PHILOSOPHICAL TRANSACTIONS B

royalsocietypublishing.org/journal/rstb

Review

Cite this article: Turner MG *et al*. 2020 Climate change, ecosystems and abrupt change: science priorities. *Phil. Trans. R. Soc. B* **375**: 20190105.
http://dx.doi.org/10.1098/rstb.2019.0105

Accepted: 8 August 2019

One contribution of 20 to a theme issue 'Climate change and ecosystems: threats, opportunities and solutions'.

Subject Areas:
ecology

Keywords:
thresholds, regime shift, resilience, ecological memory, disturbance

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Climate change, ecosystems and abrupt change: science priorities

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Ecologists have long studied patterns, directions and tempos of change, but there is a pressing need to extend current understanding to empirical observations of abrupt changes as climate warming accelerates. Abrupt changes in ecological systems (ACES)—changes that are fast in time or fast relative to their drivers—are ubiquitous and increasing in frequency. Powerful theoretical frameworks exist, yet applications in real-world landscapes to detect, explain and anticipate ACES have lagged. We highlight five insights emerging from empirical studies of ACES across diverse ecosystems: (i) ecological systems show ACES in some dimensions but not others; (ii) climate extremes may be more important than mean climate in generating ACES; (iii) interactions among multiple drivers often produce ACES; (iv) contingencies, such as ecological memory, frequency and sequence of disturbances, and spatial context are important; and (v) tipping points are often (but not always) associated with ACES. We suggest research priorities to advance understanding of ACES in the face of climate change. Progress in understanding ACES requires strong integration of scientific approaches (theory, observations, experiments and process-based models) and high-quality empirical data drawn from a diverse array of ecosystems.

This article is part of the theme issue 'Climate change and ecosystems: threats, opportunities and solutions'

1. Introduction

The magnitude and pace of anthropogenic climate change are increasing the likelihood of abrupt changes in terrestrial, aquatic and marine ecosystems worldwide [1]. As temperatures rise, coral reefs experience mass bleaching and mortality [2], kelp forests shift to seaweed turfs or sea urchin barrens [3], the duration of winter ice on lakes drops steeply [4], and aquatic and terrestrial ecosystems in the Arctic rapidly transform [5]. As droughts intensify, tree mortality soars [6], forest carbon uptake plummets [7], fires become much more frequent [8] or severe [9], and terrestrial ecosystems long considered fire-resistant begin to burn [10,11]. Although abrupt ecological changes have accompanied global climate changes during past millennia [12,13], the need to understand how ecosystems will respond to contemporary anthropogenic climate change is growing as warming accelerates. Other drivers (e.g. land cover, land use, nutrient fluxes and transport, harvest of living resources) are also changing [14]. These

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changing drivers may make ecosystems more fragile and interact with climate in novel ways [15]. Understanding the causes of abrupt change in ecological systems (ACES) is important because consequences for ecosystems and human wellbeing are profound and increasing.

Societal solutions to slow the rate of climate change are critical, but scientific research aimed at understanding why, where and when further big ecological changes are likely to occur is also sorely needed. A large body of theory has been developed around thresholds, tipping points and regime shifts (e.g. [16]), but translating this theory to real-world ecosystems has lagged [1]. Interactions among multiple drivers and feedbacks that can trigger abrupt changes are poorly understood, and consequences of slow changes (relative to human lifespan and the duration of many scientific studies) pose challenges [17,18]. We highlight five insights emerging from empirical studies of ACES across diverse ecosystems and suggest research priorities to advance understanding of ACES in the face of climate change.

2. Insights about abrupt changes in ecological systems

Well-documented case studies of ACES exist for some ecosystems, including some of the diverse systems in which we work. Here, we use case studies to highlight emerging general insights, illustrate the diversity of ACES already observed and frame ideas for future research.

(a) Ecological systems may show abrupt changes in some dimensions but not others

Ecosystem type (e.g. forest, grassland, wetland), species composition, biomass, productivity and the presence of a key species or functional group may all respond differently to changing drivers. Thus, an abrupt change in one dimension of an ecosystem does not necessarily imply an abrupt change in others, and the drivers to which they respond may also vary. For example, abrupt changes in diatom communities over the last 2600 years in tidal communities in the Galapagos were linked to extrinsic forcings from changing tidal regime, while the abrupt shift from mangroves to microbial mats was unrelated to the diatom community shifts and known external forcings [19]. Dominant drivers of abrupt changes also differ among open-ocean ecosystems and more localized aquatic ecosystems such as coral reefs, kelp beds or lakes [20]. In open-ocean ecosystems, abrupt shifts tend to follow changes in climate and circulation. In local aquatic ecosystems, harvest, predator control and trophic cascades [21] can cause abrupt shifts. When evaluating ACES, it is critical to specify the ecological dimensions (i.e. response variables) in which ACES are expected as well as the driver(s) [1,22]. It is equally important to specify the bounds of the system, which are essential for defining drivers and state and for interpreting patterns of abrupt change [23]. Studies of ACES must recognize that some dimensions of ecological systems are more prone than others to abrupt changes.

(b) Trends in climate extremes may be more likely to trigger abrupt changes in ecological systems than trends in mean climate

Climate variability is expected to increase as anthropogenic warming continues [24], and extremes (historically rare fluctuations in weather, often defined as events that fall outside the 5th–95th percentile of the historical range of variability; [25,26]) are projected to become more intense, more frequent and of longer duration in many regions globally [27,28]. Recent weather events are emblematic of expected changes in climate extremes [15,29,30]. Persistent extreme drought in 2018 set the stage for large wildfires in western North America and massive grassland yield reductions and forest canopy browning in central Europe [31,32]; a heatwave in 2017 in southern Europe and the Middle East included record-breaking temperatures in Iran [33,34]; and recent typhoons and hurricanes were accompanied by exceptionally high windspeeds (e.g. Typhoon Mangkhut) and rainfall amounts (e.g. Hurricane Harvey). However, understanding how climate extremes affect ACES is still nascent because extremes are rare [15], and not all extreme events produce abrupt changes. For instance, experimental combinations of extreme heat (43–53°C) and drought slightly altered species composition but did not fundamentally change mesic grasslands in the central USA [35]. Nonetheless, a growing number of empirical studies suggest that climate extremes can force abrupt ecological changes [36,37]. Recurrent episodes of coral bleaching and mass mortality since 1980 on reefs throughout the tropics have been driven by extreme heat waves, not average warming of sea surface temperatures [38]. In lakes and reservoirs, extreme rainfall events have produced massive nutrient pulses that cause sudden blooms of toxic cyanobacteria [39]. In Northern Hemisphere oceans, high temperatures and a strongly positive phase of the Arctic oscillation are associated with nearly synchronous abrupt shifts in pelagic food web structure [40].

Climate extremes that interact with disturbance also can produce ACES. For example, extreme drought plus wildfire quadrupled tree mortality in a tropical forest relative to similar forests that were affected by the drought but not by the fire [41]. Over millennial timescales, extreme droughts and floods have been linked to the collapses and regional abandonment of early agricultural systems [42–44]. As climate change continues, evidence increasingly suggests that climate extremes will generate ACES in advance of responses to more slowly changing average conditions.

(c) Interactions among multiple drivers often produce abrupt changes in ecological systems

Climate is one of many correlated drivers of ecosystem change in recent decades [14]. Ecosystems seldom respond to drivers in isolation, and ACES frequently arise from interactions among multiple drivers and disturbances rather than changes in a single driver. The palaeoecological record indicates that ACES have occurred repeatedly in many regions (e.g. [45–47]). Although major climate changes may have been sufficient to ensure some ACES (e.g. [48–51]), their timing and rates likely depended upon synergistic interactions among multiple drivers. For example, repeated collapses of populations of eastern hemlock (*Tsuga canadensis*) and American beech

(*Fagus grandifolia*) over the last several thousand years may be due to combined effects of climate change, density-dependent competition among trees and pathogen outbreaks [52]. Over the past several millennia, a subalpine forest in Colorado (USA) abruptly shifted from closed canopy forest to a spatially patterned habitat with open meadows and narrow bands of closed forests [53,54]. Regional cooling and increased snowpack drove this trend, but abrupt forest change was triggered after widespread wildfires burned *ca* 80% of the landscape [53,54]. These spatial patterns persist today, likely because local feedbacks were initiated among soils, snowdrifts and forest bands, which in turn stabilized a new relationship between climate and vegetation [55,56]. Contemporary studies also point to disturbance as a catalyst for climate-driven vegetation change, especially when climate conditions begin to exceed limits that allow for self-replacement of a species assemblage [57,58]. High-severity fires followed by drought years are leading to very low tree regeneration in northern conifer forests and the potential for an abrupt transition to non-forest [59,60].

Abrupt change in marine and aquatic ecosystems also often involves multiple drivers that interact with climate [20]. For example, climate change altered the thermal pattern and food web of the Black Sea after 1974. During 1988–1993, changes in fishing caused a sharp transition in the food web to a new configuration that appeared stable until at least 2005 [61]. Similar interactions occur in inland lakes. Extensive decline in the walleye (*Sander vitreus*) fishery of Wisconsin, USA, followed loss of habitat to climate warming [62]. Harvest policies designed in a more benign climate caused overharvest and recruitment failure of walleye as habitat declined [63]. Interactions among drivers had synergistic rather than additive effects.

Land-cover change can amplify or dampen effects of climate change and alter the likelihood of ACES. Surface albedo and moisture availability affect water and energy fluxes that alter conditions both locally (e.g. temperature and humidity dictate atmospheric moisture demand) and remotely (e.g. via effects on large-scale atmospheric circulation). Land-cover transitions can abruptly change surface climate if albedo and evapotranspiration rates are altered. For example, conversion of tundra to boreal forest reduces albedo and can cause warming of 1–7°C depending on season [64,65]. Conversion of forests to grasslands or unirrigated crops in the tropics also causes warming because although forest albedo is lower, transpiration rates are high [66,67]. Urbanization can lead to surprising interactions that amplify climate warming beyond the well-studied urban heat island [68–70], as in coastal southern California (USA), where urban heat and aridity have decreased the frequency and thickness of summer stratus clouds that provide critical summer shade to drought-sensitive ecosystems [71,72]. The frequency of daytime summer stratus clouds has decreased by approximately 30% over the past 45–70 years, enhancing summer solar radiation [72]. Climate–land-cover interactions can drive abrupt changes in ecosystem productivity [73,74], carbon fluxes [75], vegetation distributions [76,77] and disturbance regimes including wildfire [72].

Disease outbreaks offer additional examples of ACES driven by interactions of climate with other drivers. Pathogenic organisms (any organism that causes disease in a host) are ubiquitous in ecological systems, but emergent or introduced pathogens can have devastating impacts on ecological function, especially if infected hosts are already stressed by changing climate [78,79]. The ongoing mass extinction of amphibians infected with chytrid fungus, *Batrachochytrium dendrobatidis*, is exacerbated by changing climate [80], and some population declines are most pronounced following early spring thaws [81]. There are many arthropod, rodent and water-borne diseases for which transmission dynamics are climate-sensitive, and disease impacts are expected to shift in range and intensity with changes in temperature, seasonality and precipitation [82,83]. Mosquito-borne West Nile virus has had substantial impacts on North American avifauna since it emerged in 1999 [84,85], and the magnitude of avian mortality and human incidence is associated with changes in precipitation and milder winters [86,87]. Fungal infections and plant pests are generally expected to cause greater plant damage as climate warms [88], although pathogen-driven changes to primary productivity are likely to be highly context-dependent due to interactions with precipitation, soil nutrients and other environmental drivers [78]. Predicting ACES requires frameworks that explicitly incorporate multiple drivers, including climate, and identify the kinds, levels and interactions among drivers that are likely to produce ACES.

(d) Contingencies matter (a lot) for abrupt changes in ecological systems

The likelihood of ACES strongly depends on contingencies, and we consider four: the ecological memory in an ecosystem, the frequency and sequence of disturbances, spatial context and whether an ecosystem was preconditioned to a changing driver. These contingencies and how they may be influenced by climate change are poorly understood in most ecosystems.

Ecological memory refers to the adaptations, individuals and materials that persist during and after a disturbance event [57,89–91]. Disturbances create complex spatial mosaics of variable severity [92] that establish the post-disturbance legacies that maintain ecological memory. These contingencies depend both on the state of the system at the time of disturbance and the characteristics of the disturbance event, and they often determine the future trajectory of the ecosystem. The likelihood of ACES increases when legacies and ecological memory are diminished [57].

The frequency and order of disturbances affect the likelihood of ACES in at least two ways. *Linked disturbances* [93] occur when one disturbance interacts with a subsequent disturbance by changing its extent, severity or probability of occurrence. For example, a forest fire may reduce the likelihood of a subsequent fire until fuels again accumulate, and the severity of the first fire may influence severity of the next fire [8,94]. Similarly, invasion of cheatgrass (*Bromus tectorum*) in semiarid grasslands increases the size and severity of subsequent fires [95]. *Compound disturbances* [96] occur when two disturbances that occur in a short period of time have a synergistic effect that cannot be predicted from the sum of the individual disturbances. For example, clearcutting followed by prescribed fire in jack pine (*Pinus banksiana*) forests produced unique plant communities distinct from those found after wildfire or clearcutting alone [97]. Compound disturbances can reduce ecosystem resilience and lead to abrupt change if they disrupt recovery dynamics. Forest fires that burned within a few years of a high-severity bark beetle outbreak in Douglas-fir (*Pseudotsuga menziesii*) forests had compound effects because the seed sources needed for trees to regenerate were absent [98]. The prevalence of compound effects that produce ACES is likely to increase with warming climate because many natural disturbances are forced, in part, by climate. Furthermore, compounding effects of multiple climatic drivers can lead to extreme events that are unprecedented in the historical record, with profound consequences for ecosystems and society [15].

As disturbance frequency, severity and size change with climate, ecological memory is being altered in ways likely to produce ACES. In North American boreal forests, where black spruce has dominated for thousands of years with infrequent stand-replacing fire, more frequent, severe fires are burning deeply into the organic soil layer, reducing legacies and causing abrupt changes to a new deciduous forest state [99]. Boreal peatlands also are facing ACES. Historically, high water tables made these systems resistant to fire [100,101]. However, drawdown of the water table is now interacting with wildfire to increase the depth of burn [101] and reduce the capacity for moss regeneration [102]. The loss of surface peat—a material legacy—is causing *Sphagnum*-dominated peatlands to change abruptly to shrub- and herb-dominated meadows.

Marine ecosystems are also changing abruptly in response to compound disturbances. On the Great Barrier Reef, coral life histories, composition and distribution are shaped in part by recurrent cyclones. Historically, the interval between cyclones allowed sufficient time for reefs to recover before they were again disturbed. This disturbance regime is now being altered by successive coral bleaching events triggered by extreme heat events, recorded first in 1998 and subsequently in 2002, 2016 and 2017 [91]. The severity of bleaching and coral mortality in 2016 was unaffected by the bleaching 14 years earlier, because coral assemblages had time to recover. However, the response of corals exposed to high temperatures in 2017 depended strongly on the legacy of bleaching and mortality 1 year earlier. It took a lot more heat exposure to generate the same level of bleaching in 2017, because populations of thermally sensitive species were severely depressed by mass mortality 1 year earlier and surviving corals were more robust [91]. Additionally, coral recruitment on the Great Barrier Reef declined by 90% in 2018, following the loss of adult brood stock in the back-to-back bleaching events [103]. It seems impossible to project the future of ecosystems without better understanding of how sequences of extreme events shape ecosystem memory; it is not safe to assume that future disturbances will affect ecosystems as they did in the past. It is critically important to understand how disturbance regimes will change with climate and when linked or compound effects of disturbance interactions are likely to produce ACES.

When legacies are lost and local ecological memory diminished, the importance of *spatial context* for ACES increases because the surrounding landscape or seascape becomes the key source for new propagules [104]. Trajectories of ecosystem change also become less predictable. Distance to seed source may determine whether an abrupt change from forest to non-forest persists after fires of unusual size and severity (e.g. [105]). Similarly, coral larvae from populations adjacent to the path of a cyclone readily replenish nearby disturbed reefs, whereas the greater than 1000 km scale of mass coral bleaching has exceeded the dispersal capacity of the larvae and caused recruitment to collapse [103]. Spatial context is also important if habitat connectivity interacts with a climate driver to influence the likelihood of ACES. For example, estuarine seagrass beds will be exposed to greater wave energy as storms intensify with climate warming, and the size and connectivity of seagrasses interacts with wave energy to determine whether beds persist [106].

Pre-conditioning of a system to a changing driver can reduce the likelihood of ACES if the system has time to adapt in ways that minimize the loss of ecological memory. Experimental grasslands that experienced recurrent moderate droughts were more resilient to extreme drought than grasslands that had only experienced ambient weather conditions [107]. Pre-exposure to drought modified community response, reduced species sensitivity, shifted elemental composition in leaves and induced opposite metabolic responses of shoots and roots [107,108]. Properties such as diversity, redundancy, connectivity and biomass also become important mediators of ACES during periods of environmental change [109]. Many ecosystems become less diverse (e.g. through competitive exclusion), which can make them more prone to ACES as environmental conditions change [110–112]. A recent analysis of more than 40 grassland diversity experiments worldwide shows that ecosystem productivity is less affected by climate extremes when plant diversity is high [113]. Conversion of diverse natural communities to crop fields or tree plantations often alters predator communities, reducing natural pest control and resulting in potentially disastrous ACES [114,115]. The potential for contingencies to amplify or dampen the likelihood of ACES underscores the critical need for place-based studies and deeper understanding of mechanisms and feedbacks associated with abrupt change.

(e) Tipping points are key (but not the only) causes of abrupt changes in ecological systems

Many abrupt changes are associated with tipping points or 'critical transitions' where strong positive feedbacks within an ecosystem lead to self-sustaining change (e.g. [116–119]). Such dynamics often, but not always, result from interactions of slowly changing processes with faster ones [120–122]. A great variety of examples of such slow–fast dynamics are known from diverse social and ecological systems [123]. In ecosystems, the slow variable is often a biogeochemical reservoir, climate, water depth in lakes [124] or growth rates of slow-growing organisms such as trees or corals. The fast variable that changes abruptly at a critical value is often a fast-growing organism such as an insect pest, harmful algae in lakes or coastal oceans or a disease agent. A classic example comes from the slow growth of spruce trees interacting with the migratory cycle of forest birds and the high capacity for population growth of spruce budworm, a defoliating insect [125]. When the spruce canopy is well developed and forest bird populations are low, budworm populations expand and defoliate extensive areas of forest. Outbreaks are rapid, depending on a threshold in budworm population growth set by the slow growth of the spruce canopy. Overall, the effects of fast events (including extreme weather or disturbance events) can be large and long lasting relative to their short duration.

Identifying nonlinear responses and determining whether and where they can give rise to ACES are increasingly important as climate warms. For example, small changes in temperature or aridity can lead to surprisingly large fires because burned area increases nonlinearly with aridity [126]. Historically, a mere 0.5°C increase in the mean annual temperature during the Medieval Climate Anomaly

[127] was associated with increased fire size, frequency or severity across a range of forests [53,128–131]. During the twentieth century, years with spring and summer temperature anomalies greater than 0.5°C resulted in many large fires in western North America [132–134]. Increased frequency of dry conditions decreased habitat, recruitment and stock sizes of valuable walleye (*S. vitreus*) stocks in inland lakes of the western Great Lakes region of North America [62]. In southern Wisconsin (USA) lakes, nonlinear effects of storm size, precipitation and phosphorus loading events [39] drive blooms of cyanobacteria [135]. Events that exceed a threshold of accumulated heat exposure on Australia's Great Barrier Reef trigger extensive coral mortality and regional-scale shifts in coral assemblages based on responses of different taxa to heat stress [38].

Tipping points can occur at many scales. The concept of 'tipping elements' was introduced for large subsystems of the global climate system for which, under particular conditions, i.e. at a 'tipping point', a small perturbation could cause a qualitative change in future state [117]. Candidate tipping elements included two biomes—the Amazon rainforest and boreal forests—and the Sahel vegetation-climate system [117]. In the Amazon, rainfall–recycling feedbacks can couple the dynamics of large areas of the forest [136], while vegetation-fire feedbacks and anthropogenic ignitions can generate multiple stable states at small spatial extent [137]. In boreal forests, the area with alternative stable states of tree cover for the same levels of environmental drivers [138] is smaller than originally estimated [118], but mechanisms that can maintain alternative stable states have been identified [139]. Insect pest outbreaks [140] and feedbacks to fire regimes [141] may give rise to more ACES in boreal forests. In the Sahel, a vegetation–albedo–rainfall positive feedback mechanism was originally proposed to explain alternative stable states of vegetation [142,143], but recent observations support an alternative vegetation–rainfall–recycling positive feedback mechanism [144], potentially augmented by increased dust emission under dry conditions [145]. There are strong feedbacks between vegetation cover, soil moisture and rainfall at fine and intermediate scales [146–148], and vegetation–soil water feedbacks maintain vegetation patterns in parts of the Sahel at fine scales [149,150].

A related and largely unsolved problem is how feedbacks that cause a system to tip may interact across scales [151] and across systems [152,153]. The spatial scale of tipping is determined by several factors: the nature of the strong self-reinforcing feedback mechanisms; whether these feedbacks are coupled across scales; whether there are natural physical bounds on a system, as for a lake, and whether there is a spatially coherent change in forcing across a large area such that several otherwise independent but functionally equivalent systems tip at roughly the same time. Furthermore, the potential for *tipping cascades*, where tipping one system increases the likelihood of tipping another, potentially to where it becomes inevitable, has been recognized in the climate system [152,154,155] and for social–ecological systems [153]. If tipping cascades occur, a larger tipping element composed of the coupled components could be defined because they effectively share a tipping point. The case where tipping one system makes the tipping of another inevitable is most likely when strong positive feedbacks are present. However, causal connections can either amplify or dampen ecosystem variance, thereby intensifying [152] or removing early warnings of abrupt shifts [156]. There are counterexamples where tipping one system reduces the likelihood of tipping another [154,157]; understanding such dampening effects could also be important for avoiding undesirable change. Thus, mechanistic information about causal webs in ecosystems and the potential for such knock-on effects is critical. We see great promise in adapting the tipping element framework to encompass networks of strongly interacting variables in ecological systems.

3. Understanding the mechanisms that underpin abrupt changes in ecological systems is needed

Any research programme aimed at diagnosing ACES should investigate the mechanisms that underpin potential change. Inevitable changes after a threshold has been exceeded may be cryptic if they are lagged in time, especially in systems dominated by long-lived organisms [17,122]. Knowledge of underlying mechanisms may allow changes to be anticipated before they are observable. For example, processes that control tree regeneration determine, in part, whether forests may transition to non-forest vegetation following high-severity disturbance. Experiments can target mechanisms and identify temperature and moisture thresholds associated with key demographic rates [58], and observational studies can determine whether establishment and turnover patterns in actual landscapes are consistent with expectations [59,158]. Experiments have also identified consequences of extreme events for biotic communities [159–161]. For example, extreme drought imposed on experimental grasslands produced abrupt changes in community composition [162].

The mechanisms underpinning collapse, the most extreme form of abrupt change, warrant particular attention. Abrupt change qualifies as collapse if it meets four conditions: (i) the identity, or type, of the system [163] is lost; (ii) loss of identity happens relatively fast relative to system regeneration times; (iii) there is a substantial loss of ecological memory; and (iv) consequences are lasting [164]. The nature of collapse and the likelihood that a given system experiences collapse are closely related to system structure [164,165].

Mechanisms that underpin abrupt change are also intricately linked to feedbacks and thresholds that are sensitive to climate. During periods of plenty, individual overconsumption and explosive population growth can lead to long-term, boom–bust cycles. For example, elephant populations may prosper during wetter climate periods, with high population densities leading to negative effects on other species during drier periods [166] and creating the potential for large-scale die-offs during droughts [167]. At the same time, drought and herbivory can cause both short-term stochasticity and long-term stability in savannah understory vegetation communities [168].

Improved forecasting of ecological change must rely on mechanistic understanding. For example, different mechanisms underlie the increase in woody biomass that is observed in both wet and dry savannahs in Africa, and thus, projections for these savannahs differ [169]. Similarly, permafrost is thawing across high-latitude ecosystems as a result of climate warming [170], but variation in the mechanisms that drive thaw determines whether ACES ensue. Without mechanistic knowledge, ACES will be monitored and detected after they occur rather than forecasted in advance.

Table 1. High-priority research questions to motivate a research agenda for diagnosing ACES across a wide range of systems and scales.

Research questions
Ecological systems may show ACES in some dimensions but not others
— What constitutes sufficient observational evidence for detecting past or current ACES?
— Are ACES becoming more common, both within and across ecosystems?
— Are some dimensions of ecosystems (e.g. composition, structure, function) more prone to ACES than others, and if so, why?
— How well can early warning signs be applied to different dimensions of real-world ecosystems?
— How do ACES translate through levels of organization (e.g. species to ecosystems) and trophic networks?
Trends in climate extremes may be more likely to trigger ACES than trends in mean climate
— How is variance in drivers of abrupt change changing over time?
— How are the magnitude, duration and frequency of climate extremes changing over time and space?
— What types or sequences of extremes are likely to produce ACES?
— Under what conditions do climate extremes produce ACES?
— What ecosystems (globally) are most sensitive to climate extremes, and why?
Interactions among multiple drivers often produce ACES
— How do deterministic and stochastic drivers interact to produce ACES?
— What factors increased the frequency and extent of ACES in the past (e.g. using palaeoecological records of change)?
— Did changes in climate make past ACES inevitable?
— Are drivers of abrupt change shared or distinct among different ecosystems?
— How will ongoing climate change interact with other changing drivers, including disturbances and extreme events, to produce ACES and alter ecosystem trajectories?
Contingencies matter (a lot) for ACES
— How is ecological memory changing across different systems?
— To what degree are ACES dependent on adjacent or synchronous events?
— When does heterogeneity increase or decrease the likelihood of ACES, and does spatial heterogeneity (transient havens, refugia) buy time for systems to adapt to changing climate?
— How do slow processes mask or amplify ecological responses to rapid climate change?
— What is the role of subcontinental to global teleconnections (e.g. climate, trade) in generating ACES?
Tipping points are key (but not the only) causes of ACES
— Are threshold changing, and if so, which ones and why?
— What feedbacks stabilize new states, and what changes are reversible versus irreversible, or desirable versus undesirable?
— What are the key tipping elements within ecological systems and at different scales?
— When thresholds are exceeded, are effects likely to cascade through ecosystems and produce additional ACES? What feedbacks dampen or amplify the likelihood of tipping cascades?
— Do tipping points necessarily follow a particular sequence, and what happens if that sequence is disrupted? Can changes in the timing of different tipping points reduce the likelihood of cascades?

4. A scientific agenda for detecting abrupt changes in ecological systems

A more sophisticated and nuanced understanding of ACES—their causes and consequences, and how likely they are to manifest as climate change pushes ecosystems beyond their historical ranges of variation—should be a fundamental goal of ecological research on climate change. We suggest general questions and approaches that could form the backbone of a research agenda to understand and anticipate ACES as climate change continues (table 1). Our aim is to stimulate discussion and encourage new ways of approaching empirical study of climate change impacts.

The research required to understand ACES during this time of accelerating climate change must be multi-faceted and long term. The full arsenal of complementary research approaches, including long-term data, comparative study, experiments and models, is needed [171]. Long-term high-quality empirical time series at multiple scales, including instrumental and palaeoecological observations, are critical for detecting and understanding ACES. Comparative studies in which observations are repeated across regions in which levels or combinations of drivers vary spatially are also important, especially if manipulative experiments are infeasible. It would be unethical to conduct field experiments with many diseases, for example, and it is largely impossible to replicate many aspects of large disturbances, such as hurricanes. Experiments will retain their fundamental importance for isolating effects of individual drivers and testing for interactions. Field experiments have proven especially valuable for exploring effects of rare events, such as climate extremes [25]. Climate-extreme experiments following similar protocols have expanded to dozens of sites in Europe (e.g. [172]), and a grass-roots network aims to establish coordinated experiments across the globe [173]. Whole-ecosystem experiments have become one of the primary methods for determining how multiple drivers can result in abrupt ecological changes [171,174–177]. Natural experiments will be increasingly important, especially as ecologists strive to understand the long-term consequences of changing disturbance regimes (e.g. [91,103,178,179]).

As Earth's climate continues to warm, ACES will increasingly manifest across diverse ecosystems as drivers interact, disturbance regimes change and thresholds are exceeded. We argue that ecological research needs to reorient to a stronger emphasis on the temporal dynamics of ecosystems [180]. Such a research framework should recognize the likelihood of ACES, aim to understand the mechanisms and feedbacks underpinning such changes, and take full advantage of unplanned events. Innovative approaches for capturing long-term data sets are needed, and sustaining process-focused data collection is essential. Relevant baselines must be established now, so that further long-term changes, including ACES, can be detected and tracked. There is no equilibrial 'new normal' for the foreseeable future, but rather accelerating rates of change in multiple drivers are causing ecological changes to be hastened overall and punctuated by episodes of abrupt change. Impending fundamental changes on Earth will be widespread [181], and science is poised to extend the understanding of ecological change to diagnose ACES.

Data accessibility. This article has no additional data.

Authors' contributions. M.G.T. and S.R.C. drafted the manuscript from contributions by all coauthors based on materials presented by M.G.T. during the 2018 Sackler Forum at the National Academy of Sciences and by coauthors at an organized oral session (*Abrupt Change in Ecological Systems: When, Where, and Why?*) at the 2018 annual meeting of the Ecological Society of America. All authors contributed text, gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. We acknowledge the following sources of support to M.G.T. and S.R.C. for this work: UW2020 Initiative of the University of Wisconsin-Madison (M.G.T., S.R.C.); US National Science Foundation awards DEB-17-19905 (M.G.T.), DEB-14-55461 (S.R.C.) and DEB-14-44297 (S.R.C.); Joint Fire Science Program 16-3-01-4 (M.G.T. and Z.R.).

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