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SPECIAL FEATURE – EDITORIAL
ECOLOGICAL CONSEQUENCES OF CLIMATE EXTREMES

The ecological role of climate extremes: current understanding and future prospects

Melinda D. Smith*

Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA

Summary

1. Climate extremes, such as severe drought, heat waves and periods of heavy rainfall, can have profound consequences for ecological systems and for human welfare. Global climate change is expected to increase both the frequency and the intensity of climate extremes and there is an urgent need to understand their ecological consequences.
2. Major challenges for advancing our understanding of the ecological consequences of climate extremes include setting a climatic baseline to facilitate the statistical determination of when climate conditions are extreme, having sufficient knowledge of ecological systems so that extreme ecological responses can be identified, and finally, being able to attribute a climate extreme as the driver of an extreme ecological response, defined as an extreme climatic event (ECE).
3. The papers in this issue represent a cross-section of the emerging field of climate extremes research, including an examination of the palaeo-ecological record to assess patterns and drivers of extreme ecological responses in the late Quaternary, experiments in grasslands assessing a range of ecological responses and the role of ecotypic variation in determining responses to climate extremes, and the quantification of the ecological consequences of a recent ECE in the desert Southwest of the USA.
4. *Synthesis*. The papers in this Special Feature suggest that although the occurrence of ECEs may be common in palaeo-ecological and observational studies, studies in which climate extremes have been experimentally imposed often do not result in ecological responses outside the bounds of normal variability of a system. Thus, ECEs occur much less frequently than their potential drivers and even less frequently than observational studies suggest. Future research is needed to identify the types and time-scales of climate extremes that result in ECEs, the potential for interactions among different types of climate changes and extremes, and the role of genetic, species and trait diversity in determining ecological responses and their evolutionary consequences. These research priorities require the development of alternative research approaches to impose realistic climate extremes on a broad range of organisms and ecosystems.

Key-words: climate change, extreme events, extreme weather, global change, plant–climate interactions, state change

Introduction

An increase in the frequency and magnitude of climate (or weather) extremes, such as severe drought, periods of heavy rainfall and heat waves, has been recognized as a critical manifestation of climate change (Meehl & Tebaldi 2004; Meehl *et al*. 2007). Climate extremes have the potential to have large and widespread impacts at all levels of the ecological hierarchy from organisms to ecosystems (Easterling *et al*. 2000; Jentsch & Beierkuhnlein 2008), as well as significant economic costs and consequences for human welfare (Meehl *et al*. 2000, 2007; Garcia-Herrara *et al*. 2010). There is mounting evidence that the frequency and severity of climate extremes have already increased in many regions (Karl, Knight & Plummer 1995; Schar *et al*. 2004), and hence, there is a pressing need to understand the immediate and future consequences of climate extremes for ecological systems.

Although there have been numerous studies examining the effects of changes in climatic means on ecological processes and ecosystems, research on climate extremes is far less common

*Correspondence author. E-mail: melinda.smith@yale.edu

and is only now emerging as a distinct research field in ecology (Jentsch, Kreyling & Beierkuhnlein 2007; Jentsch *et al.* 2011). As with any emerging field, there are a number of challenges unique to this line of research including the need to develop novel research approaches and define new conceptual frameworks (Smith 2011). Despite the challenges of studying climate extremes, our understanding of this critical aspect of climate change has recently been advanced by a number of palaeo-ecological, observational and experimental studies, as exemplified by those included in this issue. Thus, although the field is nascent, there is value in providing a preliminary assessment of this rapidly growing body of research to synthesize our existing knowledge, identify and prioritize gaps in our current understanding, and build a conceptual foundation to guide future research.

The Extreme Climatic Events Symposium held at the 95th Annual Meeting of the Ecological Society of America (1–6 August 2010, Pittsburg, PA) was envisioned with these goals in mind. This symposium brought together an international group of researchers who are actively studying the ecological impacts of climate extremes. Their presentations encompassed a broad range of perspectives – from palaeo to contemporary – and their research approaches were diverse, including observational and manipulative studies that included multiple hierarchical scales. The Special Feature in this issue of the *Journal of Ecology* is a product of this highly successful symposium. In this introduction to the Special Feature, I utilize the new conceptual framework described in the first paper of this series (Smith 2011) to set the stage for interpreting the diverse set of papers that follow. These papers include an examination of the palaeo-ecological record to assess patterns and drivers of extreme ecological responses, such as abrupt ecological changes that result in regime shifts (Williams, Blois & Shuman 2011), experiments designed to impose different types of climate extremes on ecosystems and assess ecological responses (Arnone *et al.* 2011; Jentsch *et al.* 2011), an assessment of the role of ecotypic variation in determining plant species responses to a climate extreme (Beierkuhnlein *et al.* 2011), quantification of the landscape-scale consequences of an extreme drought (Royer *et al.* 2011), and finally, an alternative experimental approach for imposing climatic extremes in the field (De Boeck & Nijs 2011). Taken together, these papers represent a cross-section of current climate extremes research.

Going to the Extremes – Extreme Climate Events

Climate extremes are particularly challenging to study not only because of their rarity but also because of their context dependence, both in terms of the climate record available (or selected) and what the system and its component species have previously experienced (Smith 2011). As a consequence of this context dependence, ecological responses to climate extremes may range from little or no response (e.g. Arnone *et al.* 2011; Jentsch *et al.* 2011) to responses that are large or 'extreme' (e.g. in terms of the distribution of possible ecological responses, such as widespread mortality of an overstorey tree species, Royer *et al.* 2011). As argued in the first paper of this Special Feature (Smith 2011), the major challenges for ecologists are determining when a climate extreme occurs, when an ecological response is extreme and, most importantly, explicitly attributing the climate extreme as the driver of the extreme ecological response. This latter case is distinguished as an *extreme climatic event* (ECE), whereby extremity is coupled climatically and ecologically (Smith 2011). The value of the distinction between climate extremes and ECEs is apparent when considering palaeo-ecological records where extreme ecological responses, such as state changes or regime shifts, are a common feature but are not always attributable to climate extremes or even abrupt changes in climate (Williams, Blois & Shuman 2011). Moreover, this distinction can facilitate determining how and why ecosystems may differ in their sensitivity to climate extremes, an issue addressed in more detail below.

It follows from the conceptual arguments of Smith (2011) that both climate extremes and extreme ecological responses must be defined to determine if an ECE has occurred. Defining climate extremes is relatively straightforward and has generally been based on the statistical distribution of a climate variable for any system (Fig. 1). The expectation with changing climate means and/or variability is that climate extremes will become more frequent and intense in the future (Meehl *et al.* 2000). Due to the statistical nature of the definition, this increase in

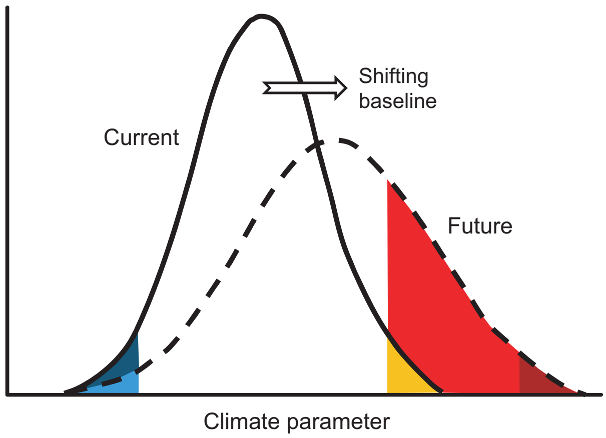

Fig. 1. Climate extremes (e.g. defined as those with ≤5% statistical probability of occurrence; dark blue and yellow portions of the 'Current' climate curve, light blue and dark red portions of the 'Future' climate curve) are expected to become more frequent and intense with changes in climate means and/or alterations in the distribution of climate variables (red shaded area). However, this increase will only be detectable with a fixed climatic baseline. With future climate change, the climatic baseline will shift (arrow), and consequently far fewer climate conditions would be deemed extreme based on the statistical definition (dark red shaded area), even though organisms in the system will be experiencing many more periods of climatic extremity (red + dark red shaded areas). Consequently, there is a clear need for the establishment of a fixed and standardized climatic baseline for ecological studies – similar to that for atmospheric CO_2 studies (e.g. c. 280 ppm) – to improve our ability to interpret how climate extremes may be altered with future climate change and more comprehensively understand their consequences for ecological systems. Modified from Meehl *et al.* 2000.

frequency and intensity must be predicated on a fixed frame of reference or climatic baseline (e.g. the historic climate record for a site). For example, a shift in mean temperatures towards warmer conditions would result in a greater number of high temperature extremes based on the current statistical distribution (red shaded area, Fig. 1), particularly if variability around the mean also is increased. However, if the climatic baseline is allowed to shift with an increase in the mean and/or alteration in the distribution of a climate variable, then substantially fewer climate conditions would be deemed extreme based on, for example, a $\leq$ 5% statistical probability of occurrence (dark red shaded area, Fig. 1). This statistically based outcome would occur even though periods of climate extremity would actually be much more common from the perspective of the organisms in the system (i.e. red + dark red shaded areas, Fig. 1) relative to the conditions they had previously experienced. This illustrates the value of establishing fixed climatic baselines for identifying climate extremes. A fixed baseline established for a standard time frame – e.g. the pre-industrial global atmospheric CO_2 concentration of *c.* 280 ppm – has proven to be invaluable for studies of elevated atmospheric CO_2. For climate extremes research, system-specific fixed climatic baselines would provide the necessary benchmarks for assessing how the frequency and magnitude of extremes may change with current and future scenarios of climate change, and allow for a more comprehensive determination of when a period of climatic extremity would occur.

In contrast to climate extremes, defining an extreme ecological response is more difficult (Gutschick & BassiriRad 2003), as it depends on the ecological system in question and the timescale considered. For example, an extreme response for a desert grassland will be very different than that for a tropical forest. Moreover, the extremity of a response for a particular system may change considerably if one considers 20 years of historic variability vs. a millennial scale palaeo-record for the same site. In response to these issues, Smith (2011) defines an extreme ecological response from both a statistical perspective, as a response that is "well outside of what is considered typical or normal variability", and from an ecological perspective, as a response that cascades across multiple hierarchical levels. The latter requirement insures that ecological responses will extend beyond the short-term fitness consequences of individual species (Gutschick & BassiriRad 2003) to changes in abundances of species, widespread species loss and/or invasion by novel species. As a result, extreme ecological responses, particularly those that involve key or common species in the system or species with novel traits, should have large and persistent effects on ecosystem structure and function (Smith, Knapp & Collins 2009). These effects may be further characterized by prolonged periods of recovery, significant hysteresis, or state changes/regime shifts (fig. 2 in Smith 2011). Although there are recent examples of extreme ecological responses, such as the widespread mortality of tree species caused by extreme drought (e.g. Allen and Breshears 1998; Breshears *et al.* 2005; Mueller *et al.* 2005; Bigler *et al.* 2006, 2007; Gitlin *et al.* 2006), the palaeo-record is rich with examples of extreme ecological responses, particularly during the late Quaternary. Williams, Blois & Shuman (2011) characterize these by their rapid shifts in species abundances and changes in community composition driven by large-scale mortality and species migration, resulting in persistent regime shifts or state changes. Thus, it is clear that extreme ecological responses as defined by Smith (2011) can be relatively common and discernable features of ecological systems. However, as with climate extremes, a baseline for the range and magnitude of responses for ecological systems is essential for providing necessary context for determining when extreme ecological responses occur, as exemplified by the case studies from the late Quaternary and early Holocene (Williams, Blois & Shuman 2011).

Once climatic and ecological extremity are recognized, explicit attribution of a climate extreme as the driver of an extreme ecological response is the next critical step in determining whether an ECE has occurred (Smith 2011). The severe drought of 2002–03 in the south-western USA provides a clear example of an extreme ecological response that can be explicitly linked to a climate extreme. Research by Breshears *et al.* (2005), Adams *et al.* (2009) and the paper by Royer *et al.* (2011) in this issue demonstrates the unprecedented magnitude of mortality of the dominant tree species, Pinyon pine (*Pinus edulis*), as a consequence of a statistically extreme drought. Royer *et al.* (2011) show that the die-off of overstorey vegetation has regional-scale effects on near-ground solar radiation, which has the potential for cascading and long-term impacts on a broad range of ecological processes. Despite this and other examples of extreme ecological responses driven by periods of climatic extremity, such as severe droughts and rapid changes in temperatures (Weaver 1968; Gitlin *et al.* 2006; Bigler *et al.* 2007; Williams, Blois & Shuman 2011), Williams and colleagues show that demonstrating causality remains a significant challenge. This raises the question of how often and under what circumstances ECEs actually occur. And when ECEs do occur, what are their consequences for ecological systems? These are critical questions that need to be addressed, and the papers in this special feature provide insight into their potential answers.

Climate Extremes are Rare, but ECEs are Even Rarer

Although the observational studies described above have increased our understanding of the causes and consequences of ECEs, the rarity and likely increased frequency and intensity of climate extremes with future climate change have prompted a number of researchers to experimentally impose climate extremes on a range of systems. The papers by Arnone *et al.* (2011), Jentsch *et al.* (2011) and Smith (2011) in this issue provide examples of such experiments.

Arnone *et al.* (2011) experimentally imposed an extremely warm year on intact tallgrass prairie monoliths from Oklahoma, USA, and found an immediate and large (~30%) reduction in above-ground productivity, driven primarily by the dominant C_4 grass species in the system. However, the change in above-ground productivity was well within the range of interannual variability observed for tallgrass prairie, was not persistent over time, and was not accompanied by changes in plant community structure or composition. Similarly, for intact tallgrass prairie in north-eastern Kansas, USA, Smith (2011) shows that over a decade of experimentally imposing an extreme precipitation regime, whereby the number and timing of rainfall events were altered well beyond historical patterns, the resulting reduction in above-ground productivity, although ecologically significant, also fell within the natural range of variation for the system and was not accompanied by substantive changes in the plant community. Finally, with a long-term field experiment where statistically extreme drought events were applied to constructed European grassland communities for five consecutive years, (Jentsch *et al.* 2011) show a lack of large effects for the majority of the 32 response parameters measured. For example, above- and below-ground productivity remained unchanged across all years of the study, i.e. as a consequence of complementary responses among plant species, and without a concomitant change in plant community composition.

The lack of extreme ecological responses in these and a number of other recent experiments (Van Peer *et al.* 2001, 2004; Marchand *et al.* 2005, 2006a,b; Milbau *et al.* 2005; Bokhorst *et al.* 2008; Kreyling *et al.* 2008; De Boeck *et al.* 2010b) suggests that ECEs probably occur much less frequently than their potential drivers – the climate extremes themselves – and possibly much less frequently than that suggested by observational studies. This may be due in part to the fact that observational studies are often conducted only when a climate extreme evokes an obvious extreme response (i.e. widespread mortality of a species). Therefore, our view from observational studies may be biased towards equating climate extremes with extreme climatic events. In addition, one might conclude from these experiments that the systems being studied are resistant to the type and/or time-scale of climate extremes experimentally imposed. However, it is difficult to rule out alternative possibilities, such as: (i) that the length of these studies was insufficient to capture an extreme response for the system in question, (ii) that the climate extremes were actually not sufficiently extreme in terms of the historic climate record or what the system and its component species had previously experienced, or (iii) that unique or rare combinations of climate extremes (e.g. temperature and precipitation with severe drought, see above) may be required to evoke an extreme ecological response. Overall, these studies suggest that ECEs may be difficult to induce experimentally, and that a diversity of approaches and a broad assessment of different types of climate extremes may be required to determine the causes and consequences of ECEs.

The Future of Climate Extremes Research

The papers in the Special Feature and others recently published (Jentsch, Kreyling & Beierkuhnlein 2007; Jentsch & Beierkuhnlein 2008; De Boeck *et al.* 2010a; Gutschick & BassiriRad 2010) provide a roadmap of research priorities and the types of research approaches needed to further our understanding of the role of climate extremes in ecological systems. A diversity of approaches that capture a broad hierarchy of ecological responses should continue to be employed and expanded upon. Moreover, there is a need to establish both climatic and ecological baselines to provide context for determining whether climate extremes occur and whether they result in an extreme ecological response.

As previously mentioned, a key knowledge gap is our lack of understanding of the types and time-scales of climate extremes that will lead to ECEs, as it is clear that statistically extreme climatic conditions often do not result in extreme ecological responses. It is likely that the intensity, timing and duration of periods of climatic extremity will interact in important and surprising ways (De Boeck *et al.* 2010b). However, we know very little about how ecological systems will respond to these potential interactions and whether or not they will result in extreme ecological responses. In addition, because the frequency of climate extremes are expected to increase in the future, research is needed that addresses how repeated climate extremes may impact ecological systems and whether resistance or resilience develops over time or if ECEs will become more frequent. As increases in climate extremes will be accompanied by changes in climatic means, climatic variability or both (Fig. 1), a key question is whether these aspects of climate change will increase or decrease the vulnerability of ecological systems to climate extremes. Research is also needed that addresses the role of multiple levels of diversity – genetic, species and trait – in determining the ecological and evolutionary consequences of climate extremes for organisms and their potential feedbacks on ecological processes (Schoener 2011). In this issue, Beierkuhnlein *et al.* (2011) show how ecotypes of a key European grass species, each adapted to differing climate means, respond differently to climate extremes. However, the performance of these ecotypes could not be predicted from the climate in which they originated. This suggests that genetic and phenotypic diversity can play an important role in determining ecological responses to climate extremes, but that these effects are complex. Without doubt, much more research is needed here.

Finally, advances in experimental infrastructure need to be made to allow researchers to impose realistic climatic extremes on organisms and entire ecosystems. Particularly challenging is imposing extremely high temperatures (more than 10 °C above ambient) under field conditions (see Box 1 in Smith 2011) without potentially confounding artefacts (De Boeck & Nijs 2011). In the last paper of the Special Feature, De Boeck & Nijs (2011) describe an alternative control method for infrared heaters, which are often employed to impose heat waves on terrestrial ecosystems, to avoid the potential confounding factors of plant responses to heating. Many more advances like these are needed if we are to increase our understanding about the role of climate extremes in ecological systems.

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