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Review

Abrupt Change in Ecological Systems: Inference and Diagnosis

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Abrupt ecological changes are, by definition, those that occur over short periods of time relative to typical rates of change for a given ecosystem. The potential for such changes is growing due to anthropogenic pressures, which challenges the resilience of societies and ecosystems. Abrupt ecological changes are difficult to diagnose because they can arise from a variety of circumstances, including rapid changes in external drivers (e.g., climate, or resource extraction), nonlinear responses to gradual changes in drivers, and interactions among multiple drivers and disturbances. We synthesize strategies for identifying causes of abrupt ecological change and highlight instances where abrupt changes are likely. Diagnosing abrupt changes and inferring causation are increasingly important as society seek to adapt to rapid, multifaceted environmental changes.

Highlights

Abrupt ecological changes occur rapidly relative to typical rates of ecosystem change and are increasingly observed in ecosystems worldwide, thereby challenging adaptive capacities.

Abrupt ecological changes can arise from many processes, only some of which are transitions between alternative states.

Focusing solely on the mean values for drivers and states is insufficient for diagnosing abrupt changes, because abrupt changes can be produced by changes in the variability of drivers and disturbance regimes.

Diagnosing the likely causes of abrupt state changes in real-world systems remains difficult. Long-term data and experimental manipulations of drivers remains essential.

Multiple changing drivers can interact to increase the likelihood of abrupt changes. Identifying interventions that decrease the risk of undesirable abrupt changes is an urgent priority.

Defining and Diagnosing Abrupt Ecological Change

Abrupt changes (see Glossary) in ecosystems — that is, substantial changes in ecosystem **states** that occur in a short period of time relative to typical rates of change — are increasingly common (see Figure S1 in the supplemental material online). Examples of such ecosystem changes span diverse systems and scales [1–3], and include the rapid collapse of consumers, such as global fisheries [4] and large mammals in Africa (Figure 1A) [5], and declines in prey abundances, as in sudden drops in the size of some penguin and sardine populations [6]. The structure of terrestrial and aquatic ecosystems can also undergo abrupt change [7,8], as when foundation species decline suddenly, such as bed-forming seagrasses [9], forest-forming kelp species [10], and reef-forming corals (Figure 1B) [11]; or when **disturbance regimes** change, illustrated by recent increases in the extent of large wildfires (Figure 1C) [12] and insect outbreaks [13]. Abrupt and persistent changes in plant communities have also been documented, including compositional changes in conifer forests [14–17] and expansion of exotic species [2,7]. Some abrupt changes can directly affect humans, as when crop production acutely declines during extreme weather [18]. Timescales of change vary with organism lifespans and ecosystem process rates, so the relevant definition of abrupt change can range from minutes, for species with short generation times, to millennia, through earth-system change. It remains difficult to anticipate abrupt changes, diagnose causes, and determine whether changes are reversible. As a result, abrupt ecological changes can make adaptation by societies, species, and ecosystems challenging [19]. The goal of this paper is to identify general conditions likely to generate abrupt ecological change and to provide guidance on how such changes might be diagnosed and anticipated.

Abrupt ecological changes, like other **regime shifts**, are empirical phenomena that can arise from multiple causes [1–3,14]. Abrupt changes are often implicitly considered to indicate transitions between **alternative states**, precipitated by a response to changing levels of an external **driver**

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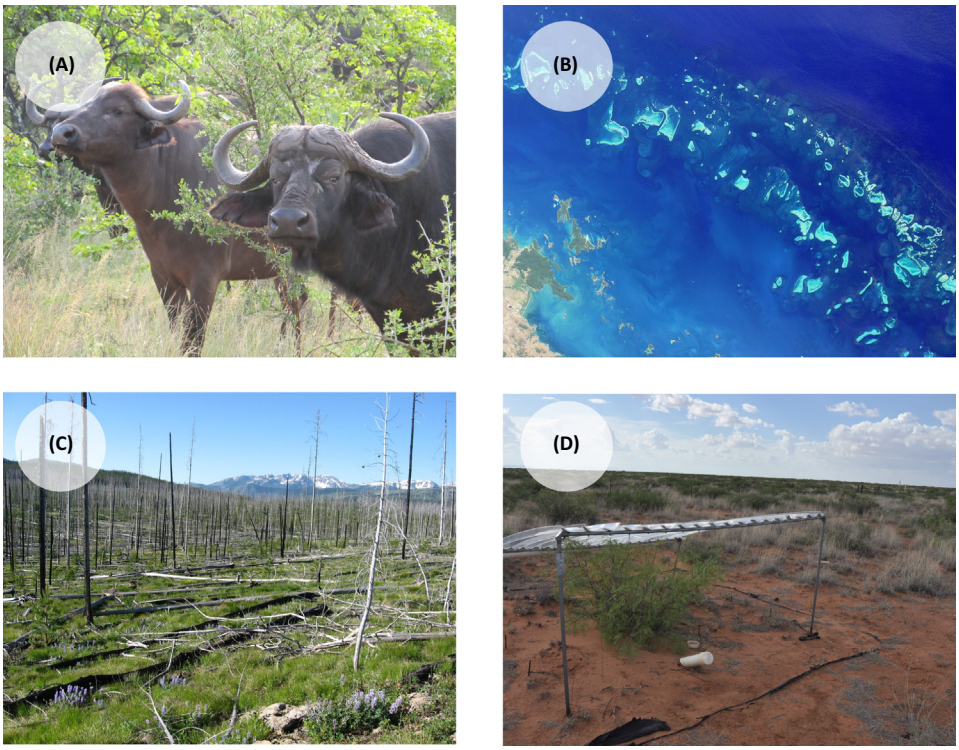

Figure 1. Examples of Systems Where Abrupt Changes Have Been Recorded. (A) in Gorongosa National Park, Mozambique, several populations of large herbivores underwent abrupt declines during a 15-year period of intense hunting. Twenty years later, some species have shown little sign of recovery, including the buffalo species shown here (*Syncerus caffer*) [5]. (B) Recent heatwaves in the Great Barrier Reef have been associated with abrupt loss of live corals [11]. Fishing and other pressures have caused abrupt declines of corals in the Caribbean [8]. (C) Many forests in Western USA have seen an abrupt increase in the area burned by large wildfires – such as the one shown here, from Grand Teton National Park – as a result of increasing growing season temperatures starting in the late 20th century [12]. (D) Depicts an experiment that increased precipitation variability in a desert grassland, resulting in abrupt decreases in net primary production [49]. Note that within the experimental plot, grasses are largely absent, compared to areas outside the experimental plot. Photo credits: (A) Jesse B. Nippert, (B) NASA, (C) Monica G. Turner, and (D) Osvaldo Sala.

variable [20–22]. Systems with alternate states exhibit hysteresis, which is the property wherein large changes in state are not easily reversed by restoring driver variables to previous levels [20,21]. Some well-studied cases of abrupt change appear to match this pattern of transitions between alternative states, including the transition of coral reefs to an macroalgae-dominated state [8,11], transitions of grassland to desert [1], transitions between strong and weak top-down control by predators [23,24], and transitions of oligotrophic lakes to a eutrophic state [25,26]. In New Mexico, USA, for instance, decades of heavy grazing and an extreme drought resulted in an abrupt change from high to low grass biomass [1]. A return to wetter conditions and lowered grazing pressure have failed to reverse this transition, indicating hysteresis [1]. However, abrupt changes can also reflect proportional and reversible ecological response to rapid changes in external **drivers**, or nonlinear but reversible responses to gradually changing drivers [1,14,27]. Changes in environmental stochasticity (e.g., increased frequency of climate extremes [28]), and disturbance regimes (e.g., decreased fire frequency [29]) can also trigger abrupt changes in ecosystem state. Thus, abrupt changes and transitions to alternative states are not synonymous [1,14,20,21,27,30–32], and inferring causes of an observed abrupt change in an ecosystem is not straightforward.

Glossary

Abrupt change: substantial changes in the mean or variability of a system that occur in a short period of time relative to typical rates of change.
Alternative states: two or more states at which an ecosystem can persist, within the same range of driver variables. The alternative states of stochastic processes are characterized by different means, variances, and other statistical moments. Alternative stable state is the term often used in reference to **deterministic processes**, whereas work focused on stochastic processes often favors terms such as alternative attractor. Often used synonymously with multiple stable states, multiple equilibria, and basins of attraction.
Critical transitions: transitions that occur when a threshold is passed, causing the disappearance or appearance of alternative states. Often used synonymously with bifurcations.
Deterministic process: a process that has no random component and is, therefore, theoretically predictable. For instance, at a given combination of a drivers and state variables, a deterministic process consistently repeats the same behaviors.
Disturbance: relatively discrete event in time that alters the biotic and/or abiotic components of an ecosystem.
Disturbance regime: the spatial and temporal patterns of disturbances over a long period of time. A disturbance regime is characterized by multiple factors including frequency, return interval, size, intensity, and severity.
Drivers or driver variables: we use 'driver' to refer to external factors that influence the dynamics of a system without themselves being affected by the system. Often synonymous with external forcing or extrinsic processes.
Hysteretic systems: ecosystems characterized by two or more alternative states, critical transitions between states, and sensitivity to initial conditions. In hysteretic ecosystems, the conditions required to change state in one direction differ from the conditions required to change back to the original state.

While theoretical frameworks for understanding regime shifts, hysteresis, and alternative states are well developed (e.g., [1,14,20,21,30]), they are often difficult to apply in real-world settings. A key challenge to diagnosis is that changes in both the mean and variability of external drivers can result in abrupt changes, and multiple drivers are often changing simultaneously [28,33]. Additionally, the underlying relationships among drivers and ecological states are often poorly understood [34]. These knowledge gaps make it especially difficult to determine the cause of past abrupt changes and even more difficult to anticipate future abrupt changes.

In this paper, we work through the intertwined relationships among system state and environmental drivers to identify conditions likely to produce abrupt ecological change. The recent growth of literature on abrupt change (Figure S1) has prompted spirited discussion about fundamental concepts (e.g., [19,35]) and the most likely causes of abrupt change [32,36,37]. Part of the challenge is a fragmentation of the literature: many different systems in diverse fields exhibit abrupt change, gaps between theory and empirical research can be wide, and subdisciplines tend to emphasize different terms and governing processes (Figures S1 and S2). Here, we build a synthesis that blends our conceptual understanding of abrupt change with real-world examples.

The System and the Drivers

Defining the system and identifying its key external drivers are central to understanding abrupt ecological changes [19,34]. The system (usually an ecosystem or another scale of ecological observation) encompasses state variables and their interactions. State variables are major components of the ecosystems that change over time. Examples of state variables include the abundance of a species, functional group, or trophic level, as well as stocks of matter (e.g., nitrogen, phosphorus, and soil moisture). External drivers (drivers hereafter), by contrast, are external to the system, affecting the system without the system affecting them. Resource addition rates, population extraction rates, regional temperature, and land-use change are common examples of driver variables, but of course, what is external depends on how the system is bounded. In reality, all drivers are stochastic, being described by not only a mean, but also variance, skew, covariance through time (i.e., temporal autocorrelation), and other statistical moments. Because real-world drivers are stochastic, the systems they affect are often stochastic as well. Many models that ecologists use, however, are deterministic, containing no random component (Box 1).

Making a clear distinction between system and drivers allows cataloging the ways in which changes in drivers alter systems [19,34]. For example, changes in the mean value of a driver could cause changes not only in the mean state of an ecosystem but also in its variability. Similarly, changes in variability of a driver, such as a disturbance regime, could alter both the mean and the variability of the system over time (Box 1). Below, we discuss the possible ways in which drivers could cause abrupt changes to a system; starting with how changes in the mean of drivers affect the mean state of a system, and then turning to cases involving variability of drivers and disturbance regimes, and their effects on both the mean and variability of ecosystems. We conclude with interactions among multiple drivers that generate abrupt change.

Abrupt Changes in Mean System State with Changes in Driver Means

This review starts with the familiar practice of asking how changes in driver means affect the mean values of system state. We consider five driver–state relationships (Figure 2A–E), starting with the null condition in which system state is insensitive to changes in a driver (Figure 2A) and linear relationships (Figure 2B). Nonlinear relationships include unimodal (Figure 2C) and threshold (Figure 2D) responses of system state to a driver. Nonlinear relationships can also

Regime shift: an observed large change in an ecosystem. Regime shifts can be gradual or fast, can be produced by many processes, and can involve multiple external drivers and/or internal feedbacks. All abrupt ecological changes are regime shifts, but not all regime shifts are abrupt. A regime shift can or can not be a transition to an alternative state. Often synonymous with state transitions and phase shifts.

Resilience: (i) degree to which an ecosystem can tolerate changing driver variables and/or disturbance without shifting to a qualitatively different state. (ii) The rate of return of the system to its stable state or stationary distribution. Despite having two different definitions since the 1970s, the term resilience is often used imprecisely. All uses of resilience in this paper relate to the first definition.

Safe operating space: the combinations of states, driver variable values, and disturbance characteristics for which a system is not likely to undergo a regime shift. The boundary of a safe operating space is not a threshold; it is placed a safe distance inside any known or potential thresholds. Safe operating spaces are intended to maintain the resilience of the ecosystem, with resilience given by the first definition above.

State: the characteristics used to describe the status of an ecosystem at a particular domain in space and time. For deterministic systems, the state is the values of variables used to describe the system, and for stochastic systems it could refer to as either the probability distribution of these state variables or realized values of the state variables. In practice, definitions of system state include both the mean and variability of systems.

Stochastic process: a process that through time generates a random variable characterized by a mean, variance, and higher statistical moments of the state variables of a system (e.g., skewness). Used to contrast deterministic processes that do not involve random variables.

Box 1. Abrupt Change in Simple Ecological Models

Ecologists have discovered many simple models capable of abrupt change (e.g., [8,20,21,39,84,85]). These models generate abrupt changes that are **critical transitions**, regime shifts, or both. Critical transitions, such as abrupt changes among multiple stable states, are applicable to many instances of ecological or social change [20]. However, not all abrupt changes are critical transitions [14,27,32]. For example, some rapid changes in drivers can trigger regime shifts in the absence of critical transitions among alternate states [80]. Thus, models of regime shifts might or might not involve critical transitions. Models have also addressed critical transitions that are not regime shifts. A well-known example is transitions among stable points and stable cycles in animal populations [86] and phytoplankton blooms [87]. Most of the simple models of abrupt change are single dynamical equations or systems of a few dynamical equations. However, models have been developed and studied for abrupt change in complex systems as well, such as spatially extended simulations [37,83,88–90].

Simple models play an important role in understanding how **stochastic processes** interact with abrupt ecological change [28]. Both unstable and stable deterministic equilibria of ecosystems interact strongly with stochastic dynamics [91]. These interactions can generate long transient dynamics that cause unstable equilibria to appear stable [82,92]. This type of abrupt change is rarely addressed, but potentially important in field studies. Rather subtle changes in environmental stochasticity can also trigger abrupt change when ecosystems have low resilience [93]. For instance, noise magnitude and type (e.g., white or redness of noise) influence the probability of abrupt change in simple spatial ecosystem models [37,90]. Despite these fascinating examples, ecological studies of interactions of stochastic processes with ecosystem steady states and noise-induced abrupt change are less common in the literature than studies of directional change in deterministic ecosystem models.

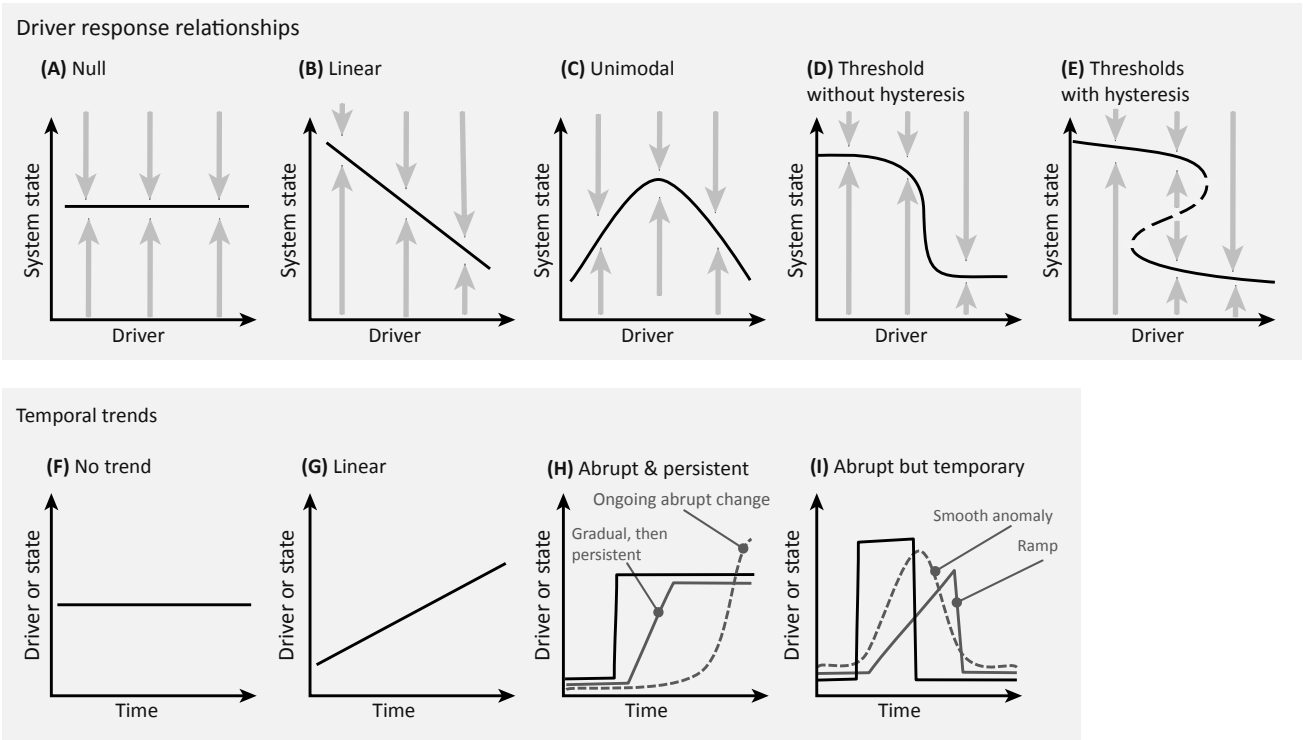

Figure 2. Potential Driver–State Relationships and Patterns of Driver and State Change over Time. (A–E) show five relationships between ecosystem state and driver variables considered in this review: (A) null, (B) linear, (C) unimodal, (D) threshold without hysteresis, and (E) thresholds with hysteresis. For all curves, unbroken black lines indicate long-term stable points, and gray arrows depict the direction a system will move to the stable point, assuming no change in the driver variable. In (E) the broken line is an unstable state, which separates two alternative states. (F–I) depict general classes of temporal trends in either driver variables or ecosystem state considered in this review: (F) stationary, (G) linear and monotonic, (H) abrupt and persistent/monotonic, and (I) abrupt but temporary changes in driver or state over time. In (F–I), black lines depict the trend considered here, and labeled gray lines represent variations on each general trend. All trends can be reversed (e.g., abruptly decreasing rather than increasing).

involve hysteresis, in which a system has two or more alternative states and the location of thresholds depends on the direction of the transition (Figure 2E). Once a **hysteretic system** transitions to an alternate state, simply bringing the driver variable back across the original threshold will not return the system to its previous state [20,30,38,39].

The mean of drivers often changes over time, and the magnitude and rates of change in mean system state depend both on the rate of change of the driver and the underlying relationship between driver and state. We focus on four kinds of trends in drivers (Figure 2F–I): no change, linear change, abrupt and persistent change, and abrupt but temporary change. We then explore possible combinations of observed trends in drivers and system state variables (Figure 3) to explore two questions: (i) which combinations of driver trend and driver–state relationships can produce abrupt changes; and (ii) which observed combinations of driver and response are most diagnostic of underlying mechanisms behind abrupt changes?

When an environmental driver exhibits no trend (Figure 3, first row), changes in system state will be uncorrelated with that driver. Therefore, if abrupt changes in mean state are observed (Figure 3C,D), another driver or mechanism is responsible. When a driver changes linearly over time (Figure 3, second row), three possible driver–state relationships can lead to abrupt ecological changes (Figure 3G,H). A unimodal driver–state relationship can produce an abrupt but temporary state change in response to a linear driver trend (Figure 3H) – as when the performance of a species is associated with optimal conditions in an external driver that are reached and then surpassed. Crop responses to temperature often follow this unimodal pattern, where rising temperatures increase photosynthetic rates until they result in water stress, after which crop production declines [40]. Both threshold and hysteretic driver–state relationships can produce abrupt and persistent state change in response to a linear driver trend (Figure 3G), and these two relationships are difficult to discriminate [31]. For example, in Northern Africa from 0 to 6000 years before present, two major drivers of vegetation – solar insolation and greenhouse gas concentrations – changed approximately linearly [41]. Over this period, many sites changed abruptly from grasslands to desert, which has been attributed to thresholds associated with feedbacks between vegetation, climate, and/or soil [41]. Whether this transition is hysteretic is debated and difficult to determine directly without a contemporary reversal of driver trends [41]. More generally, a single abrupt and persistent ecological change in response to a unidirectional driver trend usually fits a large number of possible models, and its potential reversibility cannot be evaluated [42]. This problem is known as the 'one-way trip' in fisheries stock assessment [43], and it applies to many terrestrial time series as well.

When the mean of a driver exhibits an abrupt and persistent change (Figure 3, third row), abrupt and persistent ecosystem state changes are expected but not guaranteed (Figure 3K). For linear and unimodal driver–response relationships, ecosystem state closely tracks the driver and thus, also changes abruptly [1,14,27]. For threshold driver–response relationships, ecosystem state can either change abruptly (Figure 3K) or not (Figure 3I,J), depending on whether thresholds are passed [30]. Because many driver–state relationships can cause abrupt change, diagnosing causation is especially difficult when the driver and state both change abruptly (Figure 3K). For example, an abrupt and sustained increase in the flow of saline water into a Danish fjord increased recruitment of benthic clams, triggering an abrupt increase in water clarity and decline of pelagic zooplankton [3]. However, the underlying relationship between driver (salinity and nutrient inputs) and state (community composition) is not readily apparent (Figure 3K).

An abrupt but temporary change in the mean of an environmental driver (Figure 3, fourth row) has high diagnostic potential and can also lead to abrupt ecological change, because close

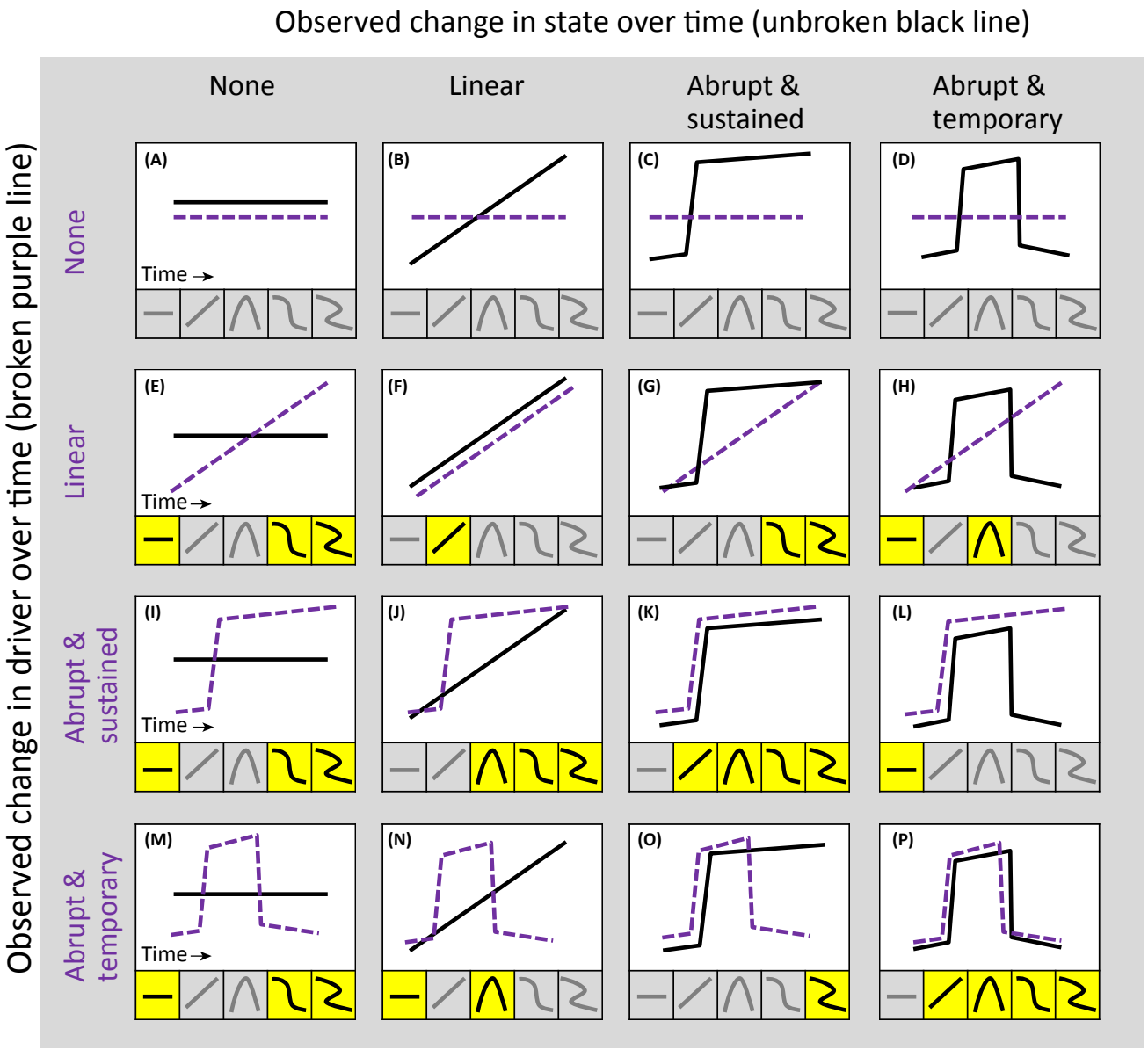

Figure 3. Using Time Series to Infer Driver–State Relationships. A matrix for interpreting time series of external drivers (broken purple line; changes across rows) and system state (unbroken black line; changes across columns), to determine whether the underlying relationship between driver and response variables is: null, linear, unimodal, a threshold without hysteresis, or a threshold with hysteresis. Driver–state relationships highlighted in yellow are consistent with the time series above. For instance, in (F), only the linear driver–state relationship is colored yellow, because a concurrent linear change in both driver and state often suggests a linear relationship between driver and state.

tracking between driver and state is common in real-world ecosystems (e.g., [15]). For example, many marine systems that were recently altered by climate anomalies or cultural eutrophication, purportedly recovered once these pressures were relaxed [3,44]. This reversal of an abrupt change in state suggests that these systems are not hysteretic or that thresholds were not crossed (Figure 3P). As with abrupt and persistent change in drivers, the ecosystem state will fail to change abruptly if thresholds are not crossed (Figure 3M,N). Hysteresis can be

detected if the ecosystem persists in its new state after the driver trend is reversed (Figure 3O), which suggests a transition between alternative states [1,20,27,30]. Consider an experiment that applied abrupt but temporary nitrogen addition to native tallgrass prairie [7]. While non-native species remained subdominant in control plots, plots affected by temporary nitrogen addition underwent an abrupt increase in non-native species that continued decades after nitrogen fertilization ended, indicating abrupt transitions to alternative states [7]. Like many transitions to an alternative state, the persistence of this abrupt change is attributed to self-reinforcing feedbacks [2,20]; in this case positive interactions between litter quantities and invasive dominance [7].

In summary, as the means of environmental drivers change over time, abrupt changes to the mean of ecological states are likely: (i) when the mean of a driver changes unidirectionally over time, and driver–response relationships are nonlinear (unimodal, threshold, or hysteretic; Figure 3G,H); (ii) when change in a driver is abrupt and sustained, and driver–response relationships take any form except null (Figure 3K); and (iii) when change in a driver is abrupt but temporary, and driver–response relationships take any form except null (Figure 3O,P). Notably, nonlinear driver–response relationships do not necessarily produce abrupt state change, because changes in drivers can fail to cross thresholds (Figure 3E,I,J,M,N).

Abrupt Changes Involving Variability in System and/or Drivers

Changes to both drivers and ecosystem states include not only means, but also variances and other statistical characteristics. For example, the variance of a driver variable can change, exemplified by forecasted increases in the frequency and magnitude of extreme weather events this century [45]. Increases in ecosystem variability are also concerning because fluctuations in resources, such as food production [18], can have serious consequences for human well-being [46]. Returning to Figures 2 and 3, all of the relationships between driver means and abrupt changes to ecosystem means hold for changes in the other stochastic properties of drivers and ecosystems, such that the vertical axes could be variability of a driver (purple broken line) and variability of system state (black unbroken line) over time. We provide several illustrative examples.

First, changes in driver variability can lead to an abrupt change in the mean state of an ecological system. For example, in grassland experiments that abruptly increased the variability of precipitation, changes in average aboveground net primary production have ranged from a 10% decrease in tallgrass prairie [47], a 20% decrease in old-fields [48], and an abrupt 50% decrease desert grassland, which was accompanied by a near-loss of grass species (Figure 1D) [49]. The responses by tallgrass prairie and old fields is most consistent with a null driver–response relationship (Figure 3E), a linear relationship with a shallow slope, or a nonlinear system that has not crossed a threshold (Figure 3K). The abrupt change in desert grassland could result from most driver–state relationships (Figure 2K), although ancillary evidence suggests potential for hysteresis (Figure 1D) [1].

Second, changes in the mean of drivers can result in abrupt changes in ecosystem variability. A familiar example is the paradox of enrichment, where increasing resource availability to prey increases the variability of predator–prey systems [50]. An experimental illustration comes from experiments with aphids and their parasitoid predators, where elevated temperature increases both population growth rate and predation rate [51]. These changing rates resulted in larger fluctuations in both prey and predator abundances [51]. An observational example comes from rangelands in South–Central Russia. After the collapse of the Soviet Union, grazing pressure decreased abruptly, which was followed by an abrupt increase in the interannual and spatial

variability of gerbil populations [52]. This increased variability persisted after grazing pressure returned to antecedent levels [52], suggesting a potentially hysteretic transition between alternative states with different variability (Figure 3O).

Finally, changes in driver variability can lead to abrupt changes in ecosystem variability. For instance, changes in the temporal pattern of variation of drivers (i.e., autocorrelation) are known to affect the variability of some ecosystems. For example, changes in the temporal autocorrelation of atmospheric forcing resulted in two abrupt changes in zooplankton abundance of coastal Central California, USA from 1950 to 2010 [53]. However, it is uncertain how future changes in temporal autocorrelation would change the variability of this system. This problem is systemic, because the few empirical studies on changes in environmental variability have focused on abrupt and persistent changes in variability, which have limited diagnostic power (Figure 3K) compared to reversed driver variable changes (Figure 3M–P). However, models suggest that certain factors can make systems sensitive to variability in drivers (Box 1). For instance, systems with slow recovery times appear particularly sensitive to changes in driver variability, because these intrinsic processes amplify rather than dampen the variance imposed by drivers [54].

Abrupt Changes and Disturbances

Natural **disturbances** (e.g., fires, floods, landslides, storm events, and volcanic eruptions) are well-known components of ecosystems that affect numerous aspects of their ecology and often result from driver variation. Disturbance regimes are typically characterized by the mean and variability in disturbance frequency, size, intensity, and severity. Biota are often adapted to their historical disturbance regimes, and disturbance followed by recovery is common in many ecological systems, exemplified by secondary succession in grasslands, forests, and elsewhere (Figure 4A) [55–57]. However, changes in the disturbance regime (e.g., altered disturbance intensity or frequency) outside of its historical range of variability [58] can alter recovery capacity of ecosystems [38,55]. It is the disruption of the disturbance–recovery cycle – the inability of an ecosystem to recover to its predisturbance state – that portends an abrupt and persistent change in state [55,59,60].

Increased disturbance intensity can result in abrupt changes, especially if thresholds associated with ecosystem recovery are exceeded (Figure 4B) [38,55,59]. For example, recovery of conifers (black spruce, *Picea mariana*) following fire in boreal forests depends on the presence of a residual soil organic layer that is not fully consumed by fire [61]. High-intensity fires can

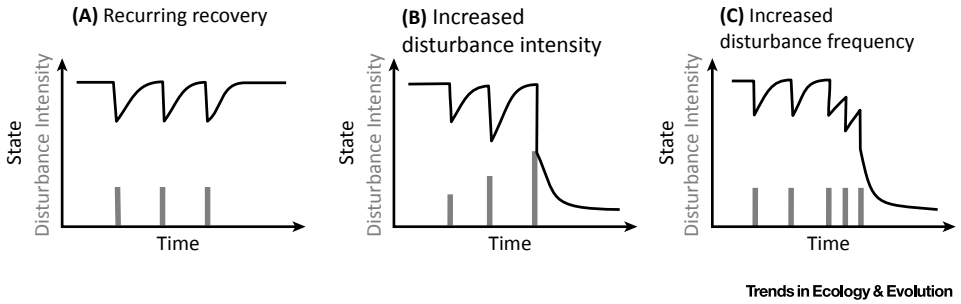

Figure 4. Disturbance Regimes and Abrupt Change. Potential effects of disturbance frequency (gray bars) and intensity (height of gray bars) on system state (unbroken black lines). (A) Depicts recurring disturbance followed by post-disturbance recovery. In (B) and (C) the system shifts to an alternative state because a threshold in system state was crossed due to an increase in disturbance intensity (B) or frequency (C).

increase disturbance severity and combust the entire organic soil layer, which exposes mineral soil and creates conditions that favor recruitment of deciduous trees rather than black spruce [59,61]. Persistence of deciduous trees is then maintained by new internal feedbacks in which plant–soil–microbial interactions support shallow soil organic soil layers and low-intensity fires that perpetuate the deciduous forest [61]. In subtropical seagrass meadows of Western Australia, a marine heat wave of unprecedented intensity was associated with a 90% dieback of seagrass, which triggered an abrupt state change with long-term impacts on the biotic community [9]. The near-complete loss of seagrass cover is likely to persist because of a new feedback where increased turbidity prevents seagrass recolonization [9].

Altered disturbance frequency can also produce abrupt ecological changes if disturbances reoccur before an ecosystem has regained its capacity for recovery (Figure 4C) [55,59,62,63]. For example, top predators of aquatic food webs can persist despite occasional recruitment failures [64]. However, repeated fishing of top predators allows increased biomass of mesopredators that consume juveniles of the top predator, eventually causing a population collapse of the top predator [64]. Similarly, the frequency of coral bleaching events has increased in Australia and in some cases, the interval between bleaching events may be too short to allow for the recovery of the reef ecosystem (Figure 1B) [11]. In some systems, new internal feedbacks that promote more frequent or severe disturbances develop [55,59,62]. A poignant example occurs with many transitions from vegetated to desert states (Figure 1D), where the expansion of bare space in arid and semi-arid ecosystems increases the frequency of sandstorms and further enlarges bare spaces [65]. Reduced disturbance frequency can also lead to abrupt state changes, allowing disturbance-sensitive species to expand and initiate feedbacks that dampen the frequency or severity of future disturbances [60,63]. For instance, reduced fire frequency in grass-dominated ecosystems can lead to an abrupt change to a wooded and fire-resistant state [29,66]. New feedbacks between trees and fuels then reduce the intensity and extent of subsequent fires, such that reintroducing fire typically fails to return the system to its grass-dominated state [60,62,63,66,67].

Abrupt Change in the Messy Real World: Interactions among Drivers of Abrupt Change

Thus far, we have parsed causes of abrupt change for single drivers, but in many systems multiple drivers change simultaneously and interact. Interactions of drivers challenge efforts to determine causation, but have great potential to produce abrupt state changes [2,20,68,69].

When drivers interact, it is difficult to separate proximate and ultimate causes. For example, even if an abrupt change coincides with a disturbance, change in a separate external driver could be the ultimate cause of abrupt change (Figure 5A). This type of interaction is likely common. In subalpine conifer forests, for instance, tree regeneration after stand-replacing fires is substantially reduced when drought occurs during the critical window of post-disturbance establishment [70] (Figure 1C). Therefore, the primary cause of recovery failure is not fire *per se*, but rather warming trends that constrains post-fire recruitment [71]. Similarly, many coral reefs in Jamaica changed abruptly to a macroalgae-dominated state after Hurricane Gilbert [8]. However, subsequent analyses and modeling revealed that the persistence of abrupt coral declines was primarily due to long-term declines in algal grazers, rather than the hurricane itself [8].

Multiple environmental drivers can have additive or synergistic interactions that cause abrupt system changes, even when altering each driver separately would have little effect. When interactions are additive, the likelihood of an abrupt state change is the summed effect of changing each driver variable separately (Figure 5B). With synergistic interactions (Figure 5C), changes in multiple drivers increase the likelihood of abrupt state changes more than additive

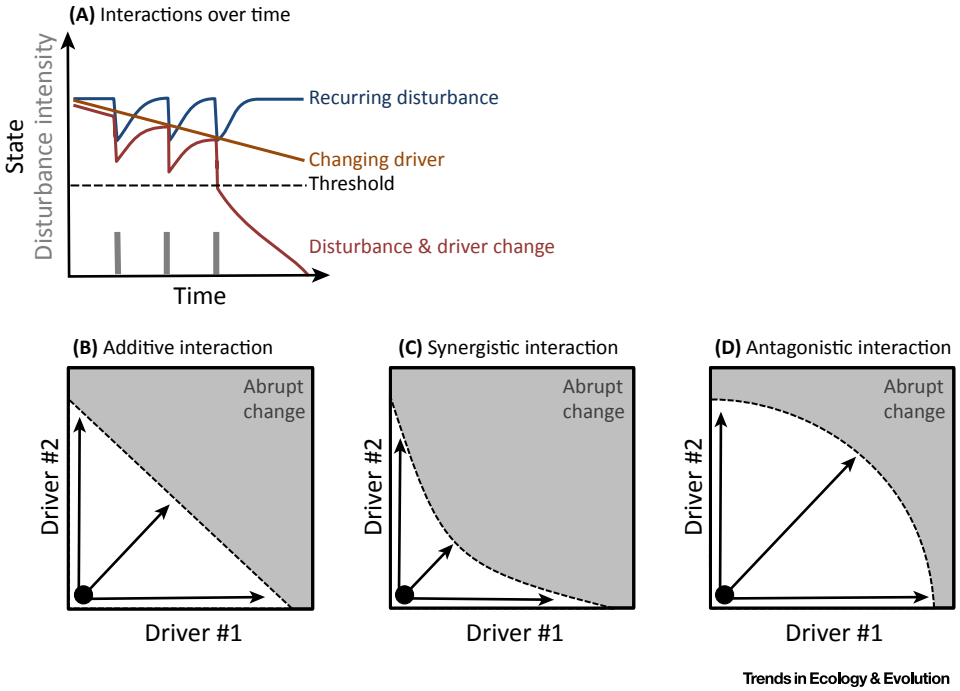

Figure 5. Interactions between Multiple Drivers. Multiple drivers often interact to change the likelihood of abrupt change. For instance, in (A) interactions between changes in the mean of one driver and the disturbance regime of another driver might cause systems to lose their ability to recover from disturbance events to which they were adapted historically. The broken line in (A) denotes a threshold in system state that, if crossed, initiates a transition to an alternative state. In (B–D), driver combinations that cross the broken line and move into the gray area produce abrupt ecological changes. Driver combinations that are unlikely to produce abrupt change are in white. Synergistic interactions (C) increase the likelihood of abrupt change, while antagonistic interactions (D) reduce the likelihood of change. The circle in the bottom left of (B–D) shows a hypothetical starting combination of both driver. Arrows show how much driver one (horizontal arrow), driver two (vertical arrow), or both drivers (diagonal arrow) would need to change to elicit an abrupt state change.

interactions would predict. Abrupt collapses of honey bee colonies in North America and Europe are a potential symptom of synergistic interactions. Exposure of bee colonies to both pesticides and pathogens (compared to exposure to either alone) caused rapid increases in honey bee mortality, with additive reductions of larva survival and synergistic reductions of adult survival [72,73]. By contrast, antagonistic interactions (Figure 5D) can make abrupt changes less likely when both drivers change (e.g. [74]). For example, it is estimated that >50% of reported interactions between warming and toxins have been antagonistic in freshwater ecosystems, resulting in attenuated changes in state when both pressures occur in concert [75]. As before, driver interactions can also apply to changes in the variability of drivers. For instance, simulations of coral reefs suggest increases in mean temperature and temperature variability (specifically heatwaves) are likely to interact synergistically, increasing the likelihood of changes to an alternative noncoral state [76].

Identifying when multiple drivers interact to cause or mitigate abrupt ecological change requires a factorial study design, in which effects of different changing drivers can be quantified separately and together [72,73,75]. Such studies can also quantify multivariate thresholds [77] that bound **safe operating spaces** [68,78] in which system state is resilient to changing drivers. Identifying additive and synergistic interactions can help force desirable abrupt changes – the goal of many restoration efforts [36,69]. Antagonistic interactions reveal opportunities wherein management interventions have more potential to avoid unwanted abrupt changes.

Looking Ahead

Humans are altering global change drivers [2,33,78] in ways that will likely lead to abrupt changes that can transform ecosystems [79]. Given the challenges of diagnosing and anticipating abrupt change, we suggest several promising avenues of research in the context of our synthetic framework (see Outstanding Questions).

Studies focused on understanding mechanisms – that is, understanding the driver–state relationships likely to influence an ecosystem, and the processes and feedbacks that confer resistance and **resilience** – remain critical to uncovering causes of abrupt state changes. Broad-scale field studies that relate system state to a spectrum of driver conditions over time and space can test whether current patterns are consistent with expected driver–response relationships over time [15,63,80]. For example, a study of pinyon woodland regeneration following a massive die-off of overstory trees in Southwestern USA spanned a wide range of moisture conditions [81]. Following the die-off, stands with hotter and drier conditions, lower soil moisture, and limited seed sources failed to recover [81]. This type of spatial variation in abrupt change along a driver gradient can suggest future consequences of continued changes in global change pressures over time. Such knowledge can also be used to parameterize models that help determine whether ecosystems have thresholds and forecast the likelihood of abrupt changes (Box 1) [8,62,74].

Designed and natural experiments should be leveraged to understand abrupt change and interactions among drivers because the clearest tests for transitions between alternative states have come from experimental manipulations and natural experiments [1,7,23,32]. Designed experiments in which drivers can be pushed in one direction and then reversed are especially powerful for identifying hysteresis (Figure 3K). Such experiments are scarce, but they have determined whether abrupt changes constitute transitions to alternative states in response to drivers ranging from nutrient addition [7] to consumer density [23,31] and disturbance suppression [66,67]. Natural experiments also offer opportunities to learn from events that cannot be implemented at broad scales. For instance, civil war in Mozambique provided a rare opportunity to quantify the large-scale effects of abrupt but temporary increases in hunting pressure of large mammals, which resulted in steep declines in several species and a 35% increase in tree cover [5]. Twenty years since the end of the war, at least three large mammal species have shown little sign of recovery [5] (Figure 1A). In the near term, resampling completed experiments – such as discontinued climate manipulations or consumer exclosures – would provide an invaluable opportunity to determine whether abrupt state changes are hysteretic.

Long-term data remain particularly important for detecting, diagnosing, and anticipating abrupt ecological change (Figures 2 and 3) [1,3,7,11,29,52,66]. The value of existing long-term data streams, including experiments, field measurements, remotely sensed Earth observations, and long-term monitoring of recovery from disturbances will only increase as the length of record grows. Similarly, many paleo-ecological records carry signals of abrupt change, which can reveal nonlinearities not apparent in shorter time series [14,15,41]. We strongly endorse calls for maintaining current long-term observations and establishing new long-term data streams [1,3].

As frameworks for diagnosing abrupt change continue to evolve, challenges posed by time lags and spatial heterogeneity remain to be addressed. Time lags can mask abrupt changes if there is a substantial delay between initiation and occurrence of a state change [1,66,82]. Additionally, when time lags are long, abrupt but temporary driver changes might fail to force transitions to alternative states that would have occurred if the same manipulations were maintained for

longer durations [66]. Spatial heterogeneity can also obscure abrupt change if systems have nonlinear driver–response relationships that differ with spatial scale or cross-scale interactions that govern ecosystem dynamics [74,83]. Finally, detecting changes in variability of ecosystems requires more data than detecting changes in means.

In conclusion, the accelerating rates of change in many drivers during the Anthropocene make abrupt ecological changes more likely in the years ahead [33,79]. Diagnosing abrupt change and inferring causation will become increasingly important as scientists and society seek to anticipate and adapt to a period of rapid change. Abrupt changes can result from changes in driver means, driver variability, disturbance regimes, and interactions among these processes. Empirical studies of abrupt change must carefully consider alternative mechanisms for observed changes. The framework we present offers a systematic approach for considering a plurality of potential causes of abrupt change that can guide empirical studies of past, present, and future abrupt ecological change. Identifying abrupt changes is relatively easy, whereas diagnosing causes and anticipating future events is difficult. Yet, few ecological challenges are more important in our rapidly changing world.

Outstanding Questions

How often are abrupt changes in either the mean or variability of ecosystem state caused by transitions between alternative states?

Changes in the mean or variability of driver variables or disturbance regimes can cause changes in the mean or variability of ecosystem parameters. Of the four possible combinations of change – mean and variability of the driver crossed with mean and variability of an external driver – which is most likely to manifest abrupt changes in ecosystem state?

When abrupt change coincides with a disturbance, is the disturbance event a proximate or ultimate cause of abrupt and persistent state changes? Or, are multiple changing drivers interacting, either additively, synergistically, or antagonistically, to promote or attenuate abrupt changes in ecosystems?

What can be learned about abrupt change by taking advantage of natural experiments or previously abandoned experiments? Have previously reported abrupt changes in response to experimental manipulations persisted to the present day, even after manipulations have been relaxed?

How can understanding past abrupt changes be used to predict where and when future abrupt changes will occur?

How can challenges posed by time lags, spatial heterogeneity, and short-term datasets be circumvented to identify abrupt changes and when they began?

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Supplemental Information

Supplemental information associated with this article can be found, in the online version, at https://doi.org/10.1016/j.tree.2018.04.013.

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Supplementary Material:

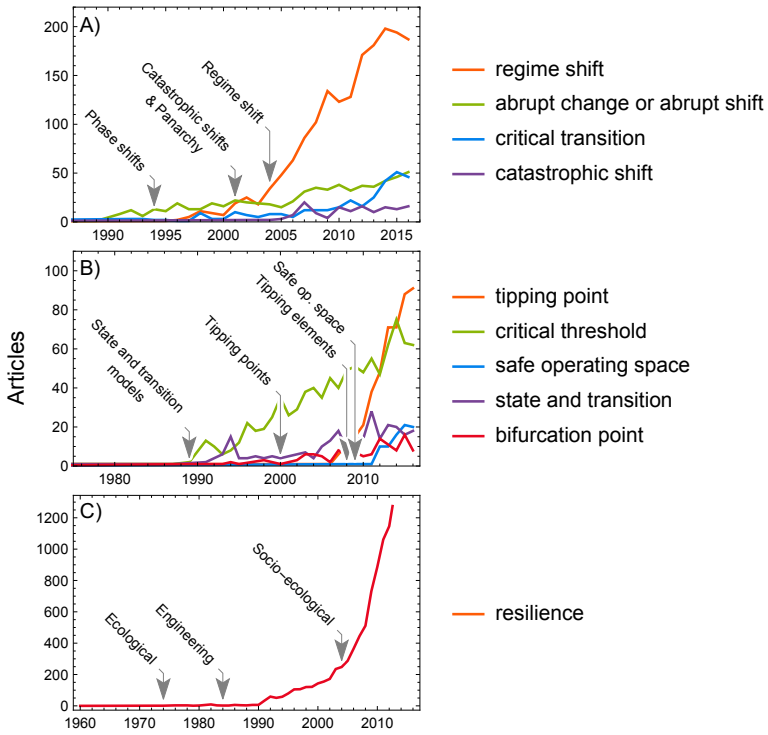

Figure S1. Number of publications per year using the terms related to (A) transitions between self-reinforcing states, (B) thresholds separating self-reinforcing states, and (C) the term resilience. Grey arrows mark influential papers that introduced, crystallized, and/or popularized concepts related to abrupt change. In (C) arrow labels denote introduction of sub-definition of resilience. Data are "from web of science" and only include papers from journals classified as "ecology," "environmental sciences," and a number of related fields in natural science. Note that "phase shifts" is not included in the data summary because this term is frequently used for describing transitions between different states of matter (i.e. melting of ice), rather than changes in ecological systems. References with arrow-markers correspond to:

Catastrophic shifts: "Catastrophic shifts in ecosystems" Scheffer, M. et al. (2001) *Nature* 413, 591-596.

Ecological resilience: "Resilience and stability of ecological systems" Holling, C.S. (1973) *Ann. Rev. Ecol. Syst.* 4, 1-23.

Engineering resilience: "The complexity and stability of ecosystems" Pimm, S.L. (1984) *Nature* 307, 321-326.

Panarchy: "Panarchy: Understanding Transformations in Human and Natural Systems" edited by Gunderson, L.H. & Holling, C.S. (2001) *Island Press.*
"Understanding the Complexity of Economic, Ecological, and Social Systems" Holling, C.S. (2001) *Ecosystems* 4, 390-405.

Phase shifts: "Phase shifts, and large-scale degradation of a Caribbean coral reef" Hughes, T.P. (1994) *Science* 265, 1547-1551.

Regime shifts: "Regime shifts, resilience and biodiversity in ecosystem management" Folke, C. et al. (2004) *Ann. Rev. Ecol. Evol. Syst.* 35: 557-581.

Resistance: "The complexity and stability of ecosystems" Pimm, S.L. (1984) *Nature* 307, 321-326.

Safe operating space: “A safe operating space for humanity” Rockstrom, J. et al. (2009) *Nature* 461, 472-475.
Social-ecological resilience: “Resilience, Adaptability and Transformability in Social– ecological systems” Walker, B. et al. (2004) *Ecology and Society* 9, 5.
State and transition: “Opportunistic management of systems not at equilibrium” Westoby, M. et al. (1989) *J. Range. Management* 42: 266-274.
Tipping element: “Tipping elements in the Earth’s climate system” Lenton, T.M. et al. (2008) *Proc. Natl. Academ. U.S.A.* 105, 1786-1793.
Tipping point: “The Tipping Point” Gladwell, M. (2000) *Hachette Book Group*.

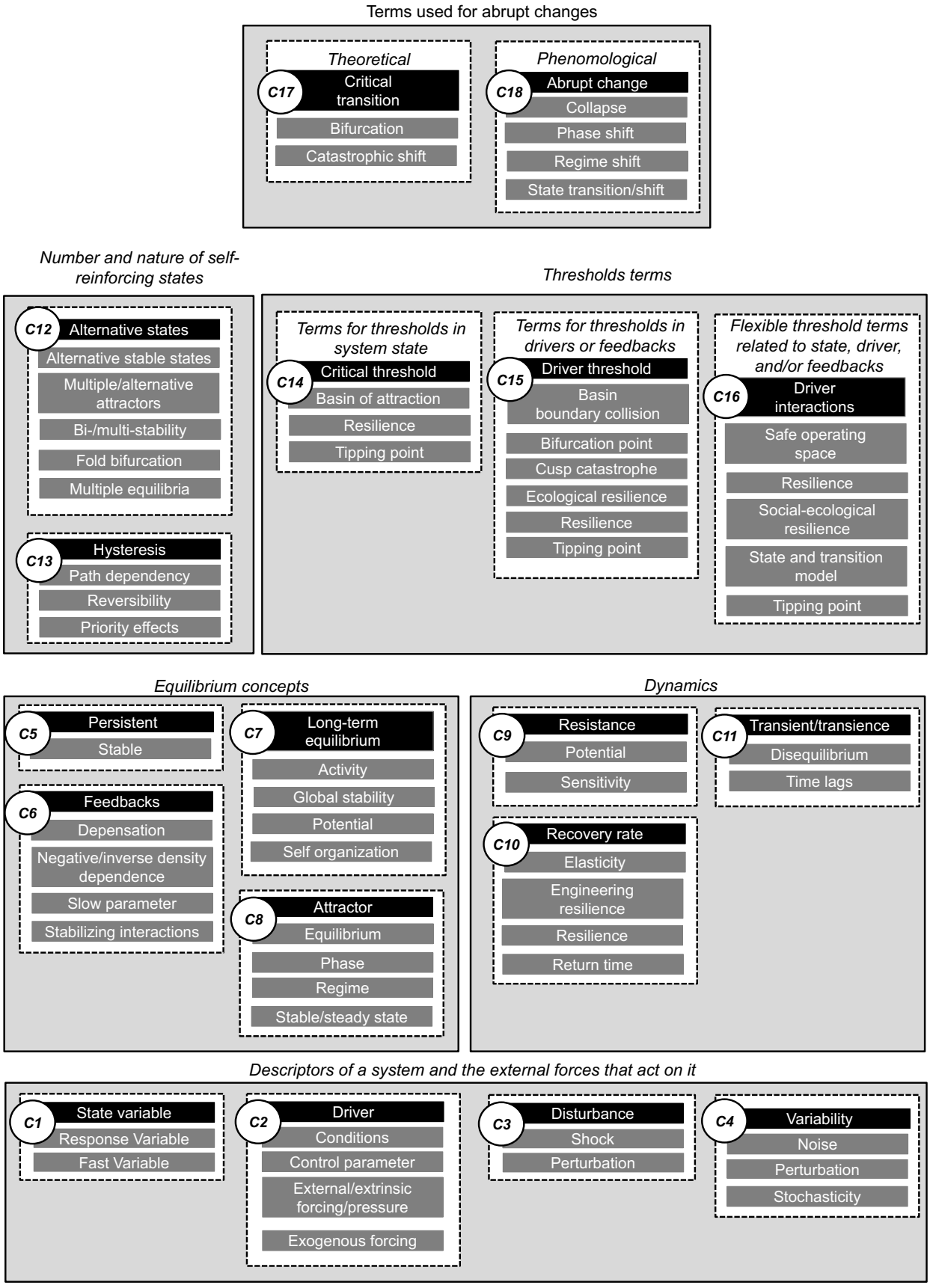
Terms used for abrupt changes
Theoretical
C17
Critical transition
Bifurcation
Catastrophic shift
Phenomological
C18
Abrupt change
Collapse
Phase shift
Regime shift
State transition/shift
Number and nature of self-reinforcing states
C12
Alternative states
Alternative stable states
Multiple/alternative attractors
Bi-/multi-stability
Fold bifurcation
Multiple equilibria
C13
Hysteresis
Path dependency
Reversibility
Priority effects
Thresholds terms
Terms for thresholds in system state
C14
Critical threshold
Basin of attraction
Resilience
Tipping point
Terms for thresholds in drivers or feedbacks
C15
Driver threshold
Basin boundary collision
Bifurcation point
Cusp catastrophe
Ecological resilience
Resilience
Tipping point
Flexible threshold terms related to state, driver, and/or feedbacks
C16
Driver interactions
Safe operating space
Resilience
Social-ecological resilience
State and transition model
Tipping point
Equilibrium concepts
C5
Persistent
Stable
C6
Feedbacks
Depensation
Negative/inverse density dependence
Slow parameter
Stabilizing interactions
C7
Long-term equilibrium
Activity
Global stability
Potential
Self organization
C8
Attractor
Equilibrium
Phase
Regime
Stable/steady state
Dynamics
C9
Resistance
Potential
Sensitivity
C11
Transient/transience
Disequilibrium
Time lags
C10
Recovery rate
Elasticity
Engineering resilience
Resilience
Return time
Descriptors of a system and the external forces that act on it
C1
State variable
Response Variable
Fast Variable
C2
Driver
Conditions
Control parameter
External/extrinsic forcing/pressure
Exogenous forcing
C3
Disturbance
Shock
Perturbation
C4
Variability
Noise
Perturbation
Stochasticity

Figure S2. Overlapping terms are currently used to describe ecological systems and abrupt change (Figure S1). As a move towards clarification, we identified clusters of terms that are frequently used to describe very similar concepts. Clusters are denoted as "*C#*" and correspond to boxes with dashed lines in Figure S2. For instance, "driver", "control parameter", and several other terms have all been used to describe exogenous factors that influence an ecological system. Therefore, these terms make up a cluster (*C2*). This process takes 69 commonly used terms and reduces them to 18 clusters, highlighting the current potential for miscommunication. Note that several terms appear in more than one cluster. Conceptual and terminological "clusters" are bounded by boxes with dashed lines. Terms within each cluster are frequently used in the abrupt change literature and have similar, but not identical meanings. Within each cluster, the term with a black background in each cluster is the term that we favor in the main text. The y-axis roughly denotes a hierarchy, where clusters higher on the y-axis are built from terms lower on the y-axis axis. There is no meaning ascribed to the x-axis.