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Forum

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

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Oikos
2022: e09616
doi: 10.1111/oik.09616

Subject Editor: Justin Travis
Editor-in-Chief: Pedro Peres-Neto
Accepted 17 November 2022

Global change has been predominantly studied from the prism of 'how much' rather than 'how fast' change occurs. Associated to this, there has been a focus on environmental drivers crossing a critical value and causing so-called regime shifts. This presupposes that the rate at which environmental conditions change is slow enough to allow the ecological entity to remain close to a stable attractor (e.g. an equilibrium). However, environmental change is occurring at unprecedented rates. Equivalently to the classical regime shifts, theory shows that a critical threshold in rates of change can exist, which can cause rate-induced tipping (R-tipping). However, the potential implications of R-tipping in ecology remain understudied. We aim to facilitate the application of R-tipping theory in ecology with the objective of identifying which properties (e.g. level of organisation) increase susceptibility to rates of change. First, we clarify the fundamental difference between tipping caused by the magnitude as opposed to the rate of change crossing a threshold. Then we present examples of R-tipping from the ecological literature and seek the ecological properties related to higher sensitivity to rates of change. Specifically, we consider the role of the level of ecological organisation, spatial processes, eco-evolutionary dynamics and pair–wise interactions in mediating or buffering rate-induced transitions. Finally, we discuss how targeted experiments can investigate the mechanisms associated to increasing rates of change. Ultimately, we seek to highlight the need to better understand how rates of environmental change may induce ecological responses and to facilitate the systematic study of rates of environmental change in the context of current global change.

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Keywords:climate change, ecological communities, eco-evo feedbacks, transitions, global change, R-tipping, temporal ecology

Introduction

Anthropogenic drivers of global change (e.g. increasing mean temperatures, nitrogen enrichment, habitat loss and fragmentation, alien species invasions) have significant effects at all levels of ecological organisation (Waters et al. 2016, IPBES 2019). A lot of attention has been drawn to critical thresholds in the magnitude of these drivers causing catastrophic regime shifts (IPCC 2022). The rate of change itself, and specifically increasing rate of environmental change, constitutes an additional threat (Pershing et al. 2015, Spooner et al. 2018, Brito-Morales et al. 2020), because it restricts the ability of organisms, populations or communities (i.e. ecological entities) to respond (Williams et al. 2021). Unfortunately, studies on the effect of different rates of change of environmental drivers on population, community and ecosystem responses are largely lacking (Pinek et al. 2020).

Most commonly, the dependence of an ecological entity on an environmental factor (e.g. temperature, salinity) is quantified via independent measurements along the gradient of this factor. Correspondingly, critical thresholds in the magnitude of environmental change have been identified when the response variable (e.g. population) undergoes a drastic change (e.g. population collapse). Therein lies a major, and usually implicit, assumption: that the rate of transition from one environmental value to the next along the gradient can be neglected. However, environmental change is occurring at rates that render this assumption problematic. It has been theoretically demonstrated how high rates of environmental change alone can trigger catastrophic responses in ecological entities (Wieczorek et al. 2011, Ashwin et al. 2012). On the other hand, empirical evidence suggests that acclimation – a time-dependent process – can alter the impact of environmental change on organisms (Kremer et al. 2018, Sohlström et al. 2021). Hence, theory and data exist to support the notion that environmental change amounts to more than its magnitude.

We aim to highlight the potential for rates of environmental change to induce catastrophic outcomes in ecology and to guide experimental studies on how to best approach this topic. In the following sections we first elaborate on the significant differences between magnitude-induced and rate-induced tipping. We then describe ecologically relevant examples of rate-induced tipping. Finally, we present a framework to guide experimental studies on rates of change in ecology based on an operational definition of rate-induced transitions. By presenting a clear definition and developing a standard framework, we aim to stimulate the debate on and facilitate the study of rate-induced phenomena in ecological systems.

B- versus R-tipping behaviour in ecology

The notion that the magnitude of an external driver crosses a critical threshold which causes a regime shift has drawn a lot of attention in ecology (Scheffer 2009). Such catastrophic transitions are mediated by a bifurcation in the underlying system, referred to as bifurcation-tipping or B-tipping (Scheffer 2009, Ashwin et al. 2012, Box 1). While such transitions 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 the 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 and Carpenter 2003, Hughes et al. 2013).

Prominent examples are shallow lake systems exhibiting shifts between a clear water state and a turbid state dominated by phytoplankton caused by eutrophication (Scheffer et al. 1993, Scheffer and Carpenter 2003); the shift of marine coastal systems to an alternative depauperate state caused by the over-exploitation of top predators (sea otters) (Estes and Palmisano 1974, Jackson et al. 2001, Estes et al. 2011); or the more frequent occurrence of cyanobacterial blooms in lakes due to warming and eutrophication causing drastic shifts in the community composition of aquatic systems (Wilkinson et al. 2018).

However, B-tipping operates under the assumption of equilibrium dynamics. Thus, the ecological entity is assumed to have attained its equilibrium for each value of the forcing parameter and we observe a transition between equilibrium points along the environmental gradient. In this sense, B-tipping neglects the temporal aspect of the change in the environmental conditions, which can be problematic if the dynamics are sensitive to this rate of change (Ashwin et al. 2017). Thus, B-tipping theory covers the potential tipping behaviours only when R-tipping cannot occur (e.g. 'forward basin unstable' systems, Ashwin et al. 2017, der Bolt and van Nes 2021). Otherwise, B-tipping cannot deal with the aspect of temporal change in the forcing parameter and a different

Box 1. Tipping

B-tipping. Bifurcation-induced tipping occurs when the system (e.g. ecological entity) shifts to an alternative state once a critical threshold in magnitude of an external driver is crossed.

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 forcing parameter. The system exhibits a tipping response when the rate of change exceeds a critical threshold and departs from the neighbourhood of the attractor.

mathematical formalism is required to study rates of environmental change as external forcing parameters.

The theory of rate-induced tipping (or R-tipping) describes how high rates of change in the forcing parameter cause the departure of the dynamical system from the stable attractor (or the quasi-stable attractor), when this rate exceeds a critical value (Ashwin et al. 2012, Box 1, Fig. 1). This departure can cause a regime shift in the classical sense with the system settling on an alternative attractor (Alkhayuon and Ashwin 2018, Gil et al. 2020, Chaparro-Pedraza 2021). In this case, the transition occurs prior to the environment crossing a critical threshold in its magnitude of change (Fig. 1A, red line). The underlying dynamics determined by the time-invariant parameters would not change and hence the magnitude threshold would remain unchanged (O'Keeffe and Wieczorek 2020); the transition would be caused solely by the extent of the departure of the ecological entity's state from the stable attractor, caused by the inability to track the rate of environmental change (Fig. 1B, solid red line).

Significantly, however, the occurrence of R-tipping does not necessitate the presence of an alternative state (Luke and Cox 2011, Wieczorek et al. 2011, Siteur et al. 2016, Vanselow et al. 2019). Two potential scenarios emerge in this case. Either the environmental change ceases and the departure from the stable attractor precedes a return to the original attractor, albeit after a transient excursion into potentially dangerously low population densities (Vanselow et al. 2019). Alternatively, if environmental change continues to unfold at above critical rates, a catastrophic departure from the current attractor could occur, triggering a cascade of species extinctions (Fig. 1B, dashed red line).

It is worth noting that the outcome of the B- and R-tipping could appear identical, i.e. as a transition to an alternative state. Thus, in an ecological setting without prior knowledge of the dynamics or the environmental driver, attributing an apparent regime shift to B- or R-tipping would be extremely hard. Being able to make this distinction could become possible if we take rate of change into account in empirical studies and aim to gain a better understanding of rate-induced phenomena. In this study we aim to facilitate this process. Therefore, we start from the causal difference identified in the theoretical studies, seek properties specific to rate-induced tipping and argue for the design of experiments accordingly.

There is a clear and significant difference in causal factors leading to B- versus R-tipping: 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 driver such as ambient temperature or atmospheric CO_2 concentrations – known drivers of the current ecological crisis – even if the magnitude of this driver remains below a B-tipping threshold. Hence, we utilise R-tipping theory to improve our understanding of ecological dynamics in the context of currently observed increasing rates of environmental change (Joos and Spahni 2008).

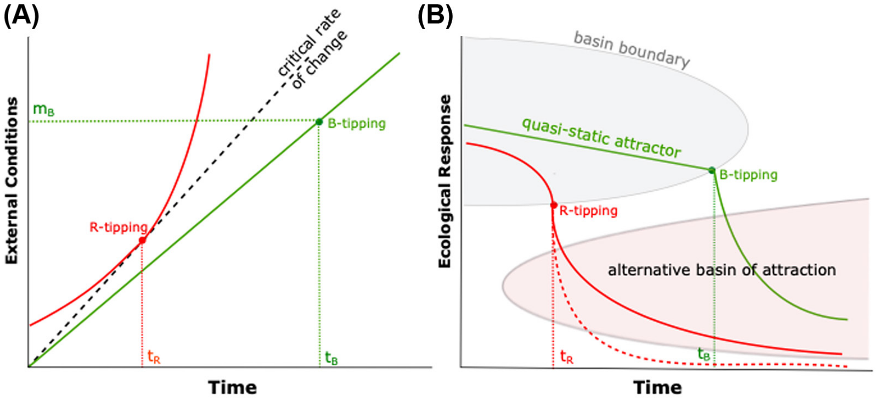

Figure 1. Illustration of how change in a forcing parameter can induce tipping in the ecological entity. We focus on bifurcation-induced tipping (B-tipping) and rate-induced tipping (R-tipping), i.e. we do not consider noise- or shock-induced tipping (Ashwin et al. 2012, Vanselow et al. 2019). (A) Change in external conditions (forcing parameter) over time. The two curves illustrate how environmental conditions can change at a constant rate (green line) or at an increasing rate (red curve). There exists a critical threshold in the magnitude of change, m_B, such that if the external conditions cross this threshold, B-tipping occurs at time t_B (green line). Independently, there exists a critical rate of change, which is determined as the magnitude of change over time, i.e. when the slope equals that of the dashed black line. When external conditions change faster (i.e. when the slope becomes steeper than the dashed black line's slope) R-tipping will occur at time t_R (red curve). Notice that the green line has a shallower slope than the critical rate of change, therefore, no R-tipping occurs. In this example, we assume that conditions continue to change at an accelerating pace even after crossing the critical rate. (B) The corresponding responses to the changing conditions. When change is 'slow' the dynamics will track the (quasi-)static attractor. Once external conditions cross the magnitude threshold m_B at time t_B, B-tipping occurs and forces the ecological entity into the alternative basin of attraction (green curve). If the rate of change increases, the dynamics cannot track the (quasi-) static attractor (red curve). If the rate of changing conditions exceeds a threshold, then R-tipping occurs at time t_R. We illustrate two different outcomes, which are not exhaustive: the dynamics settle in the alternative basin of attraction (solid red curve) or they cannot settle on an alternative attractor (especially if the rate of change remains above the critical threshold), causing a catastrophic collapse of the ecological entity (dotted red curve).

Examples for rate-induced transitions in ecology

A characteristic property of R-tipping is the coupling of fast and slow processes, which implies a separation of timescales (Ashwin et al. 2012). In a general theoretical treatment of pair–wise trophic interactions, R-tipping has been shown to occur when the resource species have fast dynamics relative to consumers (Siteur et al. 2016, Vanselow et al. 2019). Thus, the former can track rapidly deteriorating environmental conditions, while consumer behaviour corresponds to earlier (and higher) resource abundances. This lag causes the overexploitation of resources and the collapse of the community as the abundance of the resource species decreases.

In a similar way, the sustained macro-algal bloom in Caribbean coral reefs in the 1990s has been attributed to the rate of algal growth relative to consumption by grazers (sea urchins) (Scheffer et al. 2008). 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. A rapid increase in nutrient availability due to a hurricane, stimulated fast algal growth. With grazers too slow to establish effective top–down control due to a disease outbreak, a regime shift to algal dominance occurred. We should note that this scenario combines multiple stressors and different types of tipping (B-tipping, R-tipping and extreme events); however, the transition is ultimately caused by the fast algal growth – due to sudden enrichment – relative to consumption by grazers.

Two recent theoretical studies have investigated rate-induced phenomena in the context of aquatic systems (Gil et al. 2020, der Bolt and van Nes 2021). In a model of phytoplankton population dynamics, using realistic parameter values, evidence for potential R-tipping was found (der Bolt and van Nes 2021). In particular, assuming that algal growth has a hump-shaped dependence on light intensity, when light intensity increased rapidly the phytoplankton went extinct, being unable to track this change. Further, the authors suggest that the model can be tested experimentally in a chemostat.

More recently, in a model with fish as consumer and algae and corals as competing resources, the rate of fishing – rather than the amount of fish removed (i.e. the magnitude of change) – caused the loss of corals to algae (Gil et al. 2020). When fish were removed at a rate which could not be compensated by growth through the consumption of algae, the fish went extinct. Thus, algae colonised the corals uninhibited. The same amount of fishing occurring over longer time (i.e. lower rate) did not lead to the extinction of fish and corals.

For terrestrial systems, woody encroachment in tropical woodlands can be ascribed to the increased recruitment of woody plants during high rainfall years (Holmgren and Scheffer 2001, Holmgren et al. 2013). There, yearly rainfall concentrated in shorter time windows (i.e. increased intensity) can cause a mass colonisation of woody vegetation at a rate that can evade top–down control from herbivores or damage from fires, ultimately causing the encroachment of grasslands by woody plants (Scheffer et al. 2008, Kulmatiski and Beard 2013, Synodinos et al. 2018).

An interesting aspect in the context of R-tipping is the persistence of species through trait adaptation. Chaparro-Pedraza (2021) explored different organisational levels (population, predator–prey interaction and ecosystem) in which trait evolution could shift B-tipping along the forcing parameter gradient, thus creating a different range for bi-stable dynamics. Within the bi-stability regions, it was demonstrated how the relative rates of environmental change and evolution could lead to different outcomes (regime shift, transient collapse). In the absence of alternative states, Vanselow et al. (2021) demonstrated how sufficiently fast adaptation could prevent resource densities from dropping to dangerously low levels, which would constitute an effective extinction of the community. This study represents an example of indirect 'evolutionary rescue' where the adaptation of a predator trait (attack rate) led to the persistence of the resource species. It is worth noting that adaptations which improve survival chances (e.g. predator defence) are expected to trade-off with ecological processes such as lower reproduction, which might limit the ability to adapt to environmental change (Catalina Chaparro Pedraza et al. 2021).

There is also experimental evidence on the significance of rates of environmental change with respect to 'evolutionary rescue'. In a study of bacteria, rates of temperature increase induced different outcomes in the short-term compared to the long-term (Liukkonen et al. 2021). Strains subjected to slow warming had greater population growth and biomass in the short-term; however, long-term survival was higher in the strain subjected to fast warming. The authors attributed this to correlated selection. In a different experiment, the realisation of mutations allowing bacterial survival depended on the rate of antibiotic addition, with certain adaptive mutations failing to manifest under too great rates of antibiotic increase (Lindsey et al. 2013).

Not all of the highlighted studies were undertaken within the context of R-tipping. This is also true of existing frameworks. One is based on the notion of climate velocity, which measures the direction and speed of species range shifts required to stay within their climatic window (Brito-Morales et al. 2018). Thus, studies of climate velocity can quantify the impacts of the rate of climate change on species persistence (Loarie et al. 2009, Burrows et al. 2011, Garciá Molinos et al. 2016). Similarly, a framework for ecological conservation based on rates of environmental change was recently developed, seemingly independently of the R-tipping formalism (Williams et al. 2021). The authors identified rates, rather than states, as the most important indicator conservation efforts should revolve around. As with R-tipping, three potential responses to rates of change were postulated: ecological entities 1) adjust to and follow climate change, 2) follow climate change at a slower pace, creating an extinction or evolutionary debt or 3) do not respond to climate change until an abrupt shift to a new regime is forced.

Rate-induced tipping in published studies

We performed a narrative literature review (based on keywords such as 'rate of change' or 'rate-induced transition'), selecting studies which explicitly investigated the impact of the rate of change in a forcing parameter on a target variable. We found 27 studies that met our selection criteria (see the Supporting information for more information on keywords, descriptions, etc.). Within certain studies multiple target variables were investigated or distinct models compared; we treated these as independent data which increased the total number of data points to 34. From our review, we created the following categorical predictive variables with sufficient repetition between the studies to allow for a statistical analysis: level of ecological organisation (organism, population, community, ecosystem/biome), kingdom (bacteria, fungi, plants, animals), ecosystem type (terrestrial, aquatic) and study type (experiment, observation, model). Increasing rate of warming was the most common driver, though others such as rising antibiotic and CO_2 concentrations or decreasing precipitation were present. We defined the response variable as 'no effect', 'no tipping' (dynamics track the equilibrium) or 'tipping' (dynamics cannot track the equilibrium), and used the conditional inference tree algorithm of machine learning (Hothorn et al. 2006, Ryo and Rillig 2017), which classified the studies into subgroups based on the categorical variables (Fig. 2). Given the limited sample size, we employed the machine learning algorithm to uncover any interesting patterns from the qualitative attributes of the literature and to stimulate further studies, rather than identify general and robust patterns.

Study type was the strongest predictor, among the other variables, to explain the outcome (tipping or no tipping) of the rate of environmental change: modelling studies were most likely to produce 'tipping', while lab and observational studies had mixed outcomes. This could indicate a certain bias towards tipping outcomes in theoretical approaches, explicitly designed to investigate this phenomenon. At a secondary level, under modelling studies, the level of organisation was the best predictor, with community level studies always

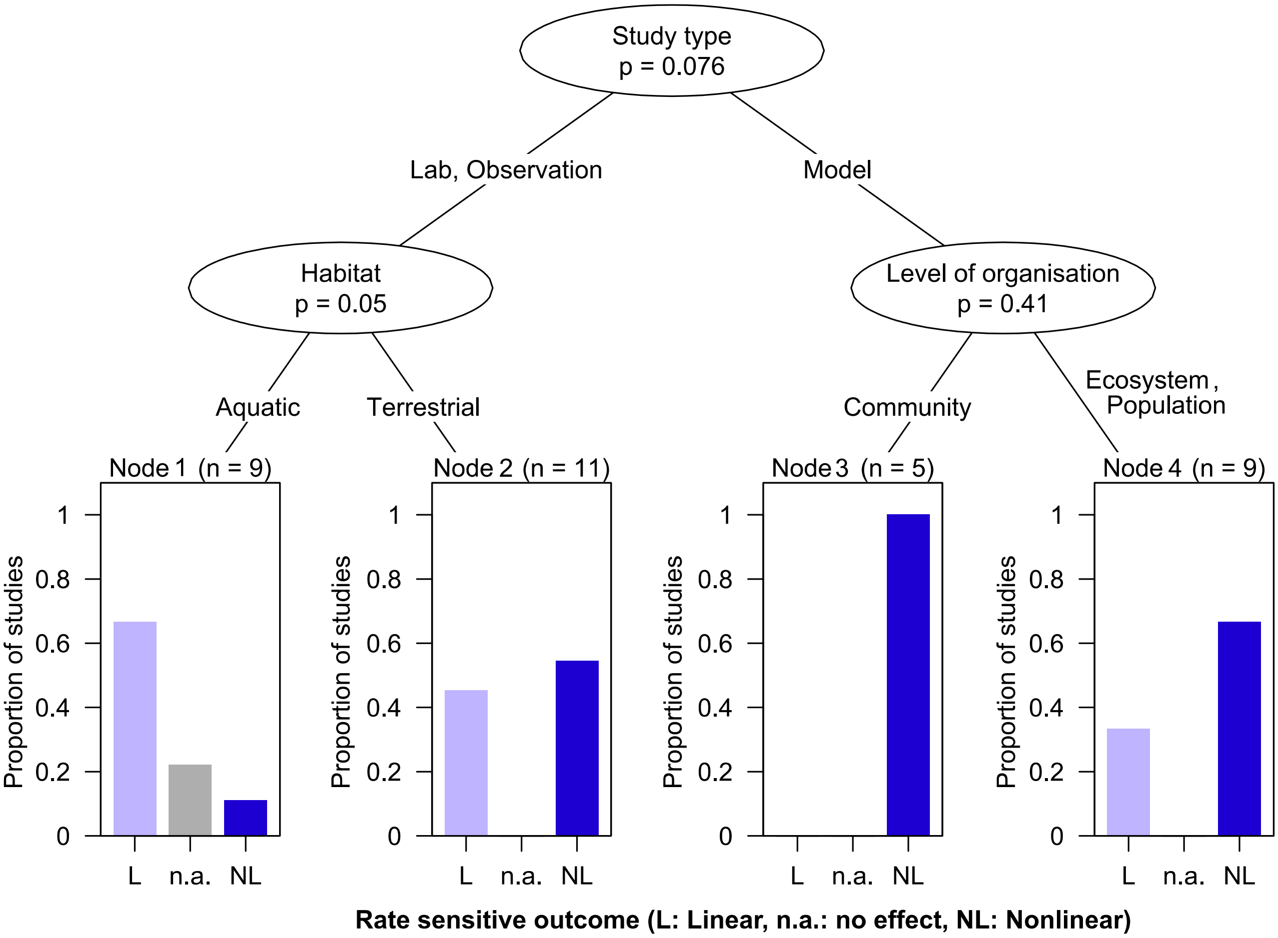

Figure 2. Conditional inference tree algorithm of machine learning for 27 studies analysing rate-induced changes, leading to 34 data points due to multiple experiments or models in certain studies. Study type was the strongest predictor to distinguish 'tipping' (i.e. N.L.) from 'no tipping' (L) outcomes, with modelling studies being a good predictor of 'tipping'. Within the modelling studies, 'level of organisation' best split 'tipping' from 'no tipping' with 'community' being the strongest predictor. Under the other study types ('lab', 'observation'), 'habitat' was the next best predictor; 'tipping' occurring more often in 'terrestrial' than in 'aquatic' habitats.

yielding tipping. Ecosystem and population level studies produced both outcomes, though tipping was more common. For lab and observational studies habitat was the next best predictor of tipping. There, studies in terrestrial habitats produced most tipping results, with aquatic habitats having a low prevalence of tipping.

However, we should remark that the very limited sample size (n = 36) and the potential bias of including certain processes (e.g. separation of timescales) in the modelling studies limit the generality of our findings. This highlights, once more, the necessity for further analyses and specifically designed studies. At the same time, we emphasise that we did not intend to conduct a full meta-analysis (i.e. statistically analysing effect sizes while accounting for sample variance). Rather, we aimed to support our findings from the literature review in a semi-qualitative manner using machine learning. To augment this statistical approach, we performed a qualitative analysis of the data (Supporting information), which also demonstrated that 'models' were most likely to produce tipping outcomes, with 'community' also strongly favouring tipping. The benefit of applying the statistical approach was to reveal connections between the different classes that could predict tipping outcomes. Nevertheless, we emphasise that our results were valuable in identifying patterns and motivating further investigation, but should not be considered as robust evidence in favour of a specific pattern.

Spatial processes can buffer against rate-induced tipping

The review by Williams et al. (2021) in the context of species distribution patterns in response to environmental change identified certain characteristics which can partially determine the impact of rates of change. For instance, the spatial properties of the environment (i.e. heterogeneity) can buffer against the temporal aspect of change (e.g. rate of warming). In particular, spatial heterogeneity increases the likelihood that some patches will be less affected by temporal changes in the environment, thus providing suitable refugia.

Movement (i.e. dispersal, migration) is a known buffering mechanism against detrimental conditions (Thomas et al. 2004) and has been linked to the notion that species will need to shift their ranges in order to follow favourable climatic conditions (Burrows et al. 2011, Sunday et al. 2015). Both marine and terrestrial species that cannot adapt fast enough due to the rate of warming, have been shifting their ranges towards higher elevations or latitudes (Parmesan and Yohe 2003, Chen et al. 2011, Pecl et al. 2017); though certain species may be able to both adapt and move simultaneously (Socolar et al. 2017, Román-Palacios and Wiens 2020). If species cannot physically move at a rate which tracks the climatic shifts, they face a high risk of extinction (Parmesan et al. 1999, Devictor et al. 2008, Feeley et al. 2011, Fadrique et al. 2018).

Thus, we can hypothesise that dispersal and migration rates will have to increase in line with the rate of environmental change. In this sense, dispersal and migration rates may be an important trait to monitor in relation to the response of populations to increased rates of environmental change (Perron et al. 2008); a mismatch between the rate of environmental change and movement rates could indicate a potential risk.

Eco-evolutionary processes in the context of rate-induced tipping

The study by Williams et al. (2021) also found indications that small body-size, life history (juvenile stages) and the number of facilitative interactions could increase the sensitivity to rates of environmental change. Multiple lines of inquiry would be necessary to fully investigate the mechanisms involved in generating this sensitivity. On the one hand, these properties refer to different levels of organisation (organism, population, community, respectively), on the other hand they could be related to various processes mediating the response to rates of change. For instance, smaller organisms, particularly terrestrial ones, may be more dispersal-limited, making them more vulnerable to environmental change (Williams et al. 2021). However, they also tend to be the ones with shorter generation times, which may provide the ability of local adaptation via evolutionary processes. The role of such eco-evolutionary feedbacks has already been explored in theoretical approaches, which demonstrated how genetic variability within populations can be vital in generating an adaptive response to high rates of environmental change (Catalina Chaparro Pedraza et al. 2021, Chaparro-Pedraza 2021, Vanselow et al. 2021). Therefore, a broader investigation of the ability of species to track increasing rates of environmental change will have to involve the study of eco-evolutionary feedbacks.

A common framework for the study of rate-induced tipping in ecology

Similar to the identification of evolutionary-driven consumer–resource dynamics which, once found, led to the re-assessment of observed dynamics in previous studies (Hiltunen et al. 2014), the occurrence of rate-induced tipping might also have gone unnoticed or been misclassified in the past (see discussion in Vanselow et al. 2019). The collection of studies presented above illustrates the potential significance of R-tipping in ecology and the rising interest on the topic. However, we currently lack a common framework within ecology that would promote generalisations through a shared terminology and understanding of the underlying theory. Moreover, it would be important to identify which characteristics of ecological entities increase or decrease the likelihood of rate-induced transitions so as to guide targeted studies in the future (der Bolt and van Nes 2021, Williams et al. 2021).

To facilitate effective studies on rate-induced transitions we provide a practical guide to the mathematical concept of R-tipping in an ecological context. Thus, we create an operational definition of R-tipping:

> *A transition classifies as a rate-induced transition if the rate of change in the environmental driver induces a catastrophic response of the ecological entity, when the magnitude of change alone would not.*

Based on this definition, the following points should guide ecological studies on rate-induced transitions:

1) The response of an ecological entity to environmental change should always be analysed considering the magnitude as well as the rate of change.
2) Rate-induced transitions should be investigated at different rates and magnitudes, seeking for thresholds along a continuum rather than by picking extreme scenarios of slow and rapid change.

The above points enable the design of empirical studies suited to distinguish the cause of transitions between magnitude and rate of change, determine critical rates of change and assess the likelihood of rate-induced transitions for different ecological entities.

Experiments investigating rates of change by varying both the magnitude and the duration of a treatment in a full factorial design could help to assess critical rates of change of specific environmental drivers like temperature for specific species (Fig. 3). If a tipping point in the magnitude of change is known to exist, then varying rates of change while keeping the magnitude of the forcing variable below this threshold could determine the potential for rate-induced transitions.

Such studies could be extended to the community level, starting with pair-wise interactions like competition or predation. In competitive communities, high rates of environmental change can induce responses in individual species which can alter the competitive balance of the community. For instance, the root niche hypothesis represents a competition-based explanation for tree–grass coexistence in savannas (Kulmatiski and Beard 2012, Ward et al. 2013). According to this hypothesis, grasses take up water from the upper soil layer while trees use longer roots to access water deeper into the soil, leading to long-term coexistence. One could test how increasing rates of rainfall (i.e. a fixed amount over a shorter period, rainfall intensity) could impact this coexistence. First, experiments should establish whether any thresholds exist in how mixed tree–grass populations respond to different total amounts of rainfall spread over a long time-window. In a

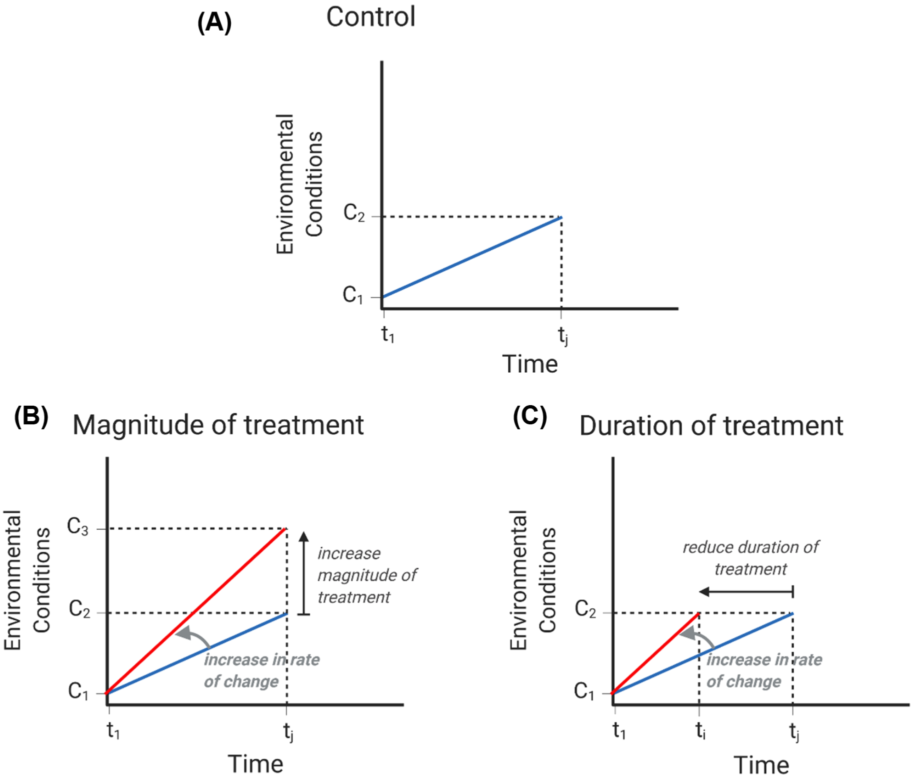

Figure 3. A visualisation of how to investigate increasing rates of change in environmental conditions. The rate of change in the treatment (i.e. environmental conditions) equals the change in magnitude over the duration of the treatment. One can investigate the same increase in the rate of change by 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. If the responses to increasing the rate of change differs between increasing the magnitude of environmental change (B) or reducing the treatment duration (C), this could disentangle the impact of magnitude and rate of change.

second step, keeping the total amount of rainfall fixed, the rainfall intensity should be increased incrementally, by reducing the time window of rainfall to simulate expected effects of climate change (Ma et al. 2015). R-tipping could occur as a result of the faster grass response outcompeting trees (Xu et al. 2015). However, if water percolates too fast into deeper soil layers, then tree colonisation could become the faster process and R-tipping would result in woody encroachment (Holmgren and Scheffer 2001, Scheffer et al. 2008, Holmgren et al. 2013).

Like competitive interactions, trophic interactions will be impacted by the rates of change in environmental drivers. For instance, the effects of the rate of increasing mean temperature could be studied using the experimental setup suggested above. First, the thermal limits of prey and predator (for the given prey) should be established. Then, within the thermal range of coexistence, the effects of different rates of temperature increase should be explored. This could lead to an outright catastrophic collapse, similar to that demonstrated by Vanselow et al. (2019) as a consequence of a reduction in prey carrying capacity. In systems with alternative stable states, too, rates of change could force transitions prior to the magnitude of change crossing a threshold. Recently, it was demonstrated how species performance curves with optima (i.e. unimodal) could be conducive to rapid rates of environmental change causing a transition to an alternative state (der Bolt and van Nes 2021). Given that thermal performance curves tend to be unimodal (Englund et al. 2011, Rezende and Bozinovic 2019), this raises questions about the potential for rapidly increasing mean temperatures to induce drastic changes in trophic communities.

Food chains can also be intrinsically prone to catastrophic collapses through an emergent Allee effect induced from specific prey life-history traits (e.g. size-dependent growth and mortality) (De Roos and Persson 2002, De Roos et al. 2003). In such cases, rates of environmental change that can significantly impact such traits (e.g. rapid warming reducing resource population growth) can lead to rate-induced population collapses, with deleterious effects for the food chain.

Any increase in complexity of the ecological entity will require significantly more laborious experimental setups. For this reason, we have focused on local and pair–wise interactions. These can form the basis for any extensions to the exploration of R-tipping in ecology. As we alluded to above, migration or dispersal should also be considered, ideally following the assessments on critical rates described above, as a buffering mechanism both in isolation (e.g. migration rates, (Higgins et al. 2003, Stefan et al. 2015)) and in the context of eco-evolutionary feedbacks (Faillace et al. 2021). Moreover, non-tipping responses at lower levels of ecological organisation could yet induce R-tipping when considered within a more complex system, especially since higher complexity increases the likelihood of differences in response rates leading to complex community feedbacks. Such complex feedbacks can – and have been – approached via modelling studies, however, often in a rather abstract way. We can hope that as more empirical evidence becomes available, the modelling assumptions will become more realistic and better suited to specific ecological scenarios. The insights gained from combining models and simple experiments should elaborate on how different mechanisms may interact (e.g. adaptation and predation) to produce rate-induced responses (e.g. loss of genetic variance) in nature. Ultimately, this could facilitate the development of appropriate tools to search for rate-induced phenomena in observational data.

Conclusion

Increasing temperature, rising CO_2 levels and other environmental changes are occurring at unprecedented, and still increasing, rates. In this study we highlighted how, beside the magnitude, the rate of change in an external driver can trigger catastrophic outcomes. The mathematical formalism of rate-induced tipping (R-tipping) provides a theoretical foundation for understanding such phenomena. Examples on the occurrence of R-tipping exist from experimental as well as observational studies. Yet, R-tipping in ecology remains largely understudied. We presented a framework to facilitate and stimulate experimental studies in search of rate-induced transitions and corresponding critical rates of change in ecological entities. To this end, we proposed an operationalised definition of rate-induced transitions, from which we deduced guidelines for their study. Combining observational studies over time and space with experimental studies will help to assess the potential of rate-induced transitions in determining the responses of ecological entities to environmental change and facilitate the development of appropriate mitigation strategies.

Glossary

Alternative stable states/attractors – When more than one dynamical attractor coexist for a fixed set of system parameter values. This parameter range is also known as hysteresis area in the bifurcation diagram.

Bifurcation – When small, smooth changes to the forcing parameter cause a sudden, qualitative change in system 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/forcing parameter – The general environment where the system is located. Typically, there exists no feedback between the ecological entity and forcing parameter, which are thus considered 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 (with an underlying smooth bifurcation), or catastrophic, i.e. the behaviour changes abruptly (with an underlying catastrophic bifurcation), 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 fixed point equilibrium, limit cycle (periodic oscillations) or a strange attractor.

Acknowledgements – ADS is thankful to Katja Geissler, Volker Grimm and Bart Haegeman for their helpful comments. Figure 3 was created with BioRender.com. Open Access funding enabled and organized by Projekt DEAL.

Funding – All authors received funding from the German Federal Ministry of Education and Research within the Collaborative Project 'Bridging in Biodiversity Science' (grant no. 01LC1501A and 01LC1501B). ADS received funding through FRAGCLIM Consolidator Grant, funded by the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 726176).

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alkhayuon, H. M. and Ashwin, P. 2018. Rate-induced tipping from periodic attractors: partial tipping and connecting orbits. – Chaos Interdiscip. J. Nonlinear Sci. 28: 33608.

Ashwin, P., Perryman, C. and Wieczorek, S. 2017. Parameter shifts for nonautonomous systems in low dimension: bifurcation- and rate-induced tipping. – Nonlinearity 30: 2185.

Ashwin, P., Wieczorek, S., Vitolo, R. and Cox, P. 2012. Tipping points in open systems: bifurcation, noise-induced and rate-dependent examples in the climate system. – Phil. Trans. R. Soc. A 370: 1166–1184.

Brito-Morales, I., García Molinos, J., Schoeman, D. S., Burrows, M. T., Poloczanska, E. S., Brown, C. J., Ferrier, S., Harwood, T. D., Klein, C. J., McDonald-Madden, E., Moore, P. J., Pandolfi, J. M., Watson, J. E. M., Wenger, A. S. and Richardson, A. J. 2018. Climate velocity can inform conservation in a warming world. – Trends Ecol. Evol. 33: 441–457.

Brito-Morales, I., Schoeman, D. S., Molinos, J. G., Burrows, M. T., Klein, C. J., Arafeh-Dalmau, N., Kaschner, K., Garilao, C., Kesner-Reyes, K. and Richardson, A. J. 2020. Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. – Nat. Clim. Change 10: 576–581.

Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., Brown, C., Bruno, J. F., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., Kiessling, W., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F. B., Sydeman, W. J. and Richardson, A. J. 2011. The pace of shifting climate in marine and terrestrial ecosystems. – Science 334: 652–655.

Catalina Chaparro Pedraza, P., Matthews, B., Meester, L. de and Dakos, V. 2021. Adaptive evolution can both prevent ecosystem collapse and delay ecosystem recovery. – Am. Nat. 198: E186–E197.

Chaparro-Pedraza, P. C. 2021. Fast environmental change and eco-evolutionary feedbacks can drive regime shifts in ecosystems before tipping points are crossed. – Proc. R. Soc. B 288: 20211192.

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. 2011. Rapid range shifts of species associated with high levels of climate warming. – Science 333: 1024–1026.

De Roos, A. M. and Persson, L. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. – Proc. Natl Acad. Sci. USA 99: 12907–12912.

De Roos, A. M., Persson, L. and Thieme, H. R. 2003. Emergent Allee effects in top predators feeding on structured prey populations. – Proc. R. Soc. B 270: 611–618.

der Bolt, B. van and van Nes, E. H. 2021. Understanding the critical rate of environmental change for ecosystems, cyanobacteria as an example. – PLoS One 16: e0253003.

Devictor, V., Julliard, R., Couvet, D. and Jiguet, F. 2008. Birds are tracking climate warming, but not fast enough. – Proc. R. Soc. B 275: 2743–2748.

Englund, G., Öhlund, G., Hein, C. L. and Diehl, S. 2011. Temperature dependence of the functional response. – Ecol. Lett. 14: 914–921.

Estes, J. A. and Palmisano, J. F. 1974. Sea otters: their role in structuring nearshore communities. – Science 185: 1058–1060.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R. and Wardle, D. A. 2011. Trophic downgrading of planet earth. – Science 333: 301–306.

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., Osinaga-Acosta, O., Malizia, L., Silman, M., Farfán-Ríos, W., Malhi, Y., Young, K. R., Cuesta C, F., Homeier, J., Peralvo, M., Pinto, E., Jadan, O., Aguirre, N., Aguirre, Z. and Feeley, K. J. 2018. Widespread but heterogeneous responses of Andean forests to climate change. – Nature 564: 207–212.

Faillace, C. A., Sentis, A. and Montoya, J. M. 2021. Eco-evolutionary consequences of habitat warming and fragmentation in communities. – Biol. Rev. 96: 1933–1950.

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla, N. S., Quisiyupanqui, M. N. R. and Saatchi, S. 2011. Upslope migration of Andean trees. – J. Biogeogr. 38: 783–791.

Garciá Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M., Poloczanska, E. S., Richardson, A. J. and Burrows, M. T. 2016. Climate velocity and the future global redistribution of marine biodiversity. – Nat. Clim. Change 6: 83–88.

Gil, M. A., Baskett, M. L., Munch, S. B. and Hein, A. M. 2020. Fast behavioral feedbacks make ecosystems sensitive to pace and not just magnitude of anthropogenic environmental change. – Proc. Natl Acad. Sci. USA 117: 25580–25589.

Higgins, S. I., Lavorel, S. and Revilla, E. 2003. Estimating plant migration rates under habitat loss and fragmentation. – Oikos 101: 354–366.

Hiltunen, T., Hairston, N. G., Hooker, G., Jones, L. E. and Ellner, S. P. 2014. A newly discovered role of evolution in previously published consumer–resource dynamics. – Ecol. Lett. 17: 915–923.

Holmgren, M. and Scheffer, M. 2001. El Niño as a window of opportunity for the restoration of degraded arid. – Ecosystems 4: 151–159.

Holmgren, M., Hirota, M., van Nes, E. H. and Scheffer, M. 2013. Effects of interannual climate variability on tropical tree cover. – Nat. Clim. Change 3: 755–758.

Hothorn, T., Hornik, K. and Zeileis, A. 2006. Unbiased recursive partitioning: a conditional inference framework. – J. Comput. Graph. Stat. 15: 651–674.

Hughes, T. P., Carpenter, S., Rockström, J., Scheffer, M. and Walker, B. 2013. Multiscale regime shifts and planetary boundaries. – Trends Ecol. Evol. 28: 389–395.

IPBES 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. – IPBES.

IPCC 2022. Climate change 2022: impacts, adaptation and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. – IPCC.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. – Science 293: 629–637.

Joos, F. and Spahni, R. 2008. Rates of change in natural and anthropogenic radiative forcing over the past 20 000 years. – Proc. Natl Acad. Sci. USA 105: 1425–1430.

Kéfi, S., Dakos, V., Scheffer, M., Van Nes, E. H. and Rietkerk, M. 2013. Early warning signals also precede non-catastrophic transitions. – Oikos 122: 641–648.

Kremer, C. T., Fey, S. B., Arellano, A. A. and Vasseur, D. A. 2018. Gradual plasticity alters population dynamics in variable environments: thermal acclimation in the green alga *Chlamydomonas reinhartdii*. – Proc. R. Soc. B 285: 20171942.

Kulmatiski, A. and Beard, K. H. 2012. Root niche partitioning among grasses, saplings and trees measured using a tracer technique. – Oecologia 171: 25–37.

Kulmatiski, A. and Beard, K. H. 2013. Woody plant encroachment facilitated by increased precipitation intensity. – Nat. Clim. Change 3: 833–837.

Lindsey, H. A., Gallie, J., Taylor, S. and Kerr, B. 2013. Evolutionary rescue from extinction is contingent on a lower rate of environmental change. – Nature 494: 463–467.

Liukkonen, M., Kronholm, I. and Ketola, T. 2021. Evolutionary rescue at different rates of environmental change is affected by trade-offs between short-term performance and long-term survival. – J. Evol. Biol. 34: 1177–1184.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. and Ackerly, D. D. 2009. The velocity of climate change. – Nature 462: 1052–1055.

Luke, C. M. and Cox, P. M. 2011. Soil carbon and climate change: from the Jenkinson effect to the compost-bomb instability. – Eur. J. Soil Sci. 62: 5–12.

Ma, X., Huete, A., Moran, S., Ponce-Campos, G. and Eamus, D. 2015. Abrupt shifts in phenology and vegetation productivity under climate extremes. – J. Geophys. Res. Biogeosci. 120: 2015JG003144.

O'Keeffe, P. E. and Wieczorek, S. 2020. Tipping phenomena and points of no return in ecosystems: beyond classical bifurcations. – SIAM J. Appl. Dyn. Syst. 19: 2371–2402.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. – Nature 399: 579–583.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., Lenoir, J., Linnetved, H. I., Martin, V. Y., McCormack, P. C., McDonald, J., Mitchell, N. J., Mustonen, T., Pandolfi, J. M., Pettorelli, N., Popova, E., Robinson, S. A., Scheffers, B. R., Shaw, J. D., Sorte, C. J. B., Strugnell, J. M., Sunday, J. M., Tuanmu, M. N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E. and Williams, S. E. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. – Science 355: eaai9214.

Perron, G. G., Gonzalez, A. and Buckling, A. 2008. The rate of environmental change drives adaptation to an antibiotic sink. – J. Evol. Biol. 21: 1724–1731.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., Sherwood, G. D. and Thomas, A. C. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. – Science 350: 809–812.

Pinek, L., Mansour, I., Lakovic, M., Ryo, M. and Rillig, M. C. 2020. Rate of environmental change across scales in ecology. – Biol. Rev. 95: 1798–1811.

Rezende, E. L. and Bozinovic, F. 2019. Thermal performance across levels of biological organization. – Phil. Trans. R. Soc. B 374: 20180549.

Román-Palacios, C. and Wiens, J. J. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. – Proc. Natl Acad. Sci. USA 117: 4211–4217.

Ryo, M. and Rillig, M. C. 2017. Statistically reinforced machine learning for nonlinear patterns and variable interactions. – Ecosphere 8: e01976.

Scheffer, M. 2009. Critical transitions in nature and society. – Princeton Univ. Press.

Scheffer, M. and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. – Trends Ecol. Evol. 18: 648–656.

Scheffer, M., Hosper, S. H., Meijer, M.-L., Moss, B. and Jeppesen, E. 1993. Alternative equilibria in shallow lakes. – Trends Ecol. Evol. 8: 275–279.

Scheffer, M., Nes, E. H. van, Holmgren, M. and Hughes, T. 2008. Pulse-driven loss of top–down control: the critical-rate hypothesis. – Ecosystems 11: 226–237.

Siteur, K., Eppinga, M. B., Doelman, A., Siero, E. and Rietkerk, M. 2016. Ecosystems off track: rate-induced critical transitions in ecological models. – Oikos 125: 1689–1699.

Socolar, J. B., Epanchin, P. N., Beissinger, S. R. and Tingley, M. W. 2017. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. – Proc. Natl Acad. Sci. USA 114: 12976–12981.

Sohlström, E. H., Archer, L. C., Gallo, B., Jochum, M., Kordas, R. L., Rall, B. C., Rosenbaum, B. and O'Gorman, E. J. 2021. Thermal acclimation increases the stability of a predator–prey interaction in warmer environments. – Global Change Biol. 27: 3765–3778.

Spooner, F. E. B., Pearson, R. G. and Freeman, R. 2018. Rapid warming is associated with population decline among terrestrial birds and mammals globally. – Global Change Biol. 24: 4521–4531.

Stefan, D., Nicolas, D., Andreas, G., Michael, L., Thomas, M., Dietmar, M., A., M. C., Christoph, P., Mark, R., Wolfgang, W., E., Z. N., Karl, H. and Ingolf, K. 2015. Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. – Divers. Distrib. 21: 1375–1387.

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A. and Bates, A. E. 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. – Ecol. Lett. 18: 944–953.

Synodinos, A. D., Tietjen, B., Lohmann, D. and Jeltsch, F. 2018. The impact of inter-annual rainfall variability on African savannas changes with mean rainfall. – J. Theor. Biol. 437: 92–100.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L. and Williams, S. E. 2004. Extinction risk from climate change. – Nature 427: 145–148.

Vanselow, A., Halekotte, L. and Feudel, U. 2021. Evolutionary rescue can prevent rate-induced tipping. – Theor. Ecol. 15: 29–50.

Vanselow, A., Wieczorek, S. and Feudel, U. 2019. When very slow is too fast – collapse of a predator–prey system. – J. Theor. Biol. 479: 64–72.

Ward, D., Wiegand, K. and Getzin, S. 2013. Walter's two-layer hypothesis revisited: back to the roots! – Oecologia 172: 617–630.

Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Gauszka, A., Cearreta, A., Edgeworth, M., Ellis, E. C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J. R., Richter, D. D., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N. and Wolfe, A. P. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. – Science 351: aad2622.

Wieczorek, S., Ashwin, P., Luke, C. M. and Cox, P. M. 2011. Excitability in ramped systems: the compost-bomb instability. – Proc. R. Soc. A 467: 1243–1269.

Wilkinson, G. M., Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R. D., Buelo, C. D. and Kurtzweil, J. T. 2018. Early warning signals precede cyanobacterial blooms in multiple whole-lake experiments. – Ecol. Monogr. 88: 188–203.

Williams, J. W., Ordonez, A. and Svenning, J. C. 2021. A unifying framework for studying and managing climate-driven rates of ecological change. – Nat. Ecol. Evol. 5: 17–26.

Xu, X., Medvigy, D. and Rodriguez-Iturbe, I. 2015. Relation between rainfall intensity and savanna tree abundance explained by water use strategies. – Proc. Natl Acad. Sci. USA 112: 12992–12996.