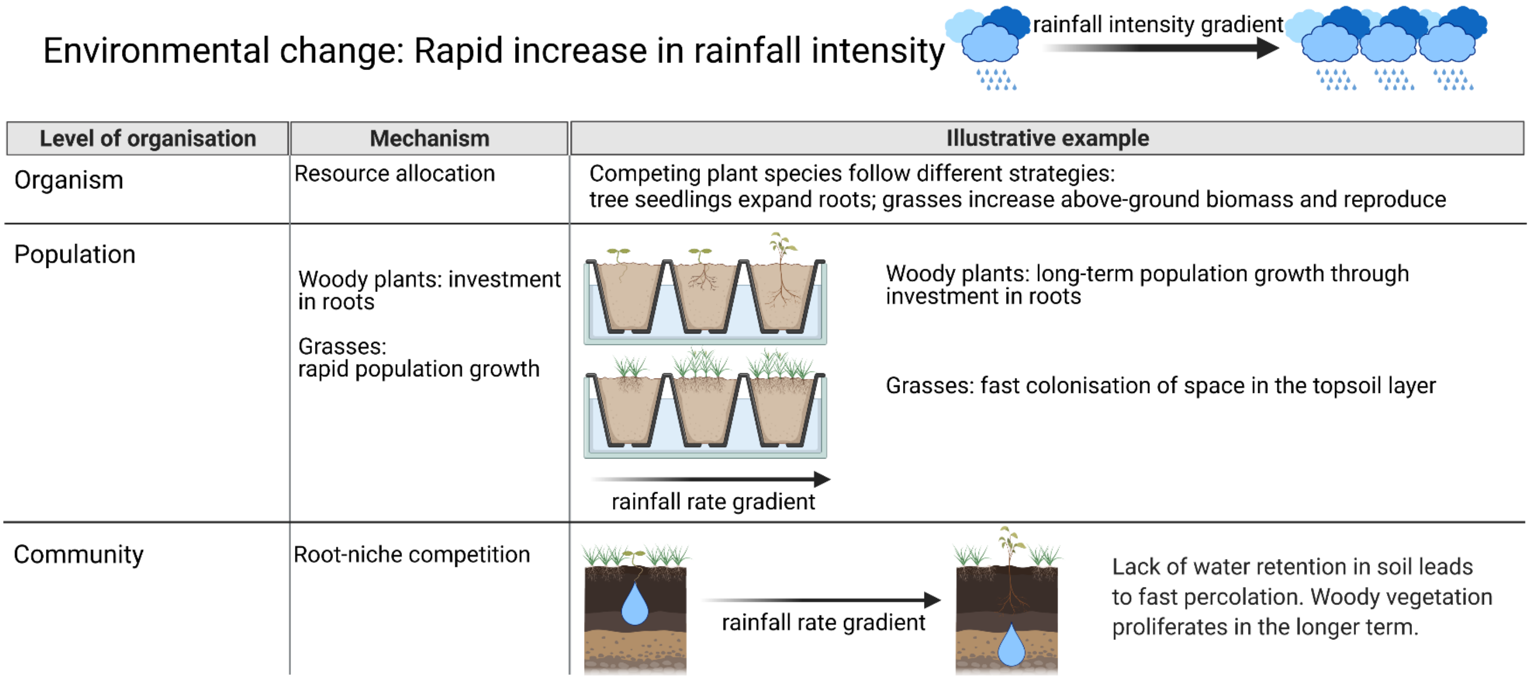
Mechanistic approach

Any environmental change will directly impact individual organisms and indirectly cause change across levels of organisation. Thus, to understand R-tipping propagation across levels of organisation, experiments and field observations can start with studying the responses at the lower levels (organism, population) focusing on a single stressor and only pair-wise interacting species. A mechanistic understanding of the given system can help produce generalisable results. Below we present different mechanisms known to buffer against environmental change at different levels of organisation and give simplified examples of potential experiments to test their susceptibility to rates of change.

At the organismal level, plasticity (Parmesan 2006; Allen *et al.* 2012, 2016; Moyano *et al.* 2017; Radchuk *et al.* 2019) or microevolution, sensu local adaptation (Hendry & Kinnison 1999; Ignacio *et al.* 2013), can buffer against environmental change. Alternatively, well-adapted species (e.g., thermal tolerance of heat shocks) can produce ecological responses (e.g., increased foraging due to higher metabolic demands with rapid warming). Observations of individual species can follow the study design described above (Fig. 3) to identify any physiological, morphological, phenological, life-history or other response induced by the rate of changing conditions. A slightly more complex experimental design could allow for individuals to disperse to account for another buffering mechanism against rapid change (Higgins *et al.* 2003; Stefan *et al.* 2015).

It should be noted that even when dynamics at one level track the equilibrium with some delay, this lag can indicate a suboptimal fit to current conditions (Williams *et al.* 2021). Such mismatches may cause evolutionary or extinction debt, ultimately impacting higher levels of organisation. Therefore, even if experiments at the organism (or population) level show that the ecological entity can track the rate of environmental change, it is critical to evaluate the impact of this response on higher levels of organisation. Such an investigation would benefit from a mechanistic approach: identifying which aspects of higher-level interactions could be impacted by the organismal level responses to the rates of change, and developing associated hypotheses. For example, a decrease in the body size of predators can lead to lower per-capita consumption of prey with consequences for top-down control. A corresponding hypothesis could be used to test how total prey and predator biomasses or population fluctuations will be affected.

At the community level, in particular in competitive communities, species can achieve stable coexistence by occupying different niches for resource acquisition (Macarthur & Levins 1967; MacArthur 1970; Tilman *et al.* 1997). High rates of environmental change can induce responses in individual species which can alter the competitive balance of the community. In drylands, for example, rainfall events will become more intense, with yearly rainfall concentrated in fewer time windows and droughts more prolonged (Ma *et al.* 2015). If we only focus on the change in rainfall, in communities of competing herbaceous and woody plants (e.g., savannas), extreme individual rainfall events could accelerate woody seed germination causing woody vegetation recruitment pulses and ultimately woody encroachment (Morrison *et al.* 2018). Alternatively, grasses can respond fastest to produce growth pulses of their own, causing the exclusion of woody vegetation (Xu *et al.* 2015). These opposing outcomes rely on different mechanisms: root-niche separation benefiting trees which can access water from deeper soils and a so-called temporal niche (i.e., fast responsiveness) benefiting grasses, respectively. Experiments can establish how isolated populations of grasses and woody plants respond to different rates of increasing rainfall intensity (i.e., rainfall amount per individual rainfall event – without altering the total amount of rainfall in a given 'year') (Fig. 4). By identifying the mechanisms responsible for the observed responses at the population level, hypotheses regarding the response patterns of competitive plant communities to altered rainfall intensity patterns can be developed and tested at the community level.



Environmental change: Rapid increase in rainfall intensity

Level of organisation	Mechanism	Illustrative example
Organism	Resource allocation	Competing plant species follow different strategies: tree seedlings expand roots; grasses increase above-ground biomass and reproduce
Population	Woody plants: investment in roots Grasses: rapid population growth	Woody plants: long-term population growth through investment in roots Grasses: fast colonisation of space in the topsoil layer
Community	Root-niche competition	Lack of water retention in soil leads to fast percolation. Woody vegetation proliferates in the longer term.

Figure 4. *Testing how the rate of increasing rainfall intensity (i.e., rainfall amount per individual event while maintaining the total 'yearly' amount constant) can alter competitive dryland plant communities, starting at the organismal level and working upwards. In this setup, we assume the rate of rainfall intensity as the single driver of the dynamics, so we will observe and hypothesise based on the associated mechanisms known from the literature. Increased rainfall intensity can be applied either by increasing the rainfall amount and maintaining the duration of the individual rainfall events or by preserving the rainfall amount and reducing the duration of the rainfall events (as explained in Fig. 3). At the organism level, the resource allocation of individuals differs between woody plants and grasses. The former expand their roots before investing in above-ground biomass accumulation, the latter increase above-ground biomass and reproduce. For trees this translates into access to water in the deeper soil layers (root-niche separation). Grasses, in the absence of inter-specific competition, can rapidly colonise the available space in the topsoil layer (so-called 'temporal niche'). With more intense rainfall events, water percolates faster into the deeper soil layer.. Given these hypotheses (separate niches), if in the presence of tree competition, grasses begin to lose out (trees take up water from the upper and lower soils, shading negatively affects grasses, etc.) and woody species expand their population, we can stipulate the root-niche competition causes R-tipping in the form of woody encroachment. Extensions to the experiment should consider other drivers of tree sapling establishment bottlenecks such as the interaction between drought duration and increased rainfall amounts (Geissler & Blaum, unpublished data) or the rate of increase in atmospheric* CO_2 *with respect to the benefits C3 and C4 photosynthetic pathways.*

As a second example at the community level, trophic interactions will also be impacted by rates of environmental change. Different evolutionary or ecological rates of resource and consumer can increase the risk of consumer extinction through long phases of low densities (Yoshida *et al.* 2003), lead to community collapse due to overconsumption (Siteur *et al.* 2016) or create resource-dominated communities (Scheffer *et al.* 2008), among others. An experimental setup which studies the potential for local adaptations of isolated prey and predator populations can generate hypotheses about potential rate-induced mismatches at the community-level (Fig. 5). The spatial extension of this example to include more patches (i.e., a metacommunity) or the addition of another trophic level (i.e., food chain) would be an important extension as it may yield unexpected results (Faillace *et al.* 2021).

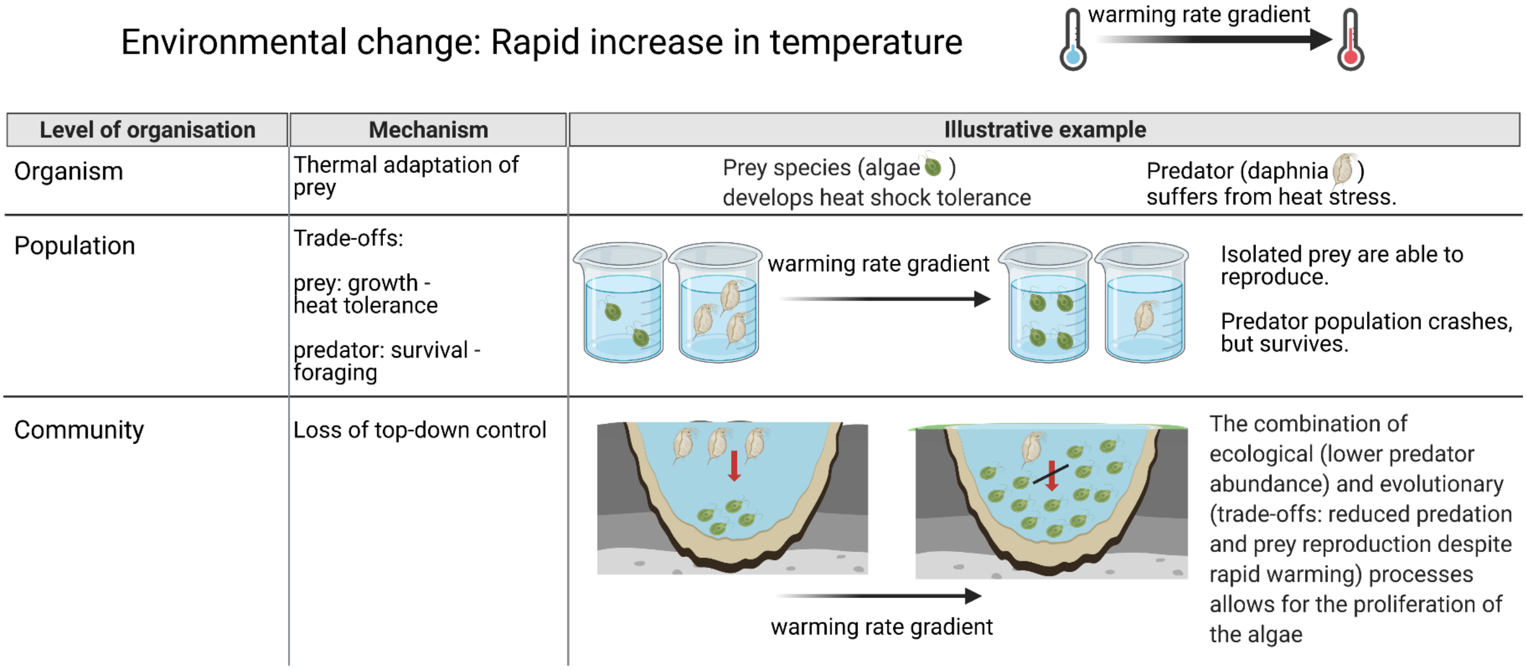


Figure 5. *An illustration of how fast rates of warming can propagate from low to higher levels of organisation in predator-prey interaction. Many eco-evolutionary feedbacks are possible, but we can assume the following: algae can respond to rapid warming by increasing their tolerance to heat shocks, through a trade-off with reproduction, i.e., improved survival at the cost of reduced reproduction (evolutionary response). The daphnia cannot adapt so they reduce their mobility to increase survival (ecological response). Already, this can be considered a form of R-tipping which propagates to the population level: algae can reproduce even as warming occurs at high rates, while daphnia populations shrink. This leads to a community where algae can grow almost uninhibited, since the ineffective daphnia population does not create a top-*

down control. This example illustrates only on a single aspect of increased warming rates; more complex eco-evolutionary feedbacks are possible, particularly in the context of a metacommunity (i.e., additional patches) (Faillace et al. 2021).

In a spatial context, the rate of fragmentation or habitat destruction could benefit habitat generalists over habitat specialists, as the latter could struggle to locate their preferred prey in fragmented landscapes (Ryall & Fahrig 2006) or to colonise new, undisturbed patches (Warren *et al.* 2001; Travis 2003). In cases where such patterns have been observed, the R-tipping framework could help develop related questions which can be tested in the same systems. For example, given a critical dispersal rate below which a species would go locally extinct, what trait trade-offs (e.g., competition-colonisation) are feasible and can buffer against extinction?

R-tipping constitutes a temporal process; therefore, it is vital to understand the interplay of interacting timescales (e.g., eco-evolutionary feedbacks, predator-prey lifecycles, 'competing' positive and negative feedbacks). Species with short generation timescales relative to their competitors or predators can evolve to track the rate of environmental change, inducing R-tipping at higher levels of organisation and setting off eco-evolutionary feedbacks. Alternatively, fast-responding species (i.e., with traits well-adapted to fast change) can immediately proliferate, thus altering their environment. This change will then select for different traits in the community, forcing eco-evolutionary feedbacks. Given that empirical – and theoretical - research on R-tipping in ecology remains in its infancy, the approaches we discussed focus on simple pairwise species interactions being driven by a single environmental factor. It is clear that in the future we should aim to incorporate a second – or even more if possible – stressor, which will impose trade-offs in the responses of individual species.

A paradigm shift is necessary

R-tipping alone will not, and indeed should not, replace the application of B-tipping theory. In fact, different mechanisms can co-occur under global change, where multiple stressors can act simultaneously (Rillig *et al.* 2019). Interactions between B- and R-tipping have been theoretically explored, yielding potentially complex dynamics (Arumugam *et al.* 2020, 2021; O'Keeffe & Wieczorek 2020). The proposed 'critical rate hypothesis' combines extreme external events, alternative states and a rapidly responding ecological entity (Scheffer *et al.* 2008). The sustained macro-algal bloom in Caribbean coral reefs in the 1990s was explained based on this hypothesis. According to this, long-term eutrophication and overfishing of grazers, though not sufficient to cause a regime shift, pushed the system close to bifurcation, thereby making it more susceptible to a transition. An abrupt loss of sea urchins (grazers) due to a disease outbreak combined with a spike in nutrient availability from a hurricane, triggered a rapid, uninhibited algal recruitment event. The authors argue that this 'critical rate of change' induced a regime shift as the algae colonised the coral reef, before grazers could re-establish effective top-down control.

Successful biological invasions can follow a similar pattern. After initial establishment in the novel environment, the exotic species will rapidly expand once physical conditions provide a window of opportunity (e. g. 'boom-bust' dynamic (Strayer *et al.* 2017)). San Francisco Bay was invaded by zebra mussels at initially low densities (Paine *et al.* 1998). Following a flood which removed the resident estuarine community, the zebra mussels' population exploded and within two years had permanently replaced the resident communities. A similar dynamic has been observed in tropical woodlands, where high rainfall years trigger mass recruitment events of woody vegetation (Holmgren & Scheffer 2001; Holmgren *et al.* 2013), which can cause a transition to an encroached state (Scheffer *et al.* 2008; Kulmatiski & Beard 2013; Synodinos *et al.* 2018).

However, temporal events are often recurrent, and thus the frequency of extreme events needs to be additionally considered due to ecological memory (Ryo *et al.* 2019). If the frequency of such events were to increase, as predicted (Rahmstorf & Coumou 2011; Myhre *et al.* 2019), existing communities' traits could become ill-suited to cope. This could yield novel communities through invasions, extinctions or a switch in competitive balance (Paine *et al.* 1998). Such considerations will inevitably overlap with studies on climate-induced changes in disturbance regimes (Johnstone *et al.* 2016; Hart *et al.* 2018; Sarneel *et al.* 2019; de Bello *et al.* 2021), providing fertile ground for theoretical synthesis.

As we have stressed above, multiple drivers acting simultaneously are impacting ecological entities from individuals to ecosystems. One theory cannot cover them all. Even though the paradigm of bifurcations and alternative states has yielded valuable insights, it cannot deal with the temporal aspect of environmental change. Given the mounting evidence on the increasing rate of change and variability in climatic regimes and environmental conditions (Waters *et al.* 2016; Pattyn *et al.* 2018; Ceballos *et al.* 2020), we propose that alternative paradigms, such as R-tipping, are explored to provide appropriate predictions. Specifically, we argue for a shift of focus to rates of change as important drivers across scales in ecology. Coupling existing theory to empirical data can be used to develop and test hypotheses and improve our predictive capabilities. We believe that anticipating and understanding rate-induced phenomena will become a major challenge for ecology as we enter a future with no analogues in the past. We hope our work will facilitate the applicability of R-tipping theory in ecology, which combined with more conservation-oriented approaches (Williams *et al.* 2021) should increase our ability to predict and mitigate adverse impacts of high rates of environmental change. Moreover, theoretical synthesis through the integration of multiple conceptual models (B-, N- and R-tipping) will become necessary. Challenging times lie ahead, and we must make sure that theory and the resulting conservation actions do not become outpaced by the rate of ecological crises.

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Data availability statement

No new datasets were generated for this study. All data used for the literature review was available in the original studies. A list of the reviewed literature is provided in the Supplementary Information.

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