Journal of Ecology

British Ecological Society

Journal of Ecology 2011, **99**, 656–663 doi: 10.1111/j.1365-2745.2011.01798.x

SPECIAL FEATURE – ESSAY REVIEW
ECOLOGICAL CONSEQUENCES OF CLIMATE EXTREMES

An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research

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Summary

1. Growing recognition of the importance of climate extremes as drivers of contemporary and future ecological dynamics has led to increasing interest in studying these locally and globally important phenomena.

2. Many ecological studies examining the impacts of what are deemed climate extremes, such as heat waves and severe drought, do not provide a definition of extremity, either from a statistical context based on the long-term climatic record or from the perspective of the response of the system – are the effects extreme (unusual or profound) in comparison to normal variability?

3. A synthetic definition of an extreme climatic event (ECE) is proposed that includes 'extremeness' in both the driver and the response: an ECE is as an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability. This definition is accompanied by a mechanistic framework based on the concept that extreme response thresholds associated with significant community change and altered ecosystem function must be crossed in order for an ECE to occur.

4. *Synthesis*. A definition and mechanistic framework for ECEs is used to identify priorities for future research that will enable ecologists to more fully assess the ecological consequences of climate extremes for ecosystem structure and function today and in a future world where their frequency and intensity are expected to increase.

Key-words: climate change, drought, ecosystem sensitivity, extreme events, extreme weather, global change, heat wave, plant–climate interactions, state change, thresholds

Introduction

A well-accepted feature of forecast alterations to the global climate is an increase in the frequency and magnitude of climate extremes, such as severe drought, periods of heavy rainfall (and associated floods) and heat waves (IPCC 2007). Indeed, the signature of an increase in the occurrence and severity of climatic extremes is already apparent (Karl, Knight & Plummer 1995; Schar *et al*. 2004; IPCC 2007), with the European and Russian heat waves of 2003 and 2010 serving as recent examples of the potential for such extremes to have profound societal and ecological impacts (Ciais *et al*. 2005; Garcia-Herrara *et al*. 2010). From an ecological perspective, the unprecedented severity of such events highlights the pressing need to better understand the role that climate extremes will play in the future.

Growing recognition of the importance of climate extremes (Easterling *et al*. 2000; Jentsch & Beierkuhnlein 2008) has spurred on a number of recent studies, both observational and experimental, focused on the ecosystem impacts of periods of climatic extremity (e.g. Jentsch, Kreyling & Beierkuhnlein 2007). What is clear from these studies is that the ecological impacts of a period of climatic extremity can be highly variable. In some cases, a climate extreme, such as a heat wave or severe drought, may result in rapid mortality of populations or species (Weaver 1968; Breshears *et al*. 2005; Bigler *et al*. 2006, 2007; Gitlin *et al*. 2006; Miriti *et al*. 2007; Thibault & Brown 2008), large-scale and/or long-term changes in community structure and ecosystem function (MacGillivray *et al*. 1995; White *et al*. 2000; Haddad, Tilman & Knops 2002; Ciais *et al*. 2005; Mueller *et al*. 2005), and even shifts in ecotone boundaries (Allen & Breshears 1998). While for others, the primary effects are limited to individuals or a few populations, often with negligible ecosystem impacts (Van Peer *et al*. 2001, 2004; Marchand *et al*. 2005, 2006a,b; Milbau *et al*. 2005; Bokhorst *et al*. 2008; Kreyling *et al*. 2008; Arnone *et al*. 2011; Jentsch

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et al. 2011). Variation among studies may, in part, be caused by species- and/or system-specific attributes, but such variation also points to the difficulty and complexity of studying climate extremes. Climate extremes are difficult to study because of their rarity, and their complexity arises from the fact that the 'extremeness' of a climatic event is highly context-dependent in terms of both the historic climate record and what the system and its component species have experienced in the past. Consequently, the 'extremeness' of ecological response (e.g. whether a period of climate extremity merely alters the physiology of individuals or causes widespread mortality of a species) will partly depend on how the climate extreme is defined by the investigator and/or imposed on or experienced by the system. Surprisingly, many ecological studies examining the impacts of what are deemed climate extremes do not provide definitions of what constitutes extremity from either the context of the long-term climatic record (i.e. is it a statistical extreme?) or its effects on the system (i.e. are the effects unusual or profound in comparison to normal variability?). Without such definitions, it is difficult to determine if a lack of response is, for example, due to the ecosystem or its component species being resistant to a particular climate extreme or because the ecosystem did not actually experience a period when the climate was truly extreme.

As the number of ecological studies of climate extremes continues to increase, it is critical that we identify when climate conditions are extreme, determine what constitutes an ecological response that is extreme, and most importantly, we must be able to attribute the extreme ecological response to the period of climate extremity. The latter is particularly critical for elucidating what factors may contribute to differential sensitivity of ecosystems to climate extremes. Here, I consider those instances in which a climate extreme results in an extreme ecological response as 'extreme climatic events' (ECEs). The goals of this paper are to (i) provide a more synthetic and comprehensive definition of an ECE, (ii) develop a conceptual framework to guide future research investigating the impacts of climate extremes on ecosystems, and (iii) suggest new approaches to climate extremes research for the future.

A synthetic definition and mechanistic framework for ECEs

Before defining an ECE, it is instructive to consider more generally the definition of an extreme event. Following Sarewitz & Pielke (2001), an extreme event can be defined as "an occurrence that, with respect to some class of occurrences, is either notable, rare, unique, profound, or otherwise significant in terms of its impacts, effects or outcomes". The use of the term 'event' denotes its short duration (discreteness) relative to the magnitude of its effects (Jentsch, Kreyling & Beierkuhnlein 2007). This definition highlights the context-dependency of extreme events – what is extreme depends on both the record of occurrences available and the type of impact, effect or outcome being considered; and, thus, emphasizes the need to define extreme events synthetically, from both the 'driver' (occurrence) and 'response' (effect) perspectives (Fig. 1).

When considering ECEs in this synthetic context, defining the driver – a climate extreme – is much more straightforward than defining what constitutes an extreme response – the ecological effect. A climate extreme can readily be represented by the tails of a distribution for a particular climate parameter (e.g. mean, maximum, minimum temperature; Fig. 1), and consequently, what constitutes a climate extreme will be highly dependent on the available climate record. It is important to note, however, that climate extremes can be more complex than just the tails of a statistical distribution of temperature or precipitation, as in the case of severe drought, which often involves the combination of low precipitation amounts, extensive dry periods and high temperatures (Jentsch, Kreyling & Beierkuhnlein 2007). Nonetheless, statistical rarity of a climate period can and should be quantified in any study of ECEs.

In contrast, an extreme response is highly context-dependent with respect to the type of climate extreme, the system in question, and the time frame of examination. From an ecological response perspective, Gutschick & BassiriRad (2003) defined an extreme event (climatic or otherwise) as one in which the ability of an organism or population to acclimate is substantially exceeded, with often persistent effects after the event, resulting in longer-term impacts on fitness. While useful, by

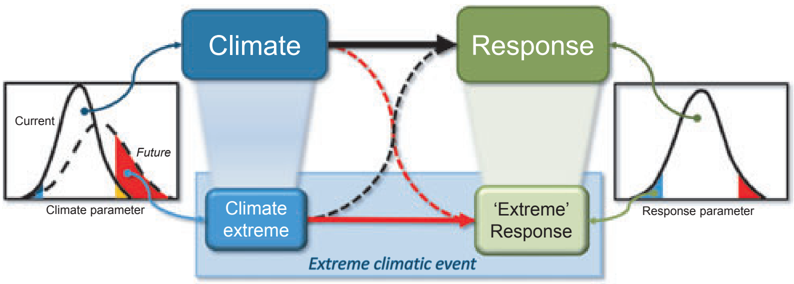

Fig. 1. Conceptual representation of an extreme climatic event. Climate variability can evoke a range of ecological responses (small to extreme, distribution on the right). Changes in climate means or variability may result in a response that is well within the range of variability for a system (solid black arrow) or one that is extreme (i.e. exceeds this range, dashed red arrow). Similarly, climate extremes (represented by tails of the distribution on the left) may (solid red arrow) or may not (dashed black arrow) result in an ecological response that is outside the typical or normal range of variability for a system. Here, an 'extreme climatic event' is defined synthetically as involving extremeness in both the climate driver and the ecological response.

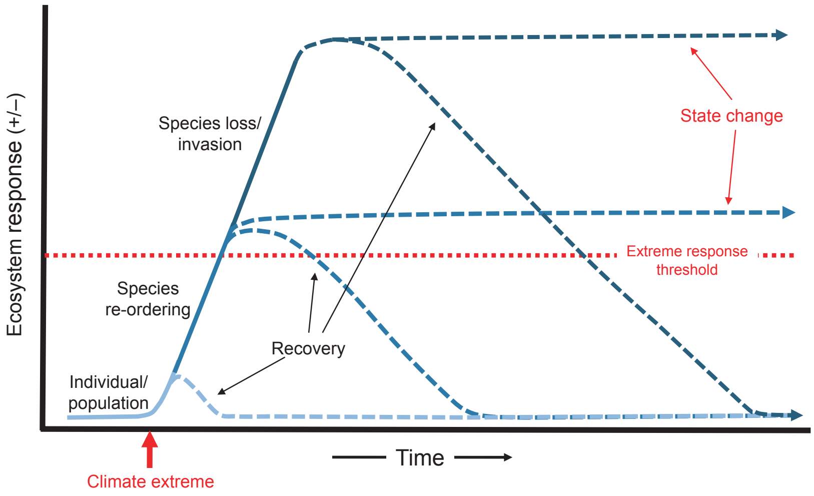

Fig. 2. A mechanistic framework for assessing responses to climate extremes. A period of climate extremity that primarily affects individual-level responses (physiology, growth, fitness) of particular organisms or populations will have a smaller effect (positive or negative) on ecosystem processes (i.e. productivity, nutrient cycling) than one that results in large shifts in species abundances (species re-ordering), or in local extinction of species or invasion by others. An 'extreme climatic event' is an episode or occurrence in which a period of statistical climate extremity alters ecosystem structure and/or function outside the bounds of what is considered typical or normal variability, as a consequence of crossing an extreme response threshold (dotted red line) in which individual-level effects cascade to higher hierarchical levels to result in significant changes in community structure and large ecosystem impacts. These alterations may be characterized by prolonged recovery and/or hysteresis, or may even lead to persistent state changes.

this definition of the most extreme response (i.e. left tail of the distribution; Fig. 1) is mortality of individuals or entire populations, and a period of climatic extremity (e.g. a 100-year drought) would not necessarily lead to an ecological response beyond the level of individuals or populations. Indeed, depending on the role and abundance of the species impacted, such responses may or may not result in changes at the community or ecosystem level that can be distinguished from background variability (see example below).

An ECE, conceptualized more synthetically to include 'extremeness' in both the driver and the response (Fig. 1), should evoke responses beyond the individual or population level, including the re-ordering of key or common species in the community, widespread species loss and/or invasion by novel species, with subsequent large and potentially persistent effects on ecosystem structure and function (Fig. 2; Smith, Knapp & Collins 2009). Certainly, mortality of individuals and/or populations and associated changes in fitness may underlie these higher-level responses, particularly if, for example, dominant species are impacted (e.g. Allen & Breshears 1998). However, to be useful in the context of large-scale change, an ECE must be defined more comprehensively to capture ecological responses that cascade across multiple hierarchical levels. Given this, I define an ECE as 'an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability' (i.e. an extreme response is evident, Fig. 2; see Landres, Morgan & Swanson 1999 for a discussion of variability). Because such profound alterations will be driven by changes in species abundances, loss of key species, and/or invasion by new species with different functional traits, likely outcomes of ECEs may include periods of prolonged recovery, significant hysteresis, and/or persistent state changes (Fig. 2; e.g. Allen & Breshears 1998; Haddad, Tilman & Knops 2002; Mueller *et al.* 2005; Thibault & Brown 2008).

There are several advantages to the more synthetic and comprehensive definition of an ECE provided above: (i) it articulates the requirements for extremity from both a driver and response perspective (Fig. 1) and (ii) it identifies *a priori* the ecological mechanisms that can lead to an ECE (Fig. 2). In doing so, this definition provides a basis for distinguishing between those instances where a statistically extreme climate period does not result in an extreme response (Fig. 1, dashed black arrow) from those instances where it does (Fig. 1, solid red arrow). It also provides a framework for elucidating the mechanisms that may give rise to these different responses (Fig. 2). Finally, the definition excludes from consideration those instances where an extreme response results from some aspect of climate other than a period of climate extremity (Fig. 1, dashed red arrow; see Smith, Knapp & Collins 2009 for examples).

The utility of this definition and accompanying mechanistic framework can be demonstrated by considering two examples. The first is from an on-going experiment designed to examine the impacts of extreme precipitation regimes on the structure and function of the tallgrass prairie ecosystem (Fig. 3; see Fay *et al.* 2000 for details). For over a decade, growing season precipitation regimes have been experimentally altered using rainfall manipulation shelters deployed over intact prairie (Fig. 3c), whereby periods of time between rainfall events have been increased by 50% without altering the total rainfall amount. The altered rainfall treatment has resulted in a threefold decrease in the mean number of growing season rainfall events, with the interval between events three times longer compared to the ambient regime (Fig. 3a,b). Such a regime is

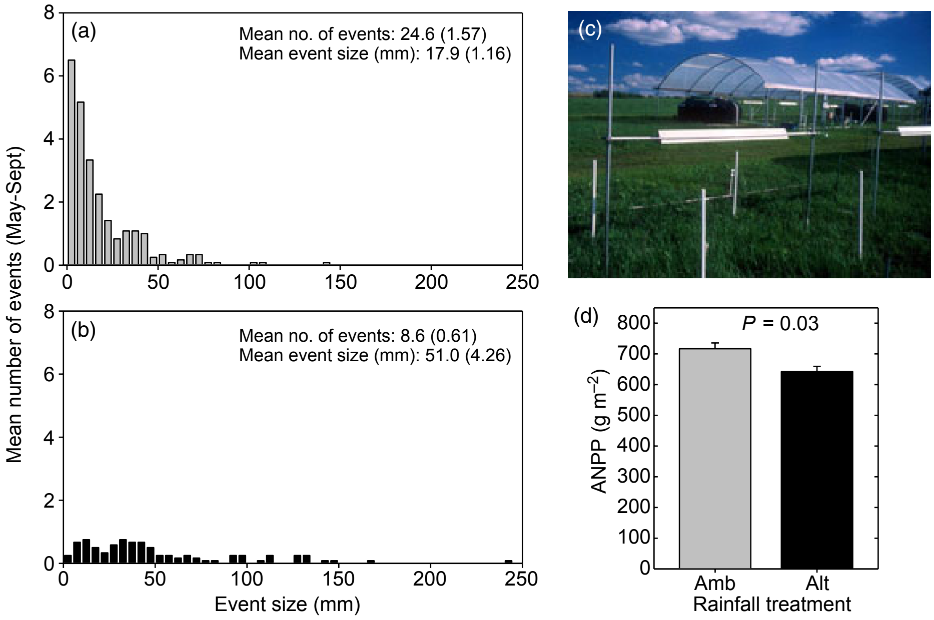

Fig. 3. The Rainfall Manipulation Plots (RaMPs) experiment, located at the Konza Prairie Biological Station (Manhattan, KS, USA), consists of 12 rainfall manipulation shelters (c) established in intact tallgrass prairie (see Fay *et al.* 2000 for details). Since 1998, growing season rainfall has been intercepted by roofs of the structures, collected and then either immediately applied (ambient regime, a) or applied as an altered regime (b), in which the time between rainfall events is increased by 50% without changing the total amount. The altered rainfall treatment has resulted in a more extreme precipitation regime, where the mean size of each event is three times larger than the ambient regime, while the number of rainfall events has decreased threefold. Despite the statistical extremeness of the precipitation regime imposed (no such regime has occurred in the documented record), the altered treatment has resulted in on average only a 10% decrease in above-ground productivity (ANPP, d). While this reduction is ecologically significant, such a decrease in production is well within the range of typical inter-annual variation in production observed for the tallgrass prairie, and thus by definition does not constitute an 'extreme' response. Photo credit: A. K. Knapp.

far beyond what has been observed in the historical climate record and thus represents a statistical extreme. However, the primary impact has been limited to reduced performance of only a few species (Fay *et al.* 2003), which has resulted on average in a 10% reduction in above-ground net productivity (Fig. 3d, Knapp *et al.* 2002). This modest alteration in ecosystem function has occurred without substantive changes in community structure, loss of species, or invasion by new species (Fig. 2), and while the reduction in production is significant ecologically, it is well within the natural range in variability observed for this system (Knapp & Smith 2001). Thus, although a period of climatic extremity has certainly been imposed, the ecosystem appears to be relatively resistant to this type of climate extreme, and according to the definition above, the grassland has not experienced an ECE. This conclusion is based on both the lack of profound impact on the ecosystem, as well as the absence of any mechanistic evidence that thresholds have been exceeded that could lead to an extreme ecological response (e.g. significant species re-ordering or loss of species, Fig. 2).

The second example involves a regional climate extreme that occurred across south-western North America in 2002–2003. This period was characterized by an extreme drought with respect to the long-term climate record and was accompanied by anomalously high temperatures. Here, the climate extreme resulted in widespread mortality of *Pinus edulis* (pinyon pine), a co-dominant species in pinyon–juniper woodland (Breshears *et al.* 2005). Such large-scale mortality events have been shown to shift ecosystem boundaries in the past (e.g. Allen & Breshears 1998) and rapidly alter ecosystem structure and function (e.g. Mueller *et al.* 2005), as well as significantly affect land surface conditions (Royer *et al.* 2011). Subsequent studies have linked Pinyon pine mortality to drought-induced carbon starvation of individual trees (Adams *et al.* 2009). In this case, we can conclude that an ECE has occurred because the statistically defined climate extreme resulted in an extreme response – one characterized by mortality of adult Pinyon pine trees, which subsequently cascaded up the ecological hierarchy to have profound and potentially long-lasting impacts on the ecosystem.

The examples above can be viewed as end-members with respect to the potential outcomes for climate extremes research. On the one hand, a statistical climate extreme was imposed but did not result in an extreme response for a tallgrass prairie ecosystem, and on the other hand, thresholds for extreme responses for pinyon–juniper woodland were clearly crossed (e.g. mortality of the dominant tree species, Fig. 2), resulting in large community and ecosystem impacts. A major challenge for the future will be for ecologists to increase our understanding of how and why ecosystems may differ in their vulnerability to experiencing an ECE, whereby an extreme ecological response can be attributed to a climate extreme. Key to this will be placing greater emphasis on quantifying thresholds for ecological processes that, when crossed, may lead to extreme responses. For example, in the case of the tallgrass prairie, independent studies of the responses of the dominant grasses, the dynamics of community structure, and the invasibility of the plant community all point to stability of the plant community as key to the resistance of tallgrass prairie ecosystem to the type of climate extreme imposed (Knapp *et al.* 2002; Nippert *et al.* 2009; Smith, unpublished data). Whether this will translate to ecosystem resistance to other types of climate extremity remains unknown but certainly demands further research.

Future research needs and approaches to the study of climate extremes

Before providing recommendations for future approaches to climate extremes research, it is important to consider how climate extremes and ECEs have been studied in the past and the advantages and limitations of these approaches. To date, the majority of studies of climate extremes might best be described as opportunistic. These opportunistic studies arise: (i) from concerted research efforts initiated after a period of climatic extremity is recognized (e.g. Allen & Breshears 1998), or (ii) when a climate extreme occurs during the course of an ongoing observational or experimental study (e.g. Haddad, Tilman & Knops 2002; Breshears *et al.* 2005; van Ruijven & Berendse 2010). Although these opportunistic studies, particularly those involving observational approaches, have the ability to capture large spatial and temporal scales, they often lack replication and cannot control for characteristics of the climate extreme (type, timing, magnitude) or for other covarying factors (e.g. disturbance regimes, pest outbreaks). Such studies also are limited in their ability to assess interactions between different types of climate extremes (e.g. severe drought vs. heat wave) or other factors, such as disturbance. And, of course, opportunistic studies are ultimately contingent upon a period of climatic extremity occurring during the lifetime of the study. To overcome these limitations, there are a growing number of studies that experimentally impose climate extremes via field experiments (e.g. Marchand *et al.* 2005; Jentsch, Kreyling & Beierkuhnlein 2007; Bokhorst *et al.* 2008; Arnone *et al.* 2011; Jentsch *et al.* 2011). While these experiments offer the advantage of greater control over the nature of the climate extreme imposed when compared to opportunistic studies, they have, to date, been limited to a single climate extreme level (e.g. a 100-year drought or 30-year heat wave) imposed at a relatively small spatial scale. Moreover, few have considered interactions between different climate extremes (but see White *et al.* 2000; Van Peer *et al.* 2004; Jentsch, Kreyling & Beierkuhnlein 2007) or other factors (e.g. disturbance, N deposition; e.g. Wang *et al.* 2008), and rarely have they addressed the role of multiple periods of climate extremity or the timing or sequence of climate extremes (Miao, Zou & Breshears 2009; De Boeck *et al.* 2010).

Opportunistic studies also are limited with respect to their ability to document the full extent of responses of ecosystems to climate extremes and their vulnerability to ECEs. However, opportunistic studies have been very successful in detailing ecosystem impacts of large magnitude as a consequence of crossing one or more thresholds for extreme responses (i.e. species re-ordering or species loss). Thus, they tend to capture the full magnitude of ECEs more often than experiments. This is because attention is typically not drawn to a climate extreme unless large ecosystem consequences are readily apparent (e.g. widespread mortality of a dominant species), and consequently those climate extremes that have limited impacts, or those that would not be considered ECEs by definition, tend to be understudied with the opportunistic approach. Experiments, on the other hand, have the potential to capture responses to multiple levels of climate extremes across the full range of hierarchical levels (Fig. 2). Clearly, for experiments to have their greatest value, they need to be imposed at large enough scales and for long enough periods of time so that responses will not be constrained to the individual or population level (Smith, Knapp & Collins 2009). Otherwise, it will be difficult to determine if the lack of large impacts or the absence of evidence for exceeding extreme response thresholds is due to the limited duration or scale of the experiment or because the system is resistant to a particular climate extreme. Despite this limitation, experiments do have the ability, if designed properly, to identify those critical ecological thresholds that may result in an extreme response, whereas opportunistic studies do not.

Given the predicted increase in frequency and severity of climate extremes with global climate change (IPCC 2007), we should continue to opportunistically study these important drivers of ecological dynamics and change. Despite their limitations, opportunistic studies have significantly advanced our understanding of the vulnerability of ecosystems to ECEs. However, more urgently needed are large-scale and long-term field experiments designed specifically to address critical gaps in our mechanistic understanding of how and why ecosystems may differ in their sensitivity to experiencing ECEs. Key elements of future experiments that can address these research gaps are summarized below, and an example of one such experiment is provided in Box 1.

1. For essentially all major ecosystems and biome types globally, we lack detailed knowledge of the magnitude, type and combination of climate extremes that are most likely to result in response thresholds being exceeded and, consequently, for ECEs occurring. This is a daunting challenge, but at the very least, future experiments should impose periods of climate extremity at multiple levels using, for example, a replicated regression approach (Box 1), whereby multiple levels of a climatic parameter can be applied in a statistically powerful way (Cottingham, Lennon & Brown 2005). With such an approach, climate extremes field experiments could follow the example of growth chamber and greenhouse studies that have successfully assessed response thresholds of individual species to temperature and water deficits (e.g. Hamerlynck *et al.* 2000; Larcher, Kainmuller & Wagner 2010).
2. Also needed are experiments that impose multiple levels of climate extremity at different times of the year, or as multiple occurrences (Box 1) and/or in different sequences within and between years. These types of experiments can address issues of timing and the potential for cumulative, compounded or sequential effects of climate extremes (Paine, Tegner & Johnson 1998; De Boeck *et al.* 2010).

Box 1. An example of a multi-factor climate extremes field experiment designed to identify thresholds of extreme ecological response.

The Climate Extremes Experiment (CEE) was established in May 2010 to examine a range of ecological responses of intact tallgrass prairie to the independent and combined effects of two statistical climate extremes: severe drought and heat waves. The CEE is unique in that heat waves are being imposed at multiple levels in plots that are either well-watered or experiencing severe drought conditions (see below for details). Such a design is relatively cost-effective (approximate cost of infrastructure, lamps and sensors = \$50k) and easy to implement in short-statured vegetation. The design allows investigators to assess not only thresholds of response to the different magnitudes of heat waves, but also to separate the direct effects of periods of extreme high temperatures from those due to the water stress that typically co-occurs with a heat wave. To determine whether an extreme response occurs and the mechanistic basis of such a response, population-, community- and ecosystem-level responses to the treatments, as well as recovery dynamics, are being assessed. In addition, genomic, physiological, growth and reproductive responses in the dominant plant species are being measured. This array of treatments (8 total) and comprehensive suite of responses should enable researchers to rigorously quantify the conditions in which a climate extreme results in an extreme ecological response, and thus in an extreme climatic event.

Experimental treatments. The severe drought treatment is applied at the whole-plot level (large greenhouse structures in the photo), where growing season rainfall is passively reduced using two rainout shelters, each 6×24 m in size. Each shelter is covered with strips of transparent polycarbonate roofing that deflect *c*. 75% of each rainfall event. The ambient rainfall treatment plots are located in two shelters covered with spectrally neutral netting that permits rainfall inputs but alters microclimate conditions similar to those in the rainout shelters (e.g. 10% reduction in photosynthetically active radiation). The heat wave treatments consist of multiple target temperature levels: +0, +5, +10 and +15 °C above ambient, each replicated five times. The 2-week heat wave is applied in mid-July to 2×2 m subplots ($n = 10$ per shelter) using a combination of passive warming chambers consisting of transparent plastic sheeting that encloses the IR lamps (small chambers beneath the shelters). Photo credit: M.D. Smith.

3. Because climate extremes often occur in combination naturally, it is also critical that we continue to assess interactions between different types of climate extremes (e.g. severe drought and heat waves) at different levels of extremity (Box 1). Other factors, such as changes in climate means, species diversity, trophic interactions or disturbance regimes (see Jentsch, Kreyling & Beierkuhnlein 2007, Jentsch *et al.* 2011) also should be considered, as these may interact with climate extremes to result in the most extreme and persistent ecological responses (i.e. state changes and hysteresis, Paine, Tegner & Johnson 1998; Smith, Knapp & Collins 2009).

4. Manipulations that may hasten or mimic the crossing of extreme response thresholds, such as removal of a dominant species from an ecosystem or experimentally invading systems to simulate the immigration of novel species, are needed to more mechanistically assess the vulnerability of ecosystems to experiencing an ECE.

5. Comparative studies of different ecosystems or biome types exposed to a range of climate extremes are also needed to elucidate the potential mechanisms underlying differential sensitivity, and whether these mechanisms are similar or different between ecosystems or biomes. Such comparative studies could include sites that differ in the longevity or diversity of species (Smith, Knapp & Collins 2009), or ecosystems that may be more or less vulnerable to climate extremes based on, for example, their sensitivity to changes in climate means.

6. Finally, experiments need to measure ecological responses at multiple hierarchical levels (individual to ecosystem; Box 1) and be conducted for sufficient periods of time and at large enough scales to ensure that the entire range of ecological responses and their respective thresholds are fully captured for the ecosystem in question.

Concluding remarks

The study of climate extremes is a relatively new emphasis in ecology. This is despite the long-standing recognition of the importance of climate extremes by paleo-ecologists (Williams, Blois & Shuman 2011) and evolutionary biologists (Combes 2008). But with forecasts predicting increases in both the frequency and severity of climate extremes and increasing recognition of their importance in driving contemporary ecological dynamics, ecologists need to bring to bear a variety of approaches to expand our mechanistic understanding of how and why ecosystems may differ in their vulnerability to climate extremes. Furthermore, knowledge of the thresholds of ecological responses that may trigger dramatic ecological consequences needs to be incorporated into scenarios of future ecosystem dynamics at the global scale.

Acknowledgements

I thank three anonymous referees for their insightful comments. I am grateful for support from the US Department of Energy, Office of Science (PER) (Grant #DE-FG92-04ER63892), the USDA CSREES Ecosystem Studies Program, and the NSF Ecosystems and LTREB programs (Grant #DBI-04214427).

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Received 17 August 2010; accepted 11 January 2011
Handling Editor : David Gibson