



When and why ecological systems respond to the rate rather than the magnitude of environmental changes

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ABSTRACT

Ecologists and conservation biologists have become quite familiar with the concept of tipping points: abrupt changes in an ecosystem's state that occur after a period of relative stasis. Most of the familiar ecological examples of tipping points occur either because a once-stable state has lost stability, or the system has been subjected to a particularly large perturbation and transitions to an alternative stable state, distinct from the pre-perturbed state. A different class of tipping points, known as rate-induced tipping (or r-tipping) points, are likely present in many ecological communities but remain little known in the field. Rate-induced tipping occurs when an environmental change is too fast for the community to track; even though the original state never loses stability, the ecological response to the change is too slow to remain in that stable state's basin of attraction. R-tipping is part of the broader phenomenon of rate dependence that arises because ecological systems cannot respond instantaneously to external changes. In this article, we provide a non-technical introduction to the theory of rate dependent responses to change, discuss the implications of this theory to conservation problems, and illustrate its application through a series of case studies. When a tipping point is rate dependent, effective management relies not only on the type of intervention used but also the rate at which it is applied. Our work highlights how a mechanistic understanding of different types of tipping points leads to stronger guidance on when, where, and how different interventions can be used to achieve conservation goals.

1. Introduction

Deep integration of the non-equilibrium perspective into conservation science is essential because conditions change and ecological systems do not sit permanently at an equilibrium state. It is well understood that some of the greatest risks to biodiversity stem from the rate, as opposed to the raw magnitude, of global changes (Vitousek, 1994; Sage, 2020). When an ecosystem responds slowly to environmental change, there is the prospect that fast rates of change may lead to a sudden shift to a less desirable state. For example, models suggest that a rapid increase in fishing intensity may interact with fish behavior to cause coral reef collapse and extinction of the fish, whereas a more gradual increase

in fishing would preserve a stable system (Gil et al., 2020). Similarly, experimental data show that rapidly increasing CO₂ concentrations cause significant shifts in soil mycorrhizal communities, while community structure is preserved if the same magnitude of change is applied slowly over several years (Klironomos et al., 2005). The rate, rather than the magnitude, of change in water temperature is also suggested to determine whether or not plankton blooms in the ocean occur (Truscott and Brindley, 1994; Freund et al., 2006).

When considering how systems respond to environmental changes, much emphasis to date has been on threshold responses known as *tipping points* (see Glossary (Section 5) for definitions of italicized words). If a tipping point is crossed, we see a *regime shift* in which the dynamics and/

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or composition of an ecological community change dramatically and sometimes irreversibly (Scheffer, 2009). Ecological theory has greatly enhanced our understanding of some classes of tipping points. For instance, some tipping points occur at threshold environmental conditions under which the existence or stability of equilibrium states abruptly changes (i.e., what was an equilibrium becomes a non-equilibrium state). These threshold responses are known as *bifurcations*, and the type of regime shift they cause is called *b-tipping* for bifurcation-induced tipping. Most of the ecological literature on early warning signals of regime shifts aims to predict impending b-tipping (Scheffer et al., 2009; Kéfi et al., 2013). A second class of tipping point, known as noise-induced or *n-tipping*, addresses the possibility that a regime shift is due instead to stochastic perturbations and has also received attention in ecology (Sharma et al., 2015).

Unfortunately, the well-developed theory of b-tipping and n-tipping does not address regime shifts caused only by the rate of environmental change (Perryman and Wieczorek, 2014; Siteur et al., 2014). Rate-induced tipping, or *r-tipping*, is an entirely different beast (Scheffer et al., 2008; Wieczorek et al., 2011; Kaur and Dutta, 2022). Imagine an ecological system at some stable state, perhaps one that a conservationist would deem desirable. Environmental conditions are changing, so the stable state changes but it is still a desirable one, and the change is not enough to push the system past this stable state's breaking point (the bifurcation threshold that would cause the desired equilibrium to be lost or destabilized). Thus, b-tipping will not occur. Stochasticity is surely present, but suppose it is not enough to cause n-tipping either. Nevertheless, if the environment changes quickly enough, a regime shift can occur in which the system transitions to a different state. This is r-tipping: it is a threshold response not to the magnitude of a change, but to its rate.

Ecological r-tipping falls into a broader class of rate-dependent responses to external change (see Table 1). For example, evolutionary rescue is the phenomenon in which r-tipping is avoided through sufficiently fast adaptive evolution (relative to the rate of change in the external conditions; Vanselow et al., 2022). Shock tipping is the infinite-rate limit of r-tipping: whereas r-tipping considers both the magnitude and duration of an environmental change (i.e., the ratio of these quantities is the rate), shock tipping considers instantaneous changes and therefore asks only what its magnitude must be to trigger a regime shift (Scheffer et al., 2008). Rate-dependent responses are consequences of the fact that ecological systems cannot respond instantaneously to change and so they must be, for some amount of time, out of equilibrium. If the response is too slow, return to a pre-disturbance state can be substantially delayed or, as in the case of r-tipping, impossible without intervention. Even when return to the pre-disturbance state is possible, the rate of the external change can still have a significant impact, shaping the path the system will take during its recovery (Vanselow et al., 2022; Feudel, 2023).

It is uncontroversial in ecology that the rate of environmental change is critical to determining its impacts, yet the application of r-tipping theory and related ideas to ecological problems is in its infancy (Ritchie et al., 2022). Developing and strengthening the applications of such theory will allow us to move beyond collecting anecdotes of rate-dependent phenomena and build a more synthetic view of when rates of change pose a risk to conservation goals. With this article, we aim to illustrate the potential role of rate-dependent responses in applied problems. We begin with a general overview of the theory of tipping points and how rate-dependent responses arise. We then present three case studies that illustrate rate dependence in different conservation-relevant contexts. Because of the state of the field, we rely on theoretical models throughout this paper. Empirically documented examples of particular rate-dependent response mechanisms are scarce, and we know of no direct experimental tests of the relevant theory. We therefore hope that this broad introduction to the theory helps to motivate new empirical and empirically-driven advances in rate dependence in ecological systems, in service of the overarching goal of enhancing the

Table 1
Various types of R-tipping with corresponding ecological examples.

R-tipping scenario	Mechanism of tipping	Ecological example (s)	References
Regime shift due to a monotonic change of a parameter	Transition from a current state of the system (equilibrium/cyclic behavior) to some different state (often an extinction state) for supercritical change of a parameter.	(i) Phytoplankton growth under gradual increase of light. (ii) Regime shift of vegetation patterns in semi-arid ecosystems under climate change	(i) van der Bolt and van Nes (2021); (ii) Siteur et al. (2014)
Shock-tipping	A single supercritical perturbation can kick the system out of its state	(i) Plant-herbivore interactions. (ii) Plant-pollinator interactions over networks	(i) Scheffer et al. (2008). (ii) Halekotte and Feudel (2020)
Excitable systems	A supercritical rate results in a long excursion before finally approaching the stable equilibrium, whereas for a slow change the system remains near the equilibrium	(i) Triggering plankton blooms by fast change of environmental conditions. (ii) Emergence of compost bombs in soil	(i) Truscott and Brindley (1994), Freund et al. (2006), (ii) Wieczorek et al. (2011), Luke and Cox (2011)
Periodic variation of parameters (daily/seasonal)	(i) An increase in the amplitude of periodic forcing (or an increase in frequency of forcing) results in a faster rate of parameter variation, which generates new patterns of dynamics, for example, chaotic oscillations	(i) Plankton communities show different patterns of oscillations (in terms of amplitude and regularity) depending on the strength of seasonality. (ii) Chaotic dynamics in periodically forced chemostat	(i) Rogers et al. (2023); (ii) Sauve et al. (2020), Clodong and Blasius (2004)
Systems with impulsive control	For the same amplitude, the frequency of control determines the conditions for population persistence and survival	Impulsive control of microorganisms in chemostat	Zhang et al. (2017)
Shifting (moving) environment	A population physically follows the vital environment: a fast shift of environment results in extinction, a slow shift ensures population survival	Survival of trees and shrubs in savannas and mangrove forests under global warming depends on the availability of plants to disperse fast	Zhou and Kot (2013), Harsch et al. (2014), Tomiolo and Ward (2018)
Anti R-tipping behavior: evolutionary rescue	Fast evolution of model parameters can prevent R-tipping	Rapid evolution of life history traits in a predator-prey system promotes species survival	Vanselow et al. (2022)

use of non-equilibrium ideas in conservation practice.

2. Theory

2.1. Where and how rate dependence arises in ecology

In its most basic form, r-tipping and other rate-dependent responses

occur when the rate of an external change is too fast relative to the ecological system's capacity to respond. Previous syntheses on *long transients* in ecology already provides the foundation for understanding which types of systems may be slow to respond to external changes (Hastings et al., 2018; Morozov et al., 2020; Francis et al., 2021; Hastings et al., 2021). For example, when fast and slow dynamics are coupled – such as when a short-lived insect interacts strongly with a long-lived tree species – the resulting “fast-slow system” can exhibit very long transients, and may be particularly vulnerable to r-tipping (Perryman and Wicczorek, 2014; Siteur et al., 2016; Feudel, 2023). High-dimensional systems (those with many interacting species or classes and/or many spatially subdivided populations) are also slower to respond, and this surely contributes to the presence of r-tipping in some spatially extended systems (Chen et al., 2015). Other causes of long transient responses, such as saddle crawlby (slow passage past certain

unstable states known as saddle points; see Hastings et al. (2018) for more explanation) and ghosts (non-equilibrium states that would be stable equilibria under only slightly different conditions), are additional viable explanations for rate-dependent responses to environmental change, though they are less well-studied in this context.

Just as an ecosystem's “slow response” can arise in several possible ways, so too can the environment's “fast change”. A common way to explore r-tipping is to ask how quickly a monotonic change of a particular magnitude can occur before a regime shift is triggered. For example, Siteur et al. (2014) determined the rate of climate change that would trigger a regime shift in the vegetation patterns of semi-arid landscapes. Others have turned this question around and asked how large an instantaneous change must be to cause a regime shift (so-called shock tipping; Scheffer et al., 2008, Halekotte and Feudel, 2020). Still others have explored rate-dependence in systems experiencing periodic

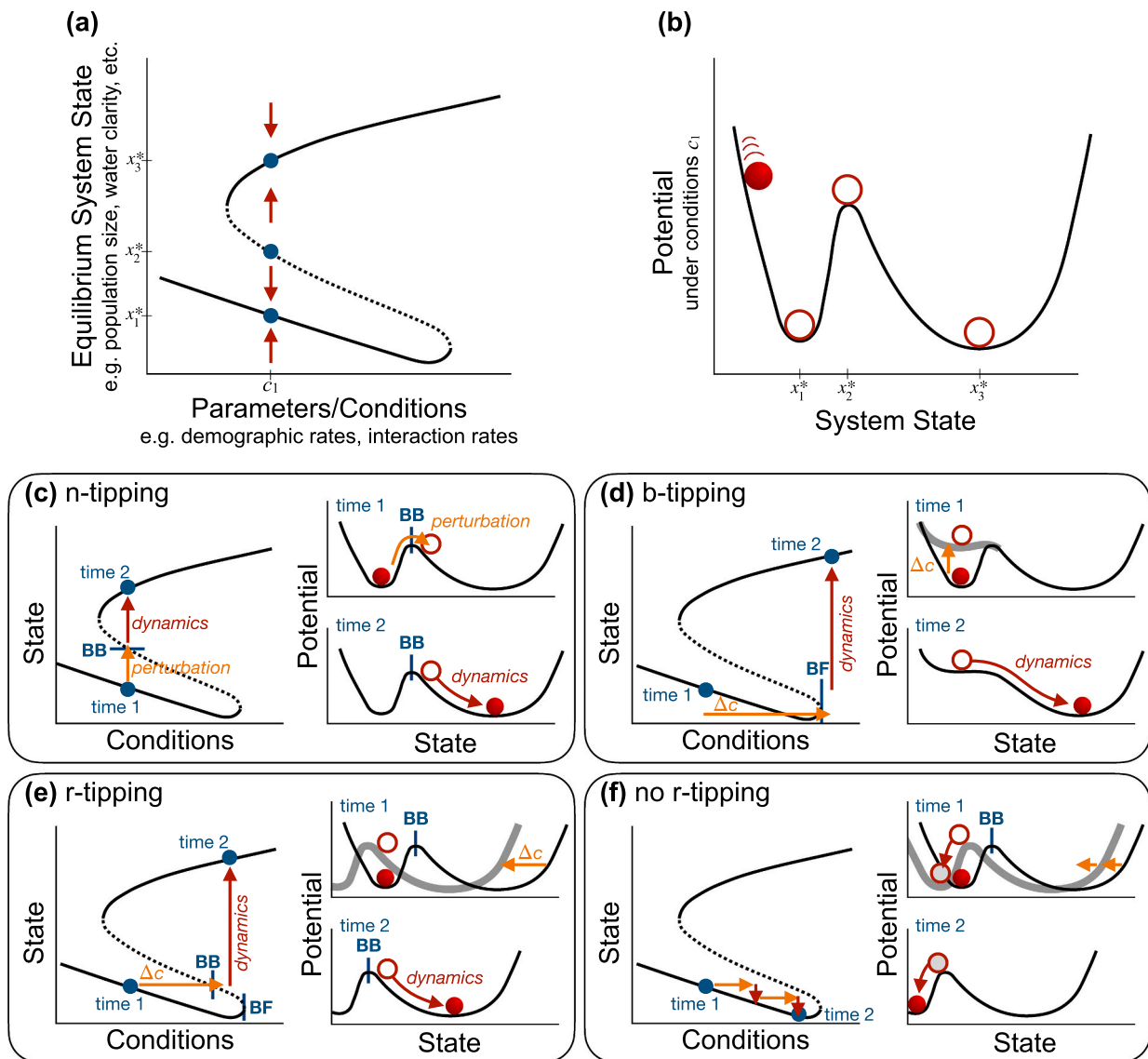


Fig. 1. Examples of (a) a bifurcation diagram and (b) a potential function for a hypothetical ecological system. The system has alternative stable states (specifically, two stable equilibria shown with solid lines and one unstable equilibrium shown with the dashed line) for an intermediate range of conditions, including the example parameter value marked c_1 in panel (a). In (a), the 3 equilibria are marked with circles while arrows indicate that the internal dynamics proceed toward stable (x_1^* or x_3^*) and away from unstable (x_2^*) equilibria. Specifically, the dynamics under condition c_1 proceed as a ball would roll on the potential surface shown in (b). The 3 open circles sit over the 3 equilibria: the states at which the ball would rest. Qualitative illustrations of the three different types of tipping points for this example are in panels (c–e), while (f) shows a lack of r-tipping to contrast with (e). On the potentials, solid balls show the state at times 1 and 2 (before and after the change that triggered tipping, respectively). Open circles show intermediate states and are repeated in the top and bottom panels to aid interpretation. See Section 2.2 for a complete explanation. Abbreviations: BB = basin boundary, BF = bifurcation point, Δc = change in conditions.

or otherwise non-monotonic changes (e.g. Rogers et al., 2023). As the amplitude of abiotic oscillations grows larger, understanding the impact of non-monotonic changes is increasingly crucial. For instance, higher annual variance in temperature necessarily means that seasonal warming and cooling must occur more rapidly, because a larger temperature oscillation must fit into the same-length year. The risk of rate-dependent responses to seasonal temperature change thus becomes elevated with higher annual variance in temperature.

2.2. Primer on tipping points

Different tipping points arise in different ways, but they can all be understood by studying an ecological system's stable and unstable equilibria (Feudel, 2023). Stable equilibria are associated with a *basin of attraction*: the set of states (e.g. population sizes) from which the stable equilibrium is approached due to the intrinsic dynamics of the system. By studying how the characteristics of both equilibria and their basins of attraction change in response to environmental change, we can understand whether a system is at risk of crossing a tipping point.

Two different types of diagrams are particularly useful for depicting how systems respond to change. The first, a *bifurcation diagram*, maps how changes in parameters or external conditions (e.g. birth and death rates, carrying capacities, etc., or the abiotic conditions that affect such quantities) change the location, presence, and/or stability of equilibrium points. The classic S-shaped bifurcation diagram for systems with alternative stable states (e.g. lake eutrophication (Carpenter et al., 1999) or herbivore outbreaks (May, 1977; Ludwig et al., 1978)) is familiar to many ecologists. The unstable equilibria are just as important in a bifurcation diagram as the stable ones, because they mark the boundaries of the basins of attraction for the stable equilibria. The logic is simplest to see in a one-dimensional system like the one shown in Fig. 1: because systems tend to move away from their unstable equilibria, any system that is currently at a state that is higher than the unstable state (e.g. $> x_2^*$ in Fig. 1a) will grow, thus preventing it from approaching a lower stable state (x_1^* in Fig. 1a). The unstable state therefore serves as the upper boundary of that lower stable equilibrium's basin of attraction. By the same logic, the same unstable state serves as the lower boundary of the next higher stable state's (x_3^* in Fig. 1a) basin of attraction.

The second type of diagram useful for understanding tipping points is the ball-in-cup or stability landscape diagrams based on the *potential function* (Fig. 1b). The potential function, $U(X)$ has a precise mathematical definition: $\frac{dU}{dX} = -\frac{dX}{dt}$ for any state variable (e.g. population size or vector of population sizes), X . Potentials – that is, functions $U(X)$ that satisfy this definition – often do not exist for multi-species ecological models, though alternatives such as the quasi-potential yield a similar interpretation (Nolting and Abbott, 2016). The potential function describes what can be thought of as the landscape on which a ball, left to roll freely, would trace out the system's internal dynamics. Since the ball would roll downhill, each well in a potential landscape corresponds to a basin of attraction for an equilibrium state that is found at its base.

Armed with these two diagrams, we can readily see how different types of tipping points arise. Noise-induced tipping (n-tipping) can occur if stochasticity pushes a system from one basin of attraction to another (Fig. 1c). An unusually large birth or death event, due to demographic noise or a warm or cold snap (or a succession of such warm/cold snaps), for example, is the type of stochastic event that could trigger n-tipping. In this example, the system begins (time 1) at the lower stable equilibrium, but a perturbation (orange arrows) moves it outside this equilibrium's basin of attraction, whose boundary is marked “BB” (basin boundary). Thus, after the perturbation, the system's dynamics (red arrows) carry it toward the higher stable equilibrium (time 2).

Note that n-tipping occurs without requiring any long-term change in the external conditions (that is, the system retained the same x -axis value in the bifurcation diagram throughout the tipping process, and the potential function also remained the same; Fig. 1c). In contrast,

bifurcation-induced tipping (b-tipping) is a response to directed external change such as a persistent trend of warming, reduced precipitation, or nutrient deposition. If conditions change in a way that alters the number of equilibria or the stability properties of the equilibria (in other words, if the conditions change such that the system crosses a bifurcation), then b-tipping can occur. This is illustrated in Fig. 1d, where a change in the conditions (orange arrows) drives the system past a bifurcation (BF) at which we switch from having three equilibria to just one. This bifurcation causes the potential function to change shape such that two of the equilibria (the lower well at x_1^* and the intermediate peak at x_2^*) are lost and the potential is left with a single well at x_3^* . The dynamics after the change thus carry the system toward this upper equilibrium, rather than returning it to the lower state, since that state is no longer a stable equilibrium under the new conditions.

In rate-dependent tipping (r-tipping), external conditions (temperature, nutrients, etc.) do change, but not in a way that causes a change in the number or stability of equilibria (O'Keefe and Wiczecek, 2020). Fig. 1e illustrates a change in conditions that is too small to cross a bifurcation point, meaning that the potential function at any of the conditions experienced during this change will have the same qualitative shape as the potential before the onset of the change. However, if the change occurs very rapidly, it can move the system outside of the lower equilibrium's basin of attraction. In a ball-in-cup diagram, picture moving the lower potential well out from under the rolling ball. A rapid change does not allow the ball enough time to respond to the change in conditions by rolling downhill back toward its original (lower) equilibrium. Instead, by the time the system responds to the change it is already in the upper equilibrium's basin of attraction, so the system tips. In contrast, if the exact same magnitude of change occurs more slowly (as illustrated in Fig. 1f), r-tipping is avoided because there is time for the internal dynamics to bring the system back toward lower stable state before the basin moves out of reach.

2.3. Context dependence and the time-varying perspective

The theory described in Section 2.2 introduced rate-dependence in terms of how basin boundaries and potentials “move” as conditions change. To do so, we treated time in a manner analogous to how animated cartoons or stop-motion films are made. The basin boundaries and potentials we drew each corresponded to a particular set of conditions along some trajectory of change. They are like the individual frames in an animation, and they correspond to the properties the system would have if we froze time at some particular point (under a particular set of conditions). Progressing through the series of “frozen-time” descriptions at different rates is an intuitive (and mathematically valid) way to understand the impact of changing conditions. However, it is not the only way. We can also consider the basin boundaries and potentials of the fully time-varying (not frozen) system, and doing so provides different insights. In Supplemental Information A, we show how to construct and interpret a potential for a time-varying physical system. We recommend that readers with an interest in time-varying potentials and those with a physics background, for whom the physical example might aid intuition, consult this supplemental material. Here, we adopt the time-varying perspective to discuss context dependence in r-tipping, before returning to the frozen-time perspective for the bulk of our case studies.

R-tipping risk is clearly tightly linked to the movement of the basin boundaries caused by changing environmental conditions. We can take a time-varying perspective to make this link explicit. Consider a pair of interacting species with alternative stable states – stable coexistence and joint extinction (Fig. 2) – separated by a basin boundary that can be described as a smooth curve (as is typical for low-dimensional dynamical systems; Hirsch, 1989, Ott, 2002, Lai and Tél, 2011). The basin boundary is a function of some parameter p (which could be a demographic rate, abiotic factor, etc.) that is changing: suppose it

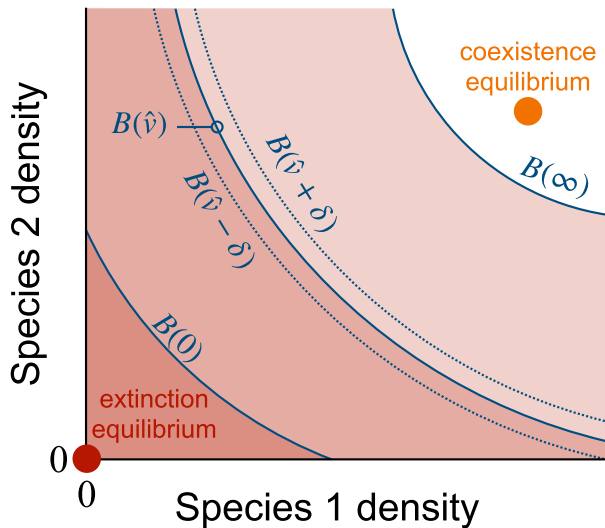


Fig. 2. Basin boundary movement in rate-induced tipping. This system has two attractors: coexistence (orange circle) and extinction (red circle). Blue curves mark the boundary between their basins of attraction, with the extinction basin shaded red. (Note that the extinction basins for the 3 solid blue curves are overlaid using semi-transparent shading, i.e., the lightest red shade is included only in the largest basin and the darkest shade occurs where all 3 basins overlap.) Conditions are described by a parameter, p that increases from p_1 to p_2 at a rate given by v . The basin boundary for any positive, finite v will lie between $B(0)$ (i.e., the boundary when p remains at p_1 indefinitely) and $B(\infty)$ (the boundary if p changes from p_1 to p_2 instantaneously). One such boundary, $B(\hat{v})$, is plotted, along with the basins for slightly slower and faster rates $B(\hat{v} \pm \delta)$ to illustrate how systems that are near the basin boundary are extremely sensitive to small changes in rate. The probability of r-tipping is related to the size of the extinction equilibrium's basin and thus increases with v , as quantitatively characterized by the scaling law (Eq. (1)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increases linearly from an initial value of p_1 to a value of p_2 at rate v . If we imagine that this change in p represents environmental degradation, we can think of the change as increasing the size of the extinction equilibrium's basin of attraction by moving the basin boundary from initially closer to the extinction equilibrium toward the coexistence equilibrium (Fig. 2).

Because the basin boundary is a function of p , its movement can be expressed in terms of how quickly p is changing (v). In the limit $v = 0$, p never changes and the basin boundary remains wherever it sits for $p = p_1$ (that is, $v = 0$ means the system is frozen at p_1). This boundary is labeled $B(0)$ in Fig. 2 since it corresponds to the $v = 0$ case. At the other extreme, p changes infinitely quickly ($v \rightarrow \infty$) and $B(\infty)$ sits at the boundary for $p = p_2$. For any positive but finite rate of change \hat{v} , the corresponding $B(\hat{v})$ sits between $B(0)$ and $B(\infty)$ (Fig. 2).

The risk of r-tipping from coexistence to extinction decreases with the size of the coexistence equilibrium's basin of attraction – that is, tipping to extinction is less of a liability when the coexistence equilibrium's basin is large. We quantify r-tipping risk as the proportion of the $B(0)$ basin's area (or, in higher dimensions, volume) that falls between $B(0)$ and $B(\hat{v})$. The rationale is that, without any change in p , $B(0)$ delineates the coexistence equilibrium's basin of attraction. Any population densities that fall between this $B(0)$ and the boundary $B(\hat{v})$ will switch from being in the coexistence basin to being in the extinction basin if conditions change at rate \hat{v} . Therefore, the larger the area between $B(0)$ and $B(\hat{v})$, the higher the risk of r-tipping.

Analyses by Panahi et al. (2023) show that R-tipping risk (Φ) scales with the quantity $T = \frac{p_2 - p_1}{v}$, which is the time required for conditions to undergo the change from the initial p_1 to some $p_2 \neq p_1$, according to,

$$\Phi \sim \exp(-CT), \quad (1)$$

where C is a positive constant that depends on the system details (Panahi et al., 2023). This scaling law has been tested and validated (Panahi et al., 2023) using a number of empirical mutualistic networks of pollinators and plants (Bascompte et al., 2003; Guimaraes et al., 2011; Nuismer et al., 2013; Lever et al., 2014; Rohr et al., 2014; Dakos and Bascompte, 2014; Guimaraes et al., 2017; Jiang et al., 2018, 2019; Meng et al., 2020; Ohgushi et al., 2012), verifying that the results described here for a two-species system successfully scale to much larger communities.

The scaling relationship in Eq. (1) contains the intuitive result that the faster the environmental change (i.e., the shorter its duration), the higher the r-tipping risk. It also reveals that the strength of this effect decreases with v (that is, $d\Phi/dv$ is a decreasing function of v). In other words, the r-tipping risk increases the most steeply when v is increased from 0 to something small, and there is less and less of an impact of increasing v if v is already large ($v \gg \sqrt{p_2 - p_1}$). Consequently, interventions that slow a rapidly changing environmental factor could have virtually no protective effect unless the rate can be brought relatively close to zero.

Mapping out the basin boundaries as in Fig. 2 helps us see that whether or not a particular rate of change will trigger r-tipping depends in part on the prior history of the system. A system that starts out close enough to the coexistence equilibrium at the onset of the change can remain in its basin of attraction even as the basin boundary retracts quickly. However, a system that happens to be at a more intermediate state between the two stable equilibria at the onset of change can experience dramatically different outcomes with only miniscule differences in the rate of change. For an initial condition along $B(\hat{v})$, say, r-tipping will occur if the rate is even slightly faster than \hat{v} ($\hat{v} + \delta$ for a small value δ), but will not occur for a rate just slightly slower ($\hat{v} - \delta$). There is thus a clear dependence on historical context underlying r-tipping risk: the history and dynamics before any environmental change will determine the pre-disturbance distribution of states and thus the vulnerability to r-tipping under any given rate of change.

3. Conservation case studies

In Section 2.1, we explained how r-tipping results from the fact that ecological systems cannot instantaneously track environmental changes, and in Section 2.2 we suggested that this may be thought of as a basin of attraction moving out from under the current system state. Section 2.3 made explicit that a system's state at the beginning of a change (i.e., the ecological context) has a major impact on its risk of r-tipping: a system whose history has brought it close to the basin boundary will tip much more readily than one in the basin's interior. In the case studies that follow, we study r-tipping in a range of settings, spanning different drivers of tipping, different contexts, and different conservation problems.

3.1. Response to environmental degradation

To begin connecting the theory in Section 2 to the natural world, consider a population with an Allee effect in which the quality of the environment in part determines the minimal population size (Allee threshold) necessary for positive population growth. Plants in arid landscapes may show this type of pattern if a higher density of plants is required to retain favorable levels of soil moisture as external conditions become drier, for example. A general model for population growth with an Allee effect is,

$$\frac{dN}{dt} = rN(N - \beta)(1 - N), \quad (2)$$

where N is the population density (measured in units such that $N = 1$ at

carrying capacity), r is the intrinsic growth rate, and β is the Allee threshold.

To represent the effect of environmental degradation on the Allee threshold, we define β_0 as the historical Allee threshold (i.e., the pre-degradation boundary between the extinction and persistence basins). We then imagine that an acute stressor, such as a severe drought, causes an initial phase of rapid population decline that moves the population toward this basin boundary. If management actions are taken to restore the Allee threshold to some level β_1 , that may be only slightly higher than β_0 , the populations may be able to recover. Given enough time in the new environmental regime, the Allee threshold will settle onto β_1 but it takes some time to do so. Specifically, using the parameter k to represent how quickly the Allee threshold tracks changes in the environment,

$$\frac{d\beta}{dt} = -k(\beta - \beta_0). \quad (3)$$

Solving Eq. (3) yields,

$$\beta(t) = (\beta_0 - \beta_1)e^{-k(t-t_0)} + \beta_1, \quad (4)$$

where t_0 is the time at which management to establish the new Allee threshold at β_1 was initiated.

Simulating Eqs. (2)–(3) shows how a small increase in the Allee threshold can result in population extinction due to r-tipping if the population dynamics is too slowly relative to the environmental tracking rate, k . Following an initial acute decline (the segment labeled 1 in Fig. 3) that brings the population below β_1 , recovery comes down to a race between the Allee threshold's rise toward β_1 and the population's ability to grow and stay above the current Allee threshold, $\beta(t)$. If population growth is fast enough relative to k that it can clear β_1 before the Allee threshold has fully adjusted to the new environmental regime, then recovery occurs (cases 2–4 in Fig. 3). However, in case 5, k is higher and the population cannot restore itself fast enough to stay above the Allee threshold. In this case, extinction due to r-tipping occurs.

In addition to illustrating r-tipping, this case study provides an interesting perspective on which rates are key. Here, it is not the rate at

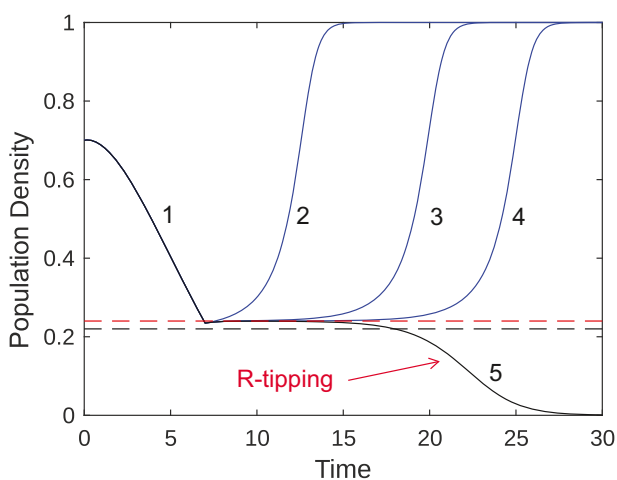


Fig. 3. Population density versus time for different rates of the environment relaxation k . The initial decline (line 1) reflects the impact of an acute stressor prior to the initiation of mitigation, and is common to the four alternative scenarios (lines 2–5) that follow. Lines 2–5 show the fates of populations with different rates of tracking the new Allee threshold ($k = 0.01$, $k = 1.4$, $k = 1.475$, and $k = 1.5$ for lines 2–5 respectively). When tracking is too fast, relative to the population's ability to grow remain above the Allee threshold, r-tipping occurs (line 5). The red and black dashed horizontal lines show, respectively, the new (β_1) and the original (pre-disturbance β_0) values of the Allee threshold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

which the environment itself changes that is important; in fact, we could transition from the historical environmental regime (characterized by an Allee threshold at β_0) to the new managed regime (with conditions that yield Allee threshold β_1) instantaneously and r-tipping might still be avoided. Instead, it is the rate at which the ecological system tracks this change (encapsulated in our parameter k), relative to the population growth rate, that determines whether r-tipping occurs.

3.2. Invasive species control

We now consider a conservation scenario that is simple enough to yield a completely tractable model so that we can more fully illustrate how the theory can be applied. In this example, imagine an invasive species that is subject to removal (for control) at rate h . We can write the population dynamics of this invader as,

$$\frac{dN}{dt} = f(N - L) - h, \quad (5)$$

where N is the population density, L is the no-removal baseline (i.e., the equilibrium density in the absence of removal), and $f(N - L)$ describes density dependence as a function of how far the population is from this no-removal equilibrium. Adapting a model studied by Ashwin et al. (2012) and Siteur et al. (2016) for our purposes, we will use $f(N - L) = (N - L)^2$.

This model has one stable equilibrium at $N_1^* = L - \sqrt{h}$ with a basin of attraction whose lower limit is $N = 0$ and upper limit is the unstable equilibrium point, $N_2^* = L + \sqrt{h}$. Outside this basin of attraction ($N > L + \sqrt{h}$), this model makes the unrealistic prediction that the population can grow infinitely large. This could be remedied by modifying $f(N - L)$, but to keep our example as simple as possible, we simply conclude that invasive species control has failed if we cannot keep the system within the basin of attraction of its lower equilibrium, N_1^* .

This scenario provides two possibilities for invasion control: increasing the removal rate (increasing h) or making the habitat less hospitable to the invader (decreasing the no-removal baseline density, L , e.g. by manipulating nutrients, pH, or some other condition that limits invader density). Increasing removal effort has the straightforward effect of reducing equilibrium invader density (Fig. 4a). Importantly, removal can be ramped up as quickly as is feasible with no risk of r-tipping. We can see this in Fig. 4a by noting that there is no horizontal path through the bifurcation diagram that begins in N_1^* 's basin of attraction but ends outside of it. There is thus no possible change in h – even one so fast that it is finished before the population density has responded at all (this would correspond to a horizontal path: change only in h with no concurrent change in N) – that places the population outside of N_1^* 's basin of attraction. The system can thus track N_1^* as the removal rate increases, no matter how fast the increase, and control is successful.

Note, however, that the removal rate h appears in a square root in the expression for N_1^* while the no-removal baseline L does not, suggesting that you could get a bigger return on investment if you can reduce L . So, should reducing habitat quality for the invader be the favored strategy? Perhaps, as long as L is not reduced too quickly. However, decreasing L comes with a risk of r-tipping (Fig. 4b): if L declines too quickly for the population to respond ($\frac{dL}{dt} = -\nu$ with a large enough ν), we lose control of the invasion (Fig. 4c). However, the exact same magnitude of reduction in L applied more slowly (smaller ν) allows the population to remain stably controlled close to N_1^* (Fig. 4d).

So, how fast of a drop in the no-removal baseline density, L , is too fast? Following Ashwin et al. (2012), we can answer this question with the aid of a *moving frame variable* that tracks population density relative to the decreasing baseline, L . Specifically, we define $y(t) = N(t) - L(t)$, which has dynamics $\frac{dy}{dt} = \frac{dN}{dt} - \frac{dL}{dt} = y^2 - h + \nu$. This moving frame variable has a stable equilibrium at $y = -\sqrt{h - \nu}$ which, given how we

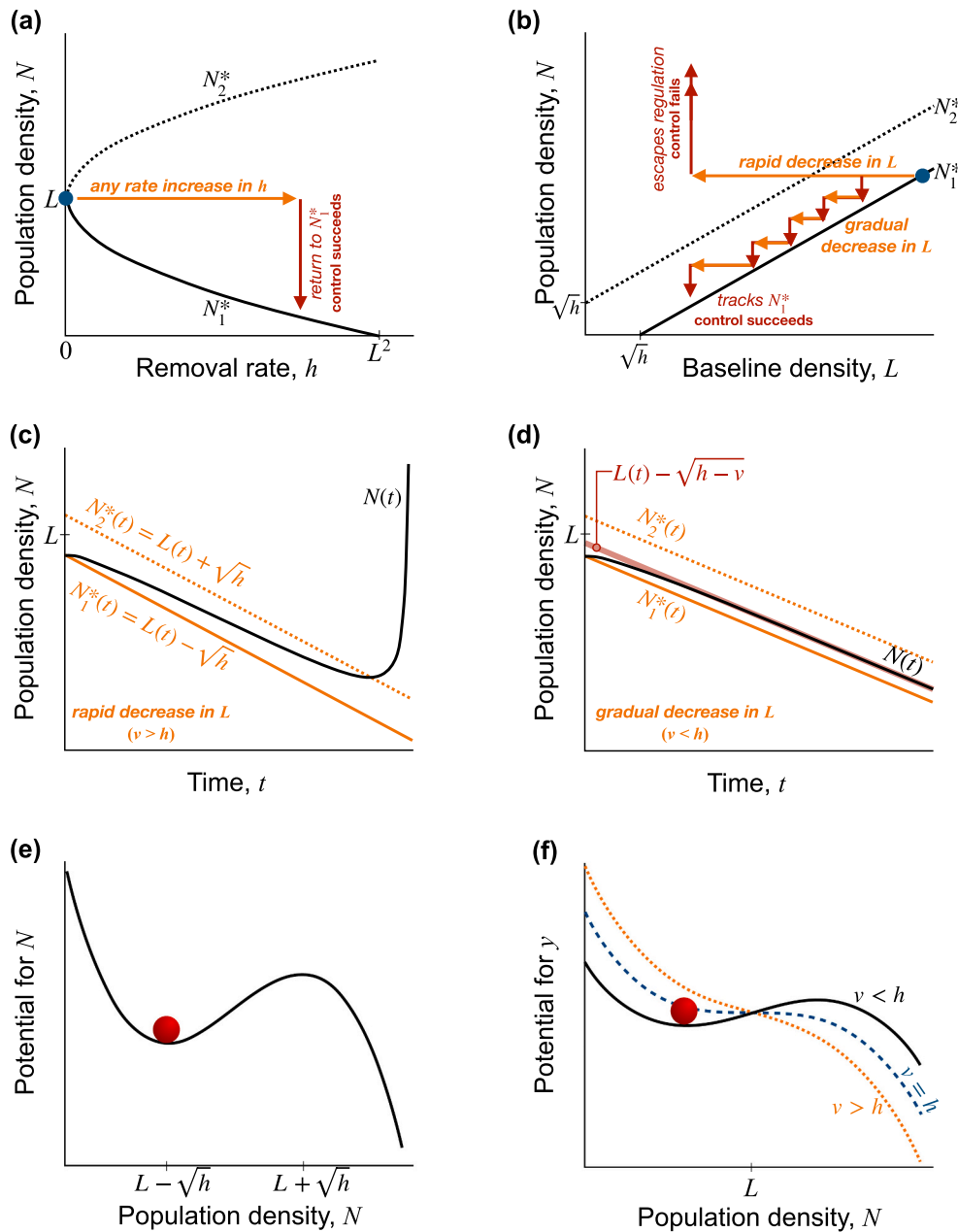


Fig. 4. Summary of r-tipping risk in an invasion example (Eq. (5)). (a–b) Bifurcation diagrams showing that r-tipping cannot occur with increases in the removal rate h , but could occur with fast enough decreases in the baseline density L . (c–d) Time series showing (c) r-tipping when the rate of decrease in the baseline density, v , exceeds the critical rate h , but (d) no r-tipping when the exact same change is made more slowly. In both, $h = 2$, $L(0) = 25$, and $N(0) = L(0) - \sqrt{h} = N_1^*(0)$; in (c) $v = 2.25$ and in (d) $v = 1.75$. Orange lines mark the equilibria (stable and unstable) of N , which change through time as L changes. The red line in (d) marks the stable equilibrium of the moving frame variable y . (e–f) Potential functions, showing that the potential for N under any fixed set of parameter values always has a well corresponding to the stable equilibrium at $L - \sqrt{h}$, but that the potential for y only has a well when $v < h$. Without a low-density well to attract the dynamics, the population grows, escaping control. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

defined y , corresponds to $N(t) = L(t) - \sqrt{h - v}$. For $v < h$ (change in L that is slower than the invasive removal rate), this value of $N(t)$ is slightly higher than the stable equilibrium density (now time-dependent due to changing L), $N_1^*(t) = L(t) - \sqrt{h}$. If we avoid r-tipping, as in Fig. 4d, the population is drawn toward $N_1^*(t)$. However, because this stable equilibrium continues to move away, the population doesn't quite catch it – instead, it settles onto $N(t) = L(t) - \sqrt{h - v}$, which is the equilibrium corresponding to the moving frame variable. Siteur et al. (2016) refer to this as the “steady lag” of the actual system state relative to where it would equilibrate without any ongoing change. When $v > h$, the moving frame equilibrium no longer exists (i.e. it is no longer a real

number) so the population cannot converge to it and r-tipping occurs such that the invader grows out of control. So, in our simple example, we can derive the critical rate of change in L beyond which invasion control fails: the no-removal baseline density must be changed more slowly than the removal rate h to keep this invader in check. By extension, increasing the removal rate would permit faster reductions in the baseline density L without r-tipping.

This example also allows us to see a connection between b-tipping and r-tipping (Siteur et al., 2016; Ashwin et al., 2017). This model cannot b-tip for $h, L > 0$ because the dynamics for N described by Eq. (5) has no bifurcation in that parameter range. The frozen potential function

for N always has a well at the stable equilibrium $N_1^* = L - \sqrt{h}$ (Fig. 4e). However, the moving frame variable y does have a bifurcation in response to parameter changes. Specifically, at the critical rate $\nu = h$, this time-varying potential function for y loses its well and the system no longer has a stable equilibrium that corresponds to successful invasion control (Fig. 4f). A ball rolling on the potential landscape for $\nu \geq h$ has no alternative but to roll toward $N \rightarrow \infty$ and uncontrolled invader growth.

In more complex models, solving for the critical rate of change at which r-tipping will occur is significantly more difficult. When the change occurs over a finite time interval, various analytical strategies can be used to make the problem of finding the critical rate tractable (Wieczorek et al., 2021). Broadly speaking, r-tipping is a risk when the external change is fast relative to the rate at which the system can respond to change (Siteur et al., 2016). Importantly, the system's response rate may be much slower than any of the component demographic rates, so a change that appears (when, for example, comparing it to a birth or death rate) to be quite slow may still be too fast to avoid r-tipping (Vanselow et al., 2019).

3.3. Human-ecological systems

For our final case study, we introduce a scenario that captures the interactions between the socio-economic and ecological dynamics involved in harmful phytoplankton blooms. The model (discussed and analyzed in detail in Heggerud et al., 2022, and summarized in Supplemental Information B) uses a stoichiometric approach to modeling phytoplankton dynamics in a lake, coupled with a model of human decision making that determines pollution levels. The biomass, B , and internal nutrient ratio, Q , of the phytoplankton are influenced by phosphorus levels in the water, P . Phosphorus levels are in turn influenced by the proportion, F , of the human population near the lake that is cooperating with anti-pollution measures aimed at limiting phosphorus runoff into the lake. Those who are not cooperating with these measures are referred to in this model as defectors.

We assume that the rate at which an individual change strategies is relatively slow (on the order of years) while the ecological dynamics have a timescale that is the order of days or weeks. Hence, we expect the ecological dynamics (phytoplankton biomass, B , internal nutrient ratio, Q , and water phosphorus level, P) to be in a quasi-steady state that is dependent on the current proportion of cooperators (F). The quasi-steady state is given in Supplemental Information B, and the corresponding social dynamics is given by,

$$\frac{dF}{dt} = \frac{s}{1 + e^{\beta(C_{\mathcal{C}} - C_{\mathcal{D}})}} - sF, \quad (6)$$

where s describes the rate at which individuals change strategies and $C_{\mathcal{C}}$ and $C_{\mathcal{D}}$ represent the cost of the cooperator and defector strategies, respectively. The parameter β scales how sensitive people's strategy decisions are to these costs.

The costs associated with each strategy are described by

$$C_{\mathcal{C}}(F, B) = \underbrace{c_{\mathcal{C}}}_{\text{baseline cost}} + \underbrace{\phi B}_{\text{cost of bloom}} + \underbrace{\delta_{\mathcal{C}}}_{\text{social norm pressure}} + \underbrace{\alpha(1 + \xi F)\psi B}_{\text{social ostracism}} \quad (7a)$$

$$C_{\mathcal{D}}(B) = \underbrace{c_{\mathcal{D}}}_{\text{baseline cost}} + \underbrace{\phi B}_{\text{cost of bloom}} + \underbrace{\delta_{\mathcal{D}}}_{\text{social norm pressure}}, \quad (7b)$$

which include costs associated with both social pressures and negative impacts of a phytoplankton bloom (see Table B1 for additional parameter definitions). The social pressures are split into social norms, through which people tend to adopt behaviors that conform with those around them or broader society, that affect both groups and an additional cost of ostracism sensu Poon et al., 2015 that may be experienced by individuals adopting non-environmentally favorable behaviors (Heggerud et al., 2022).

Because F is a function of the difference between the costs of cooperation and defection, we rewrite this difference as,

$$C_{\mathcal{C}} - C_{\mathcal{D}} = c_{\mathcal{C}} - c_{\mathcal{D}} + \delta_{\mathcal{C}} - \delta_{\mathcal{D}} - \alpha(1 + \xi F)\psi B = \eta - \sigma(1 + \xi F)B, \quad (8)$$

where $\sigma = \alpha\psi$ represents the overall cost conversion coefficient due to social pressure and concern for phytoplankton blooms and $\eta = c_{\mathcal{C}} - c_{\mathcal{D}} + \delta_{\mathcal{C}} - \delta_{\mathcal{D}}$ represents the cost differences between strategies for the baseline cost and social norm costs. Large η corresponds to high cost of participating in anti-pollution measures and/or a low cost of noncompliance.

One potential management strategy for controlling phytoplankton blooms is to implement policy that includes fines to increase the cost of defection or incentives that lower the cost of cooperating. Publicity campaigns that strengthen anti-pollution social norms might also be implemented. We can capture such changes by writing the parameter η in Eq. (8) as a function of time, $\eta_{\min} < \eta(t) < \eta_{\max}$, where η_{\min} and η_{\max} are bifurcation points discussed in detail in Heggerud et al. (2022). By keeping $\eta(t)$ between these bifurcation points, we eliminate the possibility of b-tipping in response to changing η and focus instead on the potential for rate dependence in the response to changing costs. Within the $\eta(t)$ range we allow here, the system has alternative stable states with either a low or high level of cooperation (low F and high F , respectively).

Policy changes can move the system from an intermediate state to the high-cooperation state either by exploiting r-tipping or by avoiding it, depending on the situation. If incentives to cooperate and/or fines for defection are considered excessive and policy makers choose to relax them, the relative cost of cooperation compared to defection, η , increases. A continual increase in $\eta(t)$ can be written as,

$$\eta(t) = \begin{cases} \eta_{\min} + \epsilon + \nu t & \text{while } \eta(t) < \eta_{\max} - \epsilon \\ \eta_{\max} - \epsilon & \text{otherwise,} \end{cases} \quad (9)$$

where ν is the rate of the increase and ϵ is a small parameter to ensure that η never reaches the bifurcation points at η_{\min} and η_{\max} . As long as η is increasing slowly enough (small ν), the system approaches the high-cooperation state (Fig. 5a). However, reducing incentives or fines too quickly induces r-tipping to the low-cooperation state.

In the above scenario r-tipping undermined the management objective, but r-tipping is not always problematic. If incentives to cooperate or increase fines for defecting are low and policy makers increase them, $\eta(t)$ decreases:

$$\eta(t) = \begin{cases} \eta_{\max} - \epsilon - \nu t & \text{while } \eta(t) > \eta_{\min} + \epsilon \\ \eta_{\min} + \epsilon & \text{otherwise.} \end{cases} \quad (10)$$

Here, too slow a change (small ν) causes the system to approach the low-cooperation state, but with a faster policy change, the system can r-tip into the high-cooperation state (Fig. 5b). In this scenario, r-tipping is not a phenomenon to avoid but rather a management tool to be exploited!

As we mentioned in Section 2.1, increasing the amplitude of an oscillating parameter could effectively generate rate dependence by forcing a larger change to occur over the same period of time. To conclude this case study, we consider costs that fluctuate periodically due to seasonality in social norms and associated costs. For instance, social pressure may be greater in summer when neighbors interact more frequently, and phytoplankton blooms may be more costly during peak seasons for fishing and recreation. We reflect this seasonality by using a periodic function for η . We set the period of oscillation to either 1 or 2 years and use the parameter a to govern the amplitude of oscillation, while ensuring $\eta_{\min} < \eta(t) < \eta_{\max}$ at all times.

In Fig. 5c-d we observe that the amplitude of oscillation indeed influences outcomes, but not in an entirely straightforward way. Fig. 5d confirms that increasing the amplitude of annual oscillations in η can indeed trigger r-tipping to the low-cooperation state. On the other hand,

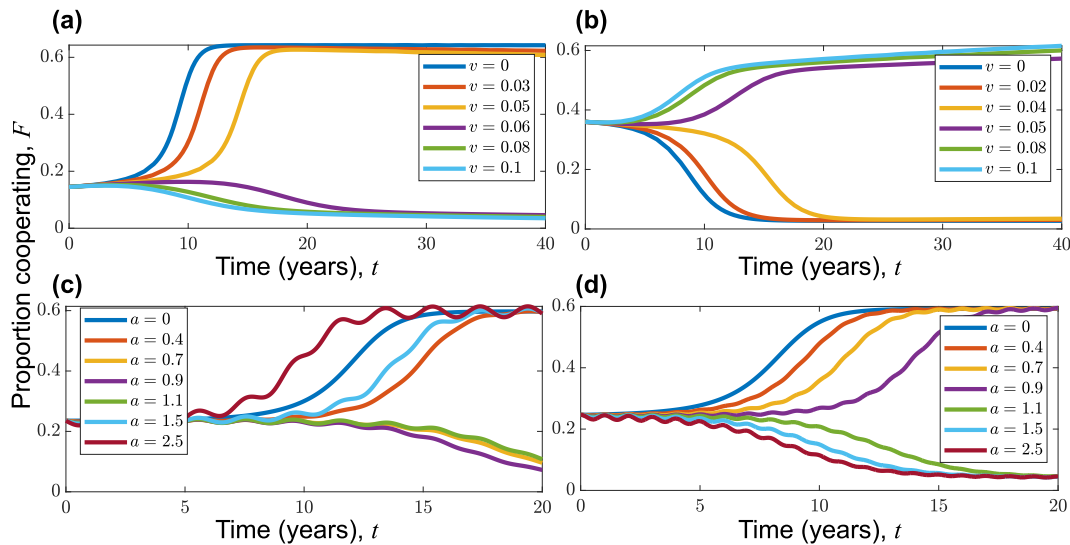


Fig. 5. Dynamics of human behavior in the human-ecological system case study. **(a)** Detrimental r-tipping to the low cooperation state occurs if η is monotonically increased too quickly (faster than a threshold ν that lies between 0.05 and 0.06). **(b)** Beneficial r-tipping to the high cooperation state occurs if η is monotonically decreased quickly (threshold between 0.04 and 0.05). **(c–d)** R-tipping to the low-cooperation state for some amplitudes (a) of periodic oscillations in η . The oscillation period is 2 years in (c) and 1 year in (d).

with longer period of 2 years (Fig. 5c), it is only the intermediate amplitudes for which cooperation is lost. The lack of r-tipping with low-amplitude oscillations is expected, but its absence at high amplitudes was a surprise. We conjecture that systems with high amplitude oscillations are rescued from r-tipping by the fact that gains in cooperation during phases of low η exceed losses during phases of high η via a nonlinear averaging effect (see Supplemental Information B). Clearly, the role of oscillation amplitude in generating rate-dependent responses warrants further research.

4. Discussion

In this article, we have presented an overview of the theory for rate dependence in how ecological systems respond to environmental change, and we have illustrated its application in conservation biology via a range of case studies. This formalism allows us to move beyond our already strong anecdotal understanding *that* rates of change are important toward a synthetic understanding of *why* and thus knowing how to mitigate undesirable responses to change.

When we wish to avoid a tipping point, or reverse a regime shift that has already occurred, it is vital that we know which kind of tipping point is present. We can only “put the ball back in the cup” if the cup still exists and if we understand where its edges are. In a sense, r-tipping tells a more optimistic story than b-tipping because with r-tipping, we have not lost the original basin of attraction. A sufficiently large one-time restoration actions or a sequence of directed smaller actions q that moves the system back into that basin could be sufficient for the internal dynamics to once again sustain that stable state. Rate-related conservation actions, such as reducing pace of change of important drivers, may, in addition be more palatable and feasible than stopping or reversing the causal activity.

Some instance of r-tipping might even give us time to preempt tipping via a very small one-time intervention. For example, the doomed population 5 in Fig. 3 could have been rescued by a small input of individuals during the long transient ($t \approx 8 - 15$) before the final decline. In low dimensional systems like this one – in which intra-population density dependence is strong relative to interactions with other species or populations in other habitat patches – r-tipping often occurs when the system crosses a saddle point (an unstable equilibrium like the Allee threshold in this example). Passage by a saddle tends to be slow

(Hastings et al., 2018), creating more time for small interventions to be effective. However, in higher dimensional systems (e.g. strongly-interacting species), saddle points have a set of states (called the stable manifold) from which the saddle is initially approached, before ultimately moving away. This phenomenon may actually promote r-tipping, as movement along the stable manifold draws the system closer to a saddle on the basin boundary (Feudel, 2023). In either case, though, understanding the basic dynamical features of the system, such as its stable and unstable equilibria (including saddles) and the geometry of their basins of attraction are key to both understanding r-tipping risk and identifying strategic interventions. In this way, pairing real-world problems with validated models is a powerful approach.

There is, of course, much work left to be done and we hope this article inspires some of that work. On the empirical side, clear demonstrations of rate dependent responses and r-tipping will be instrumental in strengthening links between theory and applications. On the theoretical side, most work to date has considered changes that occur at a constant rate over a finite interval of time, usually in a fast-slow system in which the part of the system with slow dynamics is responsible for the rate dependence. More work on other types of change (such as the oscillations considered in our final case study) and other causes of slow responses to change would be fruitful. Additionally, though much progress is possible through the use of deterministic models, theory built upon stochastic models – particular those with realistic but often neglected noise forms like red (positively autocorrelated) noise and bounded perturbations – will be needed to fully connect theoretical ideas to the real world.

5. Glossary

Basin of attraction: The set of states from which a particular stable equilibrium is attractive. For a given set of parameters (i.e. under a given set of conditions), a system tends to remain within the same basin of attraction even in the face of small magnitude disturbance.

Bifurcation: A change in the stability or existence of one or more equilibria with a change in parameter (such as an environmental factor).

Bifurcation diagram: A visual representation of how a change in a parameter value changes the location, presence, and stability of equilibria.

B-tipping, or bifurcation-induced tipping: A qualitative change in

the system's state or behavior (i.e. a regime shift) caused by crossing a bifurcation.

Long transient: A state or pattern of population dynamics that differs from the equilibrium or asymptotic state and lasts long enough (roughly dozens of generations or more) to be ecologically meaningful.

Moving frame variable: A dynamic quantity that tracks how a systems state is changing relative to a reference point, such as a property of the changing environment. Defining an appropriate moving frame variable aids in the interpretation of r-tipping risk, because the moving frame variable (but not the original state variable) undergoes a bifurcation at the critical rate of change.

N-tipping, or noise-induced tipping: A change in system behavior that occurs as a result of a sufficiently large disturbance (i.e., noise) which pushes the system out of its original basin of attraction.

Potential function: A mathematical description of a dynamical system that summarizes how the state of the system changes as a function of the current state. When we picture dynamics as a ball rolling on a surface, the potential is that surface. When a potential does not exist (as is the case in many ecological models with more than one species), extensions such as the quasi-potential can be used instead.

R-tipping, or rate-induced tipping: A change in system behavior that occurs when a parameter changes too quickly for the system to track the change to remain in the basin of attraction. This change in dynamic behavior occurs even though the original equilibrium state retains its stability.

Regime shift: A sudden, qualitative change in the state of a system. "State" here may refer to a population size, a community configuration, or some other property that summarizes a community's composition, structure, or function.

Tipping point: Threshold parameter values or magnitudes of disturbance that move a system to a new state (i.e. cause a regime shift).

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CRediT authorship contribution statement

Karen C. Abbott: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Christopher M. Heggerud:** Conceptualization, Formal analysis, Writing – review & editing. **Ying-Cheng Lai:** Conceptualization, Formal analysis, Writing – review & editing. **Andrew Morozov:** Conceptualization, Investigation, Writing – review & editing. **Sergei Petrovskii:** Conceptualization, Formal analysis, Writing – review & editing. **Kim Cuddington:** Conceptualization, Writing – review & editing. **Alan Hastings:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplemental information A: how fast is too fast? - a physical example

Potential landscapes (see Section 2.2) allow us to understand ecological dynamics by using our intuition from the physical world, and we can exploit that intuition further in a time-varying context to see what determines the critical rate of change that triggers r-tipping. Consider first an extremely simple frozen potential function consisting of two lines that meet at a point corresponding to the stable equilibrium (Fig. A1a). The simplicity of this potential means that we can fully describing it using a single parameter, α , that describes the steepness of the lines (the left wall has slope $-\alpha$ and the right has slope α). A ball positioned at the minimum of the potential is of course at rest. Now imagine moving the entire V-shaped potential to the left with acceleration a . For the ball to retain its horizontal position and maintain contact with the potential surface, this movement pushes the ball up the potential wall. The potential energy, $U(x)$, of a ball at horizontal position x is governed by two opposing forces. The movement of the potential generates a non-inertial force proportional to a . The gravitational force on the ball (g) contributes another term to the potential energy that is proportional to the ball's height $h(x) = x \tan(\alpha)$, reflecting the influence of the slope of the potential's walls. The potential function of the time-varying system is then,

$$U(x) = (g \tan(\alpha) - a)x, \quad (11)$$

given negligible friction between the ball and the ramp.

Net leftward movement of the ball is necessary if it is to remain near the stable equilibrium since the potential, and the stable state along with it, is moving left. Thus, r-tipping is avoided as long as the potential energy decreases when the ball moves left (i.e. as its horizontal position x decreases). Stated mathematically, r-tipping is avoided if $\frac{dU}{dx} = g \tan(\alpha) - a > 0$. The critical rate of change that triggers r-tipping is then the value of a at which $\frac{dU}{dx}$ crosses 0; this threshold is $a = g \tan(\alpha)$. This simple relationship shows that the critical rate of change is directly related to the steepness of the potential: a system whose potential has steeper walls can withstand a faster external change without r-tipping.

This idealized potential well with linear walls can be extended to the more general case of a nonlinear potential with arbitrary shape (Fig. A1b). The potential can still be written $U(x) = gh(x) - ax$, but the height at position x , $h(x)$, is no longer $x \tan(\alpha)$ (the relationship for a ball on an incline with slope α) but rather some other function. The law of conservation of energy gives us the velocity of the ball, r , as potential energy is converted to kinetic energy:

$$\frac{r(x)^2}{2} = -U(x) = ax - gh(x) \quad (12)$$

$$r(x) = \sqrt{2(ax - gh(x))}. \quad (13)$$

The ball must have a real-valued velocity in order to remain within the basin of attraction when the basin moves. Thus, when the expression inside square root of Eq. (12) is non-negative, r-tipping is avoided. The r-tipping threshold is therefore $a = gh(x)/x$.

Unlike the simplified V-shaped potential with linear walls, we see that the r-tipping threshold is now a function of x , and is not simply a function of the slope of the potential walls. This confirms the importance of starting position (historical context) in determining r-tipping risk. Nevertheless, we can still examine slopes to determine the impact of different rates of change. If it is possible for the ball to come to rest at a finite location x^* , then $r(x^*)$ must be 0 and so $ax^* = gh(x^*)$. In other words, the two forces (movement of the potential and gravity) must balance for the ball to come to rest, so if x^* exists, it is the point where the potential surface ($h(x^*)$) intersects a line with slope a/g that passes through the stable state. The existence of a resting point x^* means that the acceleration of the potential (the external change) is not large enough to push the ball up the steep slope, and r-tipping is avoided (as in line 1 in Fig. A1b). However, for larger acceleration and/or a shallower potential wall, no such finite x^* exists and r-tipping occurs (Fig. A1b line 3).

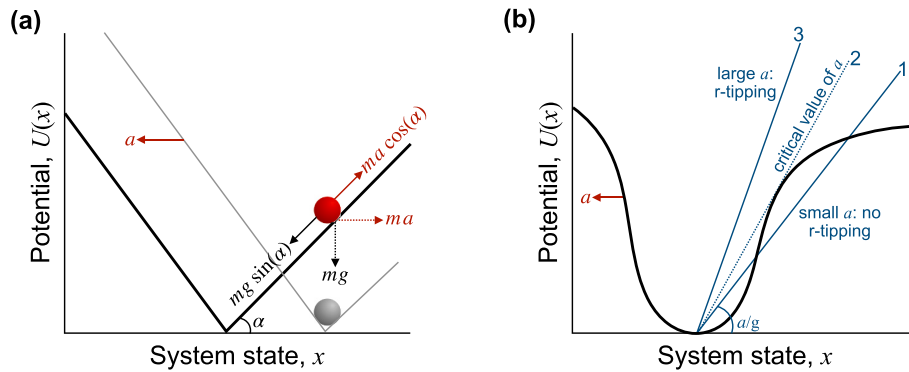


Fig. A1. A simple framework for understanding critical rates. (a) A V-shaped potential that moves left with acceleration a puts a force on the ball proportional to a (and the ball's mass m). The balance between this force and gravity, as mediated by the slope of the potential wall α , determines whether r-tipping occurs (the ball cannot achieve net downhill motion against the motion of the potential) or not. (b) Generalization to a potential with non-linear walls. R-tipping is avoided when the potential moves slowly enough that a line with slope a/g (where g is the gravitational constant) has an intersection point with the potential wall (line 1). Above a critical rate (line 2), r-tipping occurs (line 3).

Appendix B. Supplemental information B: human-ecological system case study

The dynamics of the entire system underlying our human-ecological case study are given by,

$$\frac{dB}{dt} = rB \left(1 - \frac{Q_m}{Q}\right) h(B) - \nu_r B - \frac{D}{z_e} B, \quad (14a)$$

$$\frac{dQ}{dt} = \rho(Q, P) - rQ \left(1 - \frac{Q_m}{Q}\right) h(B), \quad (14b)$$

$$\frac{dP}{dt} = \frac{D}{z_e} (p_{\mathcal{E}} F + p_{\mathcal{S}} (1 - F) - P) - B\rho(Q, Q), \quad (14c)$$

$$\frac{dF}{dt} = r_{\mathcal{S}\mathcal{E}}(F, B)(1 - F) - r_{\mathcal{E}\mathcal{S}}(F, B)F = \frac{s}{1 + e^{\beta(C_{\mathcal{E}} - C_{\mathcal{S}})}} - sF, \quad (14d)$$

where all the parameters and functions are described in Table B1.

The dynamics of the human population, F , is expected to occur on a slower timescale than the ecological dynamics when the parameter s , which describes the rate at which an individual change strategies, is relatively small. We assume that s is on the order of years while the ecological dynamics have a timescale that is the order of days or weeks. Hence, we expect the ecological dynamics to be in a quasi-steady state that is dependent on the current frequency of cooperators and we can approximate the dynamics on the slow (human) timescale as,

$$0 = rB \left(1 - \frac{Q_m}{Q}\right) h(B) - \nu_r B - \frac{D}{z_e} B, \quad (15a)$$

$$0 = \rho(Q, P) - rQ \left(1 - \frac{Q_m}{Q}\right) h(B), \quad (15b)$$

$$0 = \frac{D}{z_e} (p_{\mathcal{E}} F + p_{\mathcal{S}} F - P) - B\rho(P, Q), \quad (15c)$$

$$\frac{dF}{dt} = r_{\mathcal{S}\mathcal{E}}(F, B)(1 - F) - r_{\mathcal{E}\mathcal{S}}(F, B)F = \frac{s}{1 + e^{\beta(C_{\mathcal{E}} - C_{\mathcal{S}})}} - sF. \quad (15d)$$

To simplify the interpretation of our results, we make the following simplifications of the difference in cost functions:

$$C_{\mathcal{C}} - C_{\mathcal{D}} = c_{\mathcal{C}} - c_{\mathcal{D}} + \delta_{\mathcal{C}} - \delta_{\mathcal{D}} - \alpha(1 + \xi F)\psi B \\ = \eta - \sigma(1 + \xi F)B, \quad (16)$$

where $\sigma = \alpha\psi$ represents the overall cost conversion coefficient due to social pressure and concern for phytoplankton blooms and $\eta = c_{\mathcal{C}} - c_{\mathcal{D}} + \delta_{\mathcal{C}} - \delta_{\mathcal{D}}$ represents the cost differences for the baseline cost and social norm costs. Large η corresponds to higher cost of cooperating with anti-pollution measures. In the range of η values that we use in this paper, there are 3 equilibrium values of F (Fig. B1).

An animation showing how oscillations in the net cost of cooperation (η) drives the cooperation dynamics shown in Main Text Fig. 5d can be viewed at <https://github.com/cheggerud/Rtip>. As oscillations occur around the (oscillating) unstable equilibrium (where $dF/dt = 0$ near $F = 0.23$), increases in F when $dF/dt > 0$ exceed losses when $dF/dt < 0$. When oscillations are of large enough amplitude, this effect becomes significant and promotes increase in F toward the high-cooperation state. This preserves the high-cooperation state for high amplitude oscillations in η (that is, high values of k) despite the risk of r-tipping that exists when oscillations are not small. In comparison, medium-amplitude oscillations (intermediate k), which are also at risk of r-tipping, do not experience this effect strongly enough because the oscillations are not large enough to allow the initial decline in F to recover and tipping occurs.

Table B1

Definitions and values for ecological parameters of system 14a. PB = phytoplankton bloom.

Par.	Meaning	Biological values
r	Maximum PB specific production rate	1 /day
Q_m	PB cell quota at which growth ceases (minimum)	0.004 gP/gC
Q_M	PB cell quota at which nutrient uptake ceases (maximum)	0.04 gP/gC
z_m	Depth of epilimnion	7m
ν_r	PB respiration loss rate	0.35 /day
D	Water exchange rate	0.02m/day
H	Half saturation coefficient of light-dependent PB production	120 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$
ρ_m	Maximum PB phosphorus uptake rate	0.2 gP/gC/day
M	Half saturation coefficient for PB nutrient uptake	1.5 mgP/m ³
K_{bg}	Background light attenuation	0.3 /m
k	Algal specific light attenuation	0.0004 m ² /mgC
I_{in}	Light intensity at water surface	300 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$
$h(B)$	Light dependent growth function	see Heggerud et al. (2022)
$\rho(Q, P)$	Nutrient uptake function	see Heggerud et al. (2022)
$p_{\mathcal{C}}$	Cooperator nutrient influz.	50 mgP/m ³
$p_{\mathcal{D}}$	Defector nutrient influz.	770 mgP/m ³
s	Rate players make a decision to change strategies.	1 year ⁻¹
β	Level of determinism in changing strategies.	0.1 (costunit) ⁻¹
$c_{\mathcal{C}}$	Baseline cost to cooperate.	-
$c_{\mathcal{D}}$	Baseline cost to defect.	-
ϕ	Cost conversion coeff. for PB	10 (costunit)/mgC/m ³
α	Cost conversion for social pressure due to PB	3 (costunit)
ξ	Strength of frequency dependence for social pressure	10
ψ	Level of social concern for PB	0.02 (mgC/m ³) ⁻¹
$d_{\mathcal{D}}$	Social norm cost for defecting.	-
$d_{\mathcal{C}}$	Social norms for cooperating.	-

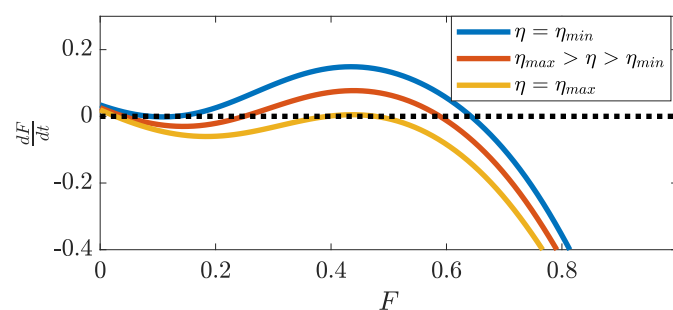


Fig. B1. The phase line of model (15) for different values of η . Equilibrium values of F occur where the curves cross the $dF/dt = 0$ line. Our case study considered only η values in the range represented by the orange curve, where there are alternative stable states with low- and high-levels of cooperation, separated by an unstable equilibrium in between.

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