

The Impacts of Extreme Climatic Events on Wild Plant Populations

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Introduction

Anthropogenic changes to the earth's climate over the past few decades have spurred a growing level of scientific interest in the impact of rapid climate change on global ecosystems. To date, the majority of studies have focused on quantifying the impact of mean climatic trends, such as warming temperatures or declining frost period, on the phenology (Menzel et al. 2006), behaviour (Parmesan et al. 2000) and distribution of individual species and biotic assemblages (Chen et al. 2011). There is now unequivocal evidence that significant shifts in both species and ecosystem attributes in response to broader climatic trends are occurring worldwide (Walther et al. 2002). So ubiquitous are these changes that they constitute a major threat to the long-term conservation of global biodiversity, and may even alter or disrupt ecosystem processes that underpin the functioning of earth's biosphere itself (Cramer et al. 2001; Hannah et al. 2002; Gerten 2013; Doblas-Miranda et al. 2014).

Arguably, much less effort has been invested in understanding the roles that extreme or unusual climatic or weather events (hereafter extreme climatic events, ECEs) play in driving population and ecosystem change. This is surprising, because climatic extremes have in the past resulted in profound human societal change, and apparently even the collapse of prehistorical cultures and the agro-ecosystems on

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Fig. 1 A stone pueblo constructed by Ancestral Puebloan (Anasazi) people at Hovenweep National Monument, Utah, USA. Hovenweep people farmed maize and other domesticated crops on surrounding terraced fields despite the semi-arid climate. As with many other Anasazi sites in the region, Hovenweep was abandoned in the late thirteenth century CE, probably at least partly in response to extreme, multi-decadal drought. [Courtesy of Holly Godfree]



which they depended. For example, multidecadal drought during the middle-twelfth and late-thirteenth-century CE (Common Era) is thought to have led to the dislocation of maize-dependent Anasazi (Ancestral Puebloan) people in the American southwest (Benson et al. 2007; Fig. 1), while the decline of the Classic Mayan civilisation coincided with a period of recurring drought between ca. 770 and 1100 CE (Hodell et al. 2005). Contemporary events, such as Australia's 1997–2009 'Millennium Drought' (Murphy and Timbal 2008; Heberger 2012) and the 2003 European heatwave (Stott et al. 2004; Ciais et al. 2005) clearly demonstrate that extreme climatic or weather conditions can be potent agents of change in anthropogenic and natural systems alike.

One reason why few studies have attempted to untangle the complex linkages that exist between climate variability, climatic trends and biotic change is that it is logistically difficult to quantify the impact of statistically improbable climatic or meteorological events on single populations, let alone entire ecosystems. Simulation of extreme climatic events and climate change under realistic field conditions, while desirable, is usually expensive, time consuming and often technically challenging (e.g., Hovenden et al. 2008; Smith 2011; Dieleman et al. 2012; Godfree et al. 2013),

and so most existing studies report on the impacts of naturally occurring ECEs on plant or animal populations or communities. Nonetheless, combined with data collected using remote sensing techniques (Zhao and Running 2010) and controlled studies that artificially induce extreme physiological stress in experimental populations (e.g., Musil et al. 2005; Marchand et al. 2006), the body of work that does exist demonstrates that relatively brief or protracted periods of unusual climate or weather can impact on biota at scales ranging from the individual organism through to entire ecosystems. In a world facing significant warming in the decades ahead, the possibility that ECEs will be fundamental drivers of ecosystem change cannot be ignored.

The objective of this chapter is to provide an overview of the nature of extreme climatic or climate-linked events and their impacts on the demography of wild plant populations. While a complete review of this subject is beyond the scope of this chapter, we focus on drawing out some of the main lessons that have been learned from the past and contemporary study of ECEs, and apply them to understanding the potential demographic and evolutionary roles that extreme events may play in the future within the context of anthropogenic climate change. While we provide a global perspective on the subject, we focus especially on specific case studies involving Australian vegetation, since the principles learned from these events are applicable to extreme events more generally. The Australian environment is highly suited to the study of ECEs, where they have left an indelible mark on both human societies and on continental biota alike. We first discuss the definition and statistical characterisation of ECEs, a source of much confusion in the literature.

Characterisation of Extreme Climatic Events

One significant complication associated with the study of climate extremes is that there is no universally accepted definition of what actually constitutes an extreme event. Many studies investigating the role of extreme events on plant populations do not quantify either the statistical probability of the climatic conditions observed during the study nor the magnitude of their effects on biota relative to what is considered background or normal variation. Hence, the notion of “extremeness” is often vague or ill-defined and provides little basis for extrapolation to other systems or events. Many simply define drought severity in terms of departure from mean rainfall, providing little, if any, data on inter-annual rainfall variability (e.g., Condit et al. 1995), despite the fact that a rigorous statistical theory of extreme events now exists that greatly facilitates the quantification of such events (Katz et al. 2005). More recently, it has been argued that one should consider both the probability of occurrence of both the climatic event and the ecosystem response, and that an ‘extreme event’ must involve both a rare climatic event and an unusually large ecosystem response (e.g., Smith 2011). To complicate matters further, the terminology used to describe climate and weather extremes in the scientific literature varies widely, often involving a mix of terms that describe attributes such as rarity, severity, magnitude of impact, and event complexity (Stephenson 2008).

To avoid confusion, we adopt the Intergovernmental Panel in Climate Change (IPCC) definition of what constitutes an extreme climate event (ECE), and provide (where possible) the statistical probability of the event using indices based on either a standard climatic reference period or a given temperature or precipitation threshold. The IPCC (IPCC 2012; Section 3.1.2) describes an ‘extreme climate or weather event’ in statistical terms: “the occurrence of a value of a weather or climate variable above (or below) a threshold value near the upper (or lower) ends of the range of observed values of the variable” (Section 3.1.2, p. 116). By following the IPCC convention we explicitly separate the concept of the rarity of a climatic event from the population- or ecosystem-level impact of the event. Indeed some extreme events appear to have little or no impact on vegetation, and so this distinction is in itself an interesting area for inquiry.

Probably the most commonly used indices quantify climatic extremes in terms of percentiles or quantiles (especially deciles) relative to a baseline distribution, often the World Meteorological Organisation’s 1961–1990 normal reference period (this is to be replaced in 2020 with a 1991–2020 reference period). For example, a tenth percentile (= first decile) annual rainfall total of 1 year duration has a 10 % chance of occurring in a given year, with an average return interval of 10 years. Others are based on frequency or duration over a specific threshold (e.g., the number of hot days exceeding 40 °C), or, in the case of chronic or multiple extremes, more complex definitions. Formal statistical distribution fitting techniques may also be used to estimate the probability of unusual events occurring in a given timeframe, in which case the choice of distribution is critically important, including from an environmental policy standpoint (Pindyck 2011).

Some of the key statistical aspects of ECEs, and the complexities associated with quantifying chronic events, can be illustrated by examining variation in total annual rainfall between 1889 and 2012 at Barraba Post Office (S 30.3781°, E 150.6096°) in northern NSW, Australia (see Fig. 2). Barraba has a nearly continuous rainfall record over this period, and shows a pattern of variability that is broadly representative of much of northern NSW. Over the entire record rainfall averaged 692 mm, with 5th and 95th percentile rainfall totals (here denoted P_5 and P_{95}) of 431 and 957 mm respectively (Fig. 3a), with high inter-annual variability (Fig. 3a). However, rainfall behaviour and the nature of extreme events have changed considerably over the past century: prior to 1950 there was a protracted period of lower (average $\mu=656$ mm) but less variable rainfall ($P_5=450$ mm, $P_{95}=887$ mm), with 1896–1946 being especially dry ($\mu=621$ mm, $P_5=442$ mm, $P_{95}=834$ mm). The 1896–1902 ‘Federation Drought’ and the 1937–1946 ‘World War II Droughts’ which devastated agricultural communities and rangelands across SE Australia (McKeon et al. 2004) both occurred during this period.

Since 1949, and especially during the 1961–1990 reference period, rainfall has been higher ($\mu=726$ mm) but generally more variable ($P_5=397$ mm, $P_{95}=1007$ mm). Five of the seven driest years have occurred since 1949, including all 4 years with <400 mm rainfall (despite the general absence of multi-year droughts), as have 6 of the 7 wettest years. Differences in the statistical behaviour of rainfall during these two periods can be clearly seen in Fig. 3c, d, where annual totals have been fit



Fig. 2 Sites and events referred to in the text. (A) Barraba, NSW. (B) General location of *Eucalyptus marginata* (Jarrah) forest in south-western Western Australia. (C) *Austrostipa aristiglumis* grassland near Wyalong, NSW. (D) Frost affected rainforest vegetation in the Atherton Tablelands region. (E) Mediterranean mallee-heathland community affected by extreme heat. (F) Drought and insect attack in *Eucalyptus* spp. near Canberra, ACT. (G) Degraded semi-arid rangeland near Carinda, NSW. (H) Barmah-Millewa Forest

with a 3-parameter Weibull function. In contrast to the near-normally distributed rainfall of 1950–2012, the distribution for the period 1889–1949 is both narrower and skewed towards lower annual totals. The prolonged nature of rainfall deficiencies in 1896–1949 is effectively shown in the associated residual mass diagram (Fig. 3b), which displays cumulative annual rainfall deviations from the 1889–2012 mean. During this period accumulative rainfall deficiencies totalled 3618 mm, or roughly five times the average annual rainfall. Since 1949 rainfall surpluses have dominated.

Delving further, we can also see that the seasonal timing of rainfall at Barraba has also changed since 1889. The most significant changes have been a 45 % increase in summer (December–February) rainfall (Fig. 4a), which has resulted in a significant reduction in the frequency and severity of dry summers in recent decades, and a weak decline in autumn (March–May) rainfall (Fig. 4b), with only one even modestly wet autumn (top 25th percentile of rainfall totals) having been recorded in the

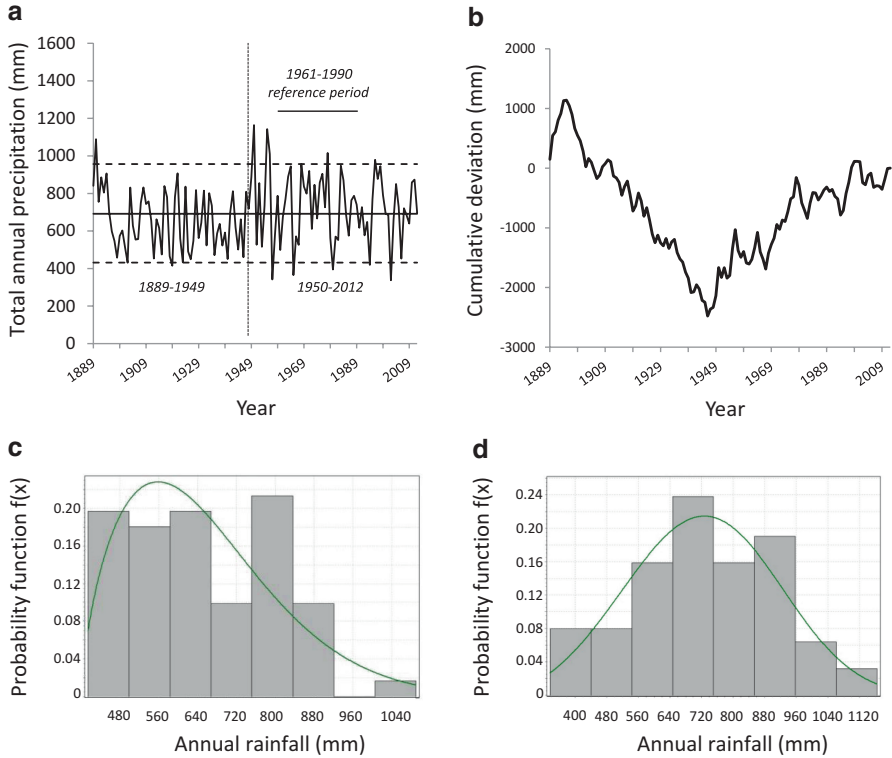


Fig. 3 Rainfall data for Barraba Post Office, northern NSW, Australia. **(a)** Total annual precipitation 1889–2012, showing the 1961–1990 reference period. **(b)** Cumulative residual mass diagram for 1889–2012 data, showing the long period of below average precipitation between 1896 and 1946 and the wetter conditions that followed. **(c)** Annual rainfall for 1889–1949 fit with a three-parameter Weibull function ($\alpha=1.6$, $\beta=282.9$ and $\gamma=402.4$). **(d)** Annual rainfall for 1950–2012 fit with a three-parameter Weibull function ($\alpha=3.4$, $\beta=626.2$ and $\gamma=163.7$)

past 21 years (Fig. 4b). A similar pattern of autumn rainfall decline has been observed across SE Australia in recent decades, especially during the 1997–2009 Millennium Drought. In a region of Australia which relies on autumn rain to establish crops, this change has significantly affected agricultural yield (Pook et al. 2009).

Collectively, these data illustrate several important features of extreme climate events and climate change. First, statistical theory indicates that the frequency of extreme events is more influenced by changes in variability than means (Katz and Brown 1992), but as the Barraba rainfall data show, both can change simultaneously, producing complex behaviour of climate extremes. Second, the statistical distribution of a climate variable, and hence estimates of the rarity of a given extreme event, can depend on the specific reference period considered. For example, the Weibull distribution model shown in Fig. 3c, based on data from 1889 to 1949, predicts a lower probability of recording a year with below 420 mm (1 %) than both

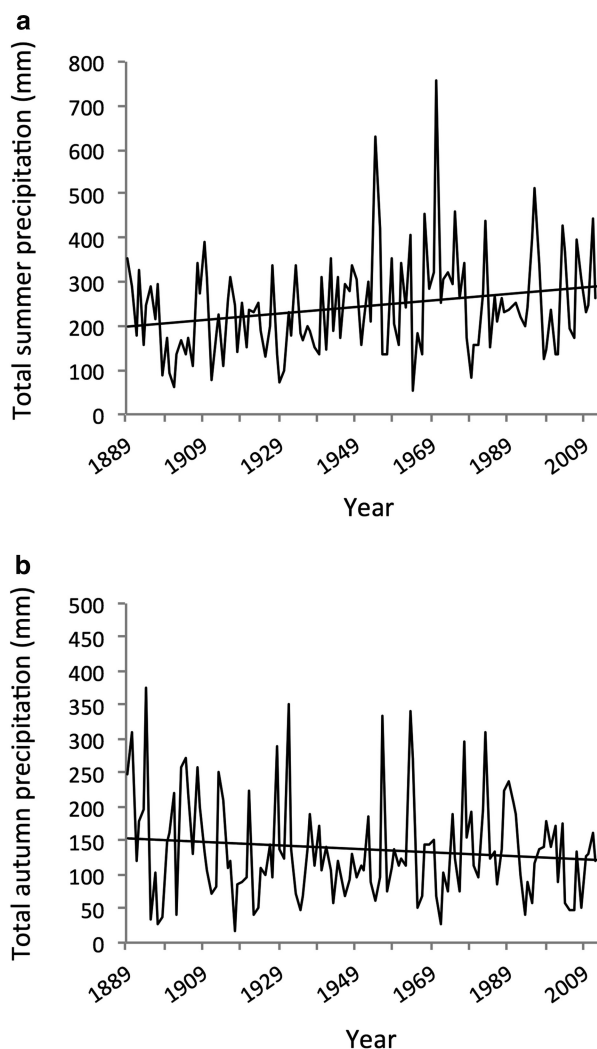


Fig. 4 Seasonal rainfall data for Barraba Post Office, northern NSW, Australia. (a) Summer (December–February). (b) Autumn (March–May)

the 1950–2012 (Fig. 3d; 5 %) and 1961–1990 reference periods (4 %). In fact, five such years have been recorded since 1889, and four since 1950. Changes can also occur in the seasonality or timing of ECEs, which may have important implications for plant adaptation. Finally, a range of statistical criteria and timeframes may be needed to adequately quantify a given ECE, especially one such as drought which may last for many years. For example, while many of the individual driest years at Barraba have occurred since 1950, the longest runs of below average rainfall years (up to seven) all occurred before 1950.

We now turn our attention to the impact of such events on wild plant populations. A review of the entire body of research relating to ECEs is well beyond the scope of this chapter, and so we focus on the phytosociological impacts of those events that drive rapid demographic changes in plant populations. Such events are of special significance given the emerging evidence for increased mortality and vegetation change in ecosystems globally in response to anthropogenic climate change.

ECEs and Population Demography

Mortality as a Key Driver of Demographic Change

By far the most well studied effects of ECEs on plant populations are those that involve the death of individuals as a direct result of water deficiencies and extremes of heat and cold. Since a comprehensive review of all such studies is beyond the scope of this chapter, the intent here is to draw key lessons from the literature.

Perhaps the most obvious conclusion to be drawn from an appraisal of the ECE literature is that most, if not all ecosystems globally can experience rapid demographic change in response to rare climatic or climate-related events, probably even in the absence of underlying climate change. Extensive mortality of plant populations directly resulting from drought stress has been observed in arid, semi-arid, temperate, subtropical and tropical forests and woodlands, arid, semi-arid and alpine grasslands and shrublands, to name but a few ecosystems. Negative effects of high temperatures, along or in combination with drought, and extremes of cold have also been reported in a great range of biomes. If we broaden our scope to include the effects of severe storms, snowfalls and hydrological events associated with extreme weather, probably few ecosystems are left untouched by extreme events at some point.

One of the earliest, yet still most comprehensive, accounts of plant population mortality and change in response to an ECE was provided by Albertson and Weaver (1944, 1945), who quantified the impacts of the 1930s “Great Drought” (Woodhouse and Overpeck 1998) on prairie and woodland ecosystems of the mid-western United States. Apparently caused by unusual tropical ocean temperatures coupled with land surface-atmosphere feedbacks (Schubert et al. 2004), this period of chronically dry conditions (punctuated by shorter periods of record low rainfall), in combination with record high temperatures and poor land management, had a catastrophic impact on agricultural and natural ecosystems alike. As vividly captured in John Steinbeck’s novel *The Grapes of Wrath*, the development of the infamous “Dust Bowl” areas of the southern Great Plains ultimately became one of the greatest catastrophes in recent North American history. During this drought, widespread desiccation and death of woody and herbaceous vegetation occurred across the Great Plains, with post-climax vegetation along the western woodland margin and prairie grassland being generally the most severely affected.

Some of the most dramatic recent examples of plant mortality in response to ECEs have come from forests and woodlands, which seem to be highly susceptible to rapid change or even collapse once certain physiological thresholds are exceeded. The recent canopy collapse observed in Mediterranean-type *Eucalyptus marginata* (Jarrah)-dominated forest in south-western Australia (Fig. 2), for instance, appears to have been caused by record low rainfall and warm temperatures (culminating in a prolonged heatwave in February 2011), possibly along with declining groundwater levels (Matusick et al. 2013). Contemporary changes in other species including *Eucalyptus gomphocephala* (Matusick et al. 2012) and *Eucalyptus wandoo* (Brouwers et al. 2012) suggest that deteriorating water balance is a phenomenon increasingly affecting much of south-western Australia. This region is highly sensitive to changes in atmospheric circulation that result in more southerly tracking of the mid latitude fronts that provide much of its precipitation, synoptic conditions which are likely to become more prevalent under global warming (Hope 2006).

Case studies such as this reinforce the view that forests and other vegetation in many areas are likely to be placed at risk by an increase in the frequency and severity of extreme drought and heat events under future climate change (Allen et al. 2010; Anderlegg et al. 2013). Critically, they also show that demographic changes associated with climate extremes are often rapid, can occur over large spatial scales, and can drive significant structural and compositional change across multiple plant communities. As we discuss below, such patterns will affect the ability of plant populations and communities to adapt to climate change, which has strong implications for biodiversity conservation on a global scale.

Nonlinearity of ECE Impacts

During the 1930s Great Drought in the mid-west US, extensive tree mortality was not only observed during the exceptionally dry years of 1934 and 1936, but also in 1939 when rainfall deficiencies were less extreme. Indeed, some populations of trees that had survived previous dry years succumbed only during 1939. As noted by Albertson and Weaver (1945), this reflects the ongoing development of soil moisture deficits over the course of the drought, the effects of repeated tissue desiccation and injury, and more complex land surface-pathogen-plant interactions. This illustrates one of the more interesting aspects of ECEs: that the relationship between the demographic response of plant populations and increasing severity of climatic extremes, and indeed abiotic stress in general, is usually strongly nonlinear. In the most striking cases, changes are minimal, often for protracted periods, until a specific threshold is reached, after which demographic change becomes extremely rapid.

Consider the behaviour of a population of the perennial tussock grass species *Austrostipa aristiglumis* in semi-arid grassland in central NSW, Australia (see Godfree et al. 2011; Fig. 2) when subjected to an exceptionally severe drought. Between 2001 and 2009 the study site was affected by drought of varying intensity,

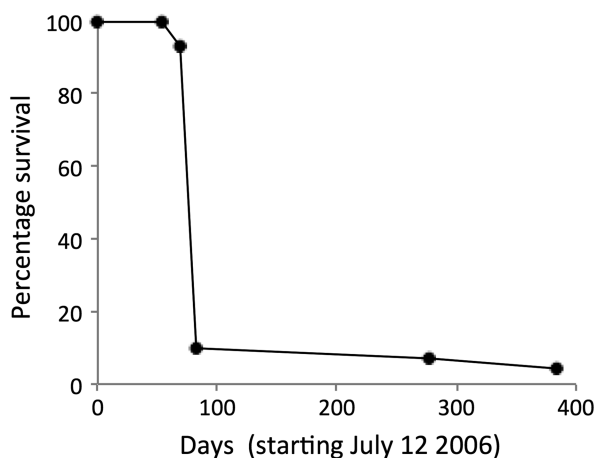


Fig. 5 Survival of adult *Austrostipa aristiglumis* during 2006–2007 at the Wyalong study site. The vast majority of mortality occurred in a 2-week period between late October and early November 2006

with 2006 being the driest year on record (181 mm; annual average=480 mm). Between January and May 2006 only 28 mm of rain fell, leaving the soil profile bereft of plant-available water, but some recharge of the upper profile occurred in June and July. To this point, virtually no mortality of *A. aristiglumis* plants was observed. However, dry conditions re-established in August 2006, and virtually all adult plants underwent complete senescence of above and below-ground tissue within a 2-week period in late October 2006 (Figs. 5 and 6a), which coincided with soil water content reaching lethal levels. In this case the population crashed to below 10 % of its original size, which then had profound effects on the post-drought recovery of the species at the study site. Interestingly, population-level mortality was visibly much lower during 2002 (the second driest year on record with 225 mm), illustrating that small rainfall differences, even among extreme events, can have great ecological significance.

Similar patterns of nonlinearity have been widely observed in response to drought, along with many other climatic cues, and often reflect the presence of discreet thermal or water stress thresholds beyond which normal physiological processes are impaired and cell death occurs. For example, a run of successive 9 days of overnight frosts in July 1984 where screen temperatures dipped to around the freezing point resulted in the widespread mortality of early-successional rainforest species at the Atherton Tablelands in northern Queensland (Fig. 2), which, like most tropical species, are frost sensitive with discrete low temperature thresholds that induce mortality (Prentice et al. 1992). Similar effects were observed in the same area in 2007 (Curran et al. 2010), and it has been suggested that occasional severe frosts are probably an important factor in determining the distribution of rainforest in Australia (Duff and Stocker 1989). Similar impacts on vegetation were observed in south-western Australian mallee-heathland vegetation during a

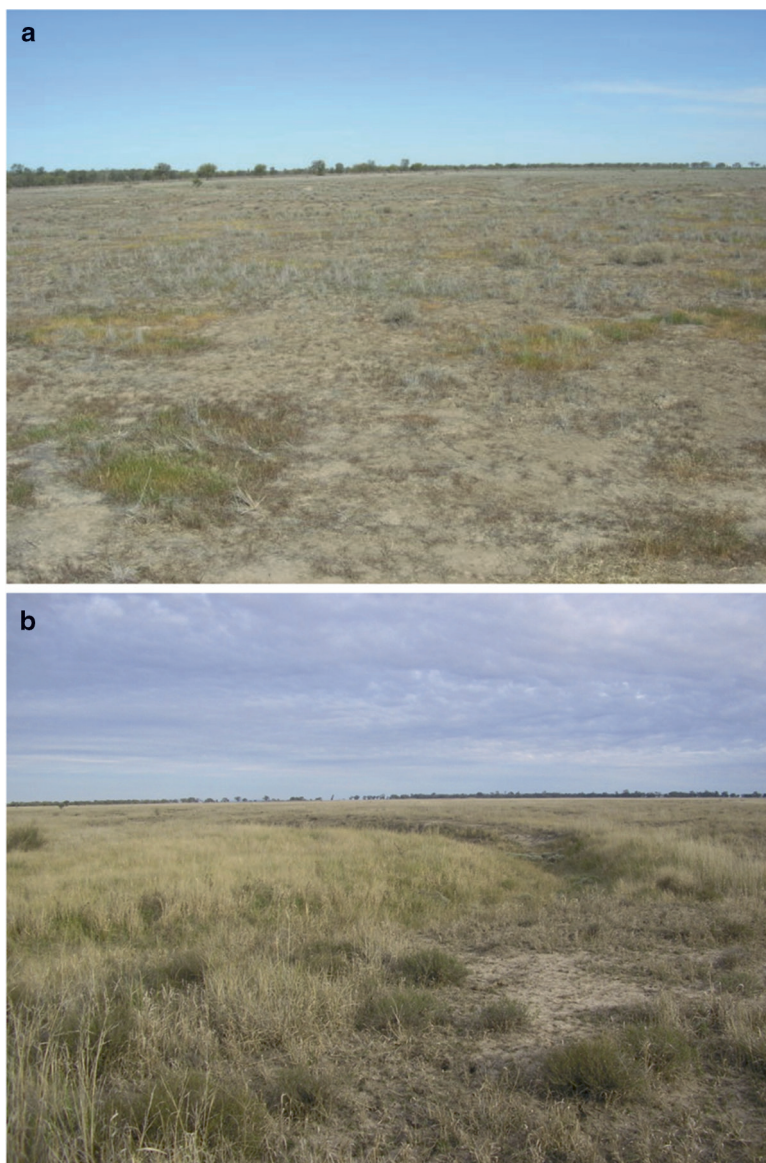


Fig. 6 The study site near Wyalong, NSW where populations of *Austrostipa aristiglumis* were tracked through the drought years of 2006–2008. (a) The study site in September 2007. Dead, gray tussocks of *A. aristiglumis* are in the background. Annuals showing varying levels of water stress are present in hollows in the foreground. (b) Topography and vegetation of the site in 2010 following drought-breaking rains, showing barer slopes dominated by *Panicum* spp. and *Leiocarpa pan-aetioides* in the foreground and wetter terrace habitats dominated by *A. aristiglumis* in the centre left. Extensive flats dominated by *A. aristiglumis* are in the background. [Courtesy of Robert C. Godfree]

record heatwave in which temperatures exceeded 45 °C on successive days (Groom et al. 2004; Fig. 2); leaf mortality in Mediterranean species is very sensitive to small (2–3 °C) differences in temperature (Larcher 2000).

Predicting the impact of specific ECEs on plant populations can be extremely challenging when physiological thresholds are involved. In the case of drought, for example, we are unlikely to know the underlying physiological responses of most wild plant populations to water stress, the level of within-population genetic variation present for stress tolerance, the potential for phenotypic plasticity to allow plants to persist through stressful periods, or even the exact nature of soil water conditions through the rooting zone over time. A secondary complication is that other landscape processes, themselves linked to specific climatic thresholds, can also result in feedback scenarios which magnify the impact of ECEs on plant populations. An excellent example of this occurred during the 1930s Great Drought in the mid-west US, when the loss of plant cover led to destabilisation of the soil surface, resulting in extensive wind erosion and soil drift. In some places, drifts covered woody vegetation altogether, or enhanced drying of the root zone by reducing the permeability of the soil surface to precipitation (Albertson and Weaver 1945). Collectively, these lines of evidence suggest that the past behaviour of plant populations to previous climate events may often be a poor or incomplete guide to their behaviour when faced with new extremes.

Species-Level Responses to ECEs, Ecosystem Change, and the Role of Environmental Heterogeneity

Interspecific differences in climate sensitivity and stress tolerance are probably ubiquitous in ecosystems globally, having been observed in drought-affected tropical rainforests and temperate woodlands, in heatwave-affected mallee-heathland, and in alpine grassy heath, subalpine woodlands and tropical rainforests affected by frost (see Fig. 2), to name but a few. These species differences fundamentally affect the way in which plant assemblages respond to severe abiotic stress, and so it appears safe to conclude that all ecosystems affected by ECEs will likely undergo at least some degree of structural and floristic change, at least temporarily.

As discussed above, ECE-induced mortality is often a key driver of vegetation change, and when stress-sensitive species are lost major shifts in plant community composition can occur. Such changes can also happen surprisingly rapidly and at landscape scales. An excellent example of this occurred in the south-western US during the 1950s, when the ecotone between ponderosa pine (*Pinus ponderosa*) forest and piñon-juniper woodland shifted significantly in response to a severe drought (Allen and Breshers 1998). Here, extensive mortality of *P. ponderosa* in response to acute soil water deficiencies resulted in ecotonal movement of 2 km or more within a <5 year period. The fact that little reestablishment of *P. ponderosa* occurred in formerly occupied parts of its range in subsequent favourable years resulted in the persistence of this ecotonal shift for at least 40 years, demonstrating that brief

climatic extremes can have long-term ecosystem-wide consequences. Interestingly, the retreat of *P. ponderosa* to higher, wetter locations was also accompanied by increased fragmentation of remaining forest patches.

Typically, however, the impacts of ECEs on population demography and community composition are more complex and occur over longer timeframes. Most plant species that occur in environments characterised by recurring abiotic stress have one or more demographic mechanisms that enable populations to either survive through, or rapidly recover from, extreme events once conditions ameliorate (e.g., the production of a persistent seedbank). Therefore changes in ecosystem structure and composition often reflect the processes of both mortality and post-event recovery. Both were shown to be of great importance in the *Austrostipa aristiglumis*—dominated semi-arid Australian grassland described above (see Godfree et al. 2011; Fig. 2) between 2006 and 2008, a period of record rainfall deficiencies, critically low soil water availability, record warmth, and elevated evaporation (Murphy and Timbal 2008). While these conditions resulted in mortality of virtually all perennial species at the study site, the subsequent recovery of populations during 2007–2009 reveal some very interesting aspects of plant population responses to ECEs that may well be generalisable to other systems.

First, drought-induced mortality differed greatly among the three dominant species at the site (*A. aristiglumis*, another perennial tussock grass *Panicum prolatum*, and the shrub *Leiocarpa panaetioides*; Fig. 6b), resulting in a considerable shift in the relative abundance of all three species over the study period. In general, *L. panaetioides* suffered much lower mortality than *A. aristiglumis* or *P. prolatum* during the drought, but in contrast to the latter species showed little evidence of population recovery after the break of the drought. Most importantly, however, minor topographic variation (<4 m across the study site) greatly influenced the rates of mortality and recovery of all species, with the composition of the different habitats investigated changing over the drought-recovery transition period (described in detail in Godfree 2012). Furthermore, the mix of strategies adopted by plant species to survive the drought period was highly habitat-dependent, and ranged from high adult survival (mesic habitats) to high post-drought recruitment (more xeric habitats). Populations of *A. aristiglumis* and *P. prolatum* virtually disappeared on the driest terrain, also demonstrating the persistent ecological impacts of transient climatic conditions.

Evidence that topographic, edaphic and microclimatic variability plays a critical role in determining the demographic responses of plant species to ECEs has been widely observed in other studies. For example, Groom et al. (2004) noted that species-level differences in the extent of damage caused by heatwave conditions appeared to be linked to the degree of pre-adaptation of plant species in habitats varying in exposure to heat and desiccation, while similar microclimatic impacts associated with the degree of canopy cover influenced the impact of frost on tropical vegetation in northern Australia (Curran et al. 2010). At a larger scale, Albertson and Weaver (1945) noted that woody vegetation mortality varied widely in different topographic positions under drought conditions, and it is typical for the first plant communities to be stressed under increasingly dry conditions to be those growing

on elevated terrain or in shallow soils. These case studies also indicate the potential importance that refugial habitats can play in both maintaining viable plant populations during and after an ECE and by acting as a source of propagules following amelioration of climatic conditions.

The Importance of Complex ECE-Population-Environment Interactions

Above, we focused primarily on the direct impact of acute and chronic extreme abiotic stress on plant population dynamics and some of their impacts at local to landscape scales. In perhaps the majority of cases, however, climatic extremes drive demographic and ecosystem change via interactions that involve a broader range of abiotic and biotic processes. These often involve secondary indirect or feedback mechanisms that amplify the initial direct effects of ECEs on plant populations, leading to even greater ecosystem change.

Among such processes, the amplifying effects of disease and insect attack on forest tree populations under stress from climate change, rising atmospheric CO₂ levels, soil nitrification and other drivers of global change have arguably received the greatest attention. Many recent studies suggest that the mortality rate of mature and old trees has risen in ecosystems globally, with insect attack and disease likely playing an increasingly important role in these systems (Harvell et al. 2002; Kurtz et al. 2008; Anderlegg et al. 2013). Such concern is not new, however: the interactive effects of disease and climate extremes, particularly drought, have been widely implicated in the widespread dieback of forest across southern and eastern Australia over the past century. While climate is thought to be only one of many factors which have led to increased impacts of defoliating insects and pathogens on tree health, the link between extreme or unprecedented drought and subsequent insect or pathogen behaviour has been well documented in some situations.

An excellent example was reported by Pook et al. (1966) and Pook and Forrester (1984), who studied the effects of an acute drought between December 1964 and August 1965 in Canberra, ACT, Australia (Fig. 2) on naturally occurring tree populations. During this drought, Canberra received only 64 mm of rain in the first half of 1965 (the driest such period on record), and also experienced well above-normal pan evaporation. The ensuing exhaustion of soil moisture, which extended for over 30 weeks, severely stressed trees in the region, with many experiencing extensive canopy defoliation, wilting, and bark injury associated with desiccation. Bark fissures and cracks provide favourable oviposition sites for longicorn beetles, and subsequent larval feeding resulted in the girdling, and ultimately death, of the most severely drought-affected trees, well after the drought had broken. Interestingly, there is also some evidence that growth and survival of longicorn beetle larvae is higher in water-stressed than well-watered trees (Caldeira et al. 2002). This case study not only demonstrates that lag-effects can be important in drought-affected systems, but also that differences in susceptibility to insect attack can significantly

affect the expression of ECEs at both intraspecific and interspecific scales; here, bark damage and beetle infestation were most prevalent in younger age classes of smooth-barked tree species.

Even more complex interactions occur in systems where plant-climate relationships are affected by a high level of ecosystem sensitivity to other biotic and abiotic variables, especially where rapid transitions between alternative (stable) states can arise. Semi-arid rangelands are perhaps the biome most sensitive to such changes, since they are usually episodic or 'event driven' systems in which plant survival and recruitment disproportionately reflect the occurrence of rare climatic events or sequences of events (Walker 1993). Indeed, failure to realise the critical sensitivity of these systems to changes in land management and climate has, in the past, resulted in the tragic collapse, and, in some case permanent damage, of semi-arid ecosystems in many parts of the world.

This lesson was learned the hard way in the semi-arid rangelands of western NSW (along with much of the rest of semi-arid Australia) during the first half of the twentieth century, a period of generally reduced rainfall punctuated by extended droughts of great severity that affected much of the continent. In this region significant changes in rangeland vegetation occurred following settlement in the mid 1800s (for example woody weed invasion and the loss of palatable species), but it was the 1896–1902 "Federation Drought" which first resulted in severe rangeland degradation as a direct consequence of overstocking and massive loss of perennial vegetation. During this drought (Verdon-Kidd and Kiem 2009), much of inland NSW was affected by extensive wind erosion, drifting sand and dust storms. While rangeland conditions improved somewhat after 1903, chronically dry conditions were again experienced repeatedly in the 1910s–1930s, culminating in the successive extreme drought years of 1943–1945 when much of south-western NSW and northern Victoria suffered the lowest 36-month rainfall on record. During this period rangeland collapse was general, dust storms occurred regularly, and wind- and water-driven soil loss occurred on a massive scale (reviewed in McKeon et al. 2004).

Fortunately, the astute observations of landowners and government officials at the time and decades of subsequent research provide a clear picture of the interactions between grazing, plant cover, and climatic conditions that led to the degradation and subsequent (partial) recovery of western NSW rangelands during and after this period. By far the most important factor throughout the period was livestock grazing pressure, which prior to 1880 had been restricted by water availability. However, an increase in watering points, generally favourable (wet) conditions years in the 1870s and early 1890s, and a great plague of rabbits which migrated across inland NSW in the 1870s and 1880s caused grazing pressure to rise to unsustainable levels. During the ensuing 7-year drought perennial groundcover was reduced to low levels by grazing, while trees and shrubs were ringbarked by starving rabbits. Defoliated grasses lacked the photosynthate reserves to re-allocate growth to roots during dry periods, and suffered extensive mortality. Wind erosion then exposed less fertile and permeable subsoils, which in turn reduced water filtration and increased scalding of the soil surface. Extensive mobilisation of sand during windstorms blasted the remaining perennial vegetation even on better managed



Fig. 7 Extensive surface scalding and loss of vegetation in north-western NSW. Extreme drought combined with poor land management practises resulted in rangeland degradation and erosion on a massive scale between the 1890s and 1940s. While many areas have recovered, there remains widespread evidence of these past events. Near Carinda, NSW, in 2006 (Fig. 2). [Courtesy of Robert C. Godfree]

properties. The destruction of the pre-existing soil crust, which was strengthened by lichen and other microflora, then reduced soil microbial activity and nutrient cycling, which limited vegetation recovery. The resulting collapse of vital ecosystem processes, which even today have not fully recovered (Figs. 2 and 7), demonstrates how the impact of extreme climatic conditions can be augmented by complex landscape-level feedback loops.

As a postscript to this case study, it is interesting to reflect on the factors which led to the dramatic improvement of the NSW rangelands beginning in the 1950s. The most important factor was certainly a shift towards generally higher rainfall, and in particular the exceptionally wet years of 1950, 1955–1956, and 1973–1976, when annual precipitation was at or above 90th percentile totals over most of eastern Australia. A decline in rabbit density following the release of the myxoma virus in 1950, along with the new ability to move stock during drought periods using road trains allowed perennial vegetation (including woody weeds, which themselves are considered a driver of rangeland degradation) to re-establish across most of the region. Soil stabilisation was also assisted by coordinated engineering and land management strategies aimed at reducing water movement and re-establishing vegetation, and probably by a general decline in wind speeds. Severe droughts still result in degradation, but there is hope that the unique combination of climatic and anthropogenic processes that led to the events of the 1890s–1940s may not again be repeated.

Extreme Events in Aquatic Systems

Above, we have focused on the impacts of extreme climatic events on terrestrial systems. However, extreme events, such as floods and droughts, can also be important drivers of the structure, composition, assembly, and function of aquatic systems (Lytle and Poff 2004; Naiman et al. 2008). Ecologically, aquatic ecosystems are extremely diverse, and unsurprisingly, the impacts and indeed the very nature of ECEs vary widely among these different systems; here we focus on the impacts of extreme hydroclimatic events on freshwater aquatic ecosystems.

Extreme hydrological events are a natural part of many aquatic ecosystems, some of which may even rely on both extreme floods and droughts to maintain their composition and structure over time (Lytle and Poff 2004). The study of extreme events in aquatic systems is complicated by the tendency for associated hydrological regimes to reflect not only prevailing climatic or meteorological conditions at a given location but also a myriad of water balance-related processes operating at site to landscape scales. For example, river flow rates, groundwater availability, and the timing of seasonal inundation often substantially lag changes in rainfall, temperature, evapotranspiration and land surface runoff rates. Some aquatic ecosystems also require a very long historical record to characterise long-term variability in flow, particularly in highly variable or intermittent systems (Lake 2011; Reid and Ogden 2006), a difficulty compounded by anthropogenic river regulation, which alters the statistical distribution and timing of flows, directly uncouples meteorological and hydrological drought, and generates new or “non-natural” types of extreme events. In many cases, the frequency and severity of extreme events have actually been *reduced* by river regulation and water extraction for human purposes (Walker et al. 1995; McMahon and Finlayson 2003; Lytle and Poff 2004; Vivian et al. 2014a).

Numerous indices have been developed to quantify both the hydrological regime of an aquatic ecosystem and the thresholds that define extreme events; events can be extreme in terms of magnitude, frequency, seasonality, duration, or spatial factors. As with climatological parameters there will always be a selection of events that can be classified as statistically extreme (e.g., beyond the 95 % percentile), but we are usually interested in those that elicit a biotic response in which the adaptive capacities of an organism are exceeded. This distinction is especially relevant for aquatic ecosystems, in which many species have evolved traits (e.g., life history, morphological plasticity, different regeneration or reproductive strategies) that allow them to survive extreme disturbances (Lytle and Poff 2004). Particular adaptations can carry costs as well as benefits, and changing the timing, magnitude, duration and predictability of extreme events can shift the balance to cause the costs of the adaptation to outweigh the benefits (Lytle and Poff 2004), thus inevitably affecting species survival and persistence.

Case Study: The Murray-Darling Basin and the Millennium Drought

Australia's Murray-Darling Basin (MDB) is a region where the impacts of extreme events on aquatic vegetation have been highly visible in recent years. While inflows in the MDB have traditionally exhibited high variability on annual to multi-decadal timeframes, between 1997 and 2009 (the "Millennium Drought") much of south-eastern Australia and the MDB suffered from severe meteorological drought, with many areas recording record low rainfall in this period. Low rainfall was exacerbated by high evaporation rates (due to above average temperatures), which resulted in an even larger decline in runoff and the establishment of extreme (90th–95th percentile) or even unprecedented hydrological drought across much of the region (Leblanc et al. 2012; Cai and Cowan 2008). The Millennium Drought was finally broken by flooding rains during the La Nina years of 2010–2011 (Leblanc et al. 2012).

The nature of these extremes can be illustrated by stream flow records from Yarrawonga weir, located approximately 192 km upstream from the mouth of the Murray River, and the impacts on downstream vegetation in the Barmah-Millewa Forest (BMF) (Fig. 2). The BMF contains a range of high conservation-value floodplain vegetation, including extensive stands of the iconic *Eucalyptus camaldulensis* (river red gum), many of which are flooded when flow in the Murray River exceeds the channel capacity of 10,600 mL day⁻¹ at Yarrawonga weir. Prior to the regulation of the Murray River in the mid-1930s, in most years BMF experienced deep winter-spring floods and a generally dry summer-autumn period. Flow during the latter part of the Millennium Drought was very low, remaining approximately at or below channel capacity (<ca. 11,000 mL day⁻¹) for a continuous period of over 1600 days between February 2006 and 2010, resulting in the absence of significant flooding in the BMF. This was by far and away the longest duration of low flow on record, the two previous being 626 days (December 1943 to August 1945) and 582 days (March 1940 to October 1941).

Interestingly, the statistical 'extremeness' of daily flows during the Millennium Drought and the subsequent La Nina flood peaks is strongly influenced by the choice of reference period. For example, when compared to the post-regulation reference period of 1960–1990, daily flow during the last 2 years of the Millennium Drought (2008–2010) only occasionally dropped below the fifth percentile (Fig. 8a). In contrast, when compared to the pre-regulation period of 1905–1935, daily flow was well below the fifth percentile for multiple lengthy periods, including during every winter and spring (i.e., June to November) from 2006 to 2009 (Fig. 8b). Collectively, daily winter and spring flows during the Millennium Drought were thus more extreme when compared with the pre-regulation period than the post-regulation period.

Multiple floods occurred from late 2010, ending the long-term drought conditions (Fig. 8). The flood peaks that occurred in winter-spring 2011 and 2012 were well within the normal bounds of daily low rates, but other peaks were clearly unusual.

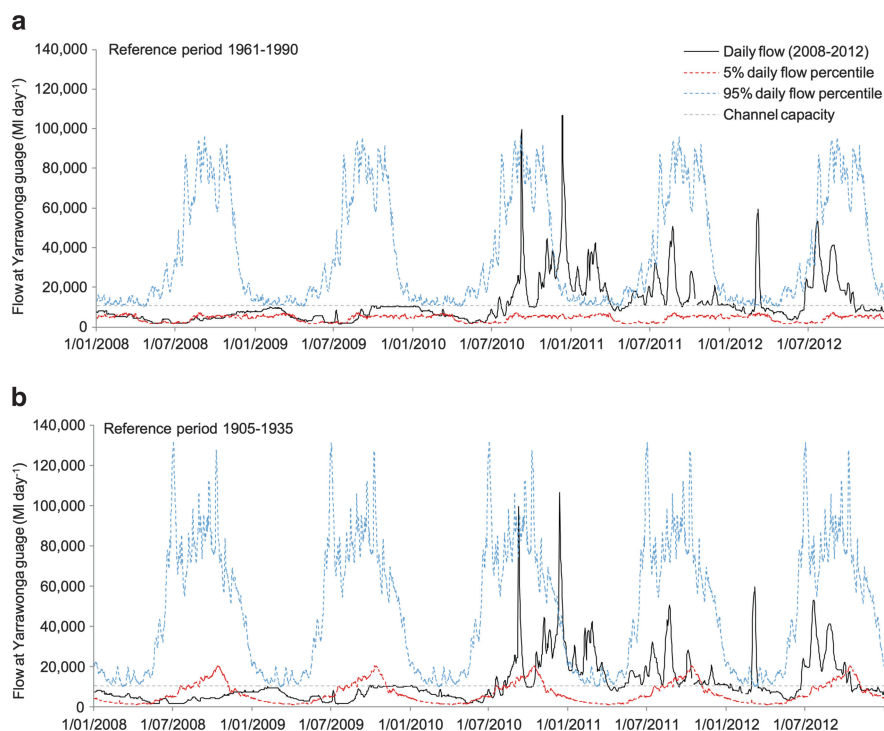


Fig. 8 Daily flow at Yarrawonga weir (black line) during the final 2 years of the Millennium Drought (2008–2010) and the floods of 2010–2012. Dotted grey line indicates the bank threshold of ca. 10,600 ml/day above which flooding occurs in the downstream Barmah-Millewa Forest. Flow is shown compared to 95 % (blue line) and 5 % (red line) flow percentiles of two reference periods: (a) 1960–1990 (post-regulation) and (b) 1905–1935 (pre-regulation)

In particular, the unseasonal flooding that occurred in summer 2010–2011 can be considered extreme with respect to both reference periods, extending for several months above the 95 % percentile of daily flows. In particular, peak flows in March of both 2011 and 2012 were the two highest March flood peaks on record, and occurred at a time when river flow is normally below channel capacity and flood-plains are consequently dry.

Given the extremes in flow seasonality, depth and duration described above, it is not surprising that these drought and flood events had a significant impact on major species and ecosystems across the BMF. Perhaps most dramatic was the widespread dieback of *E. camaldulensis*, a situation also observed widely across the Murray-Darling Basin (Fig. 9). During latter stages of the drought *E. camaldulensis* located away from the Murray River were in poorest condition (Cunningham et al. 2009), reflecting the decline in flood extent within the forest. Interestingly, Horner et al. (2009) showed that annual *E. camaldulensis* mortality increased substantially between 1996 and 2007, but that the impact was limited to higher density stands.



Fig. 9 Extreme drought stress in *Eucalyptus camaldulensis* (river red gum) during the Millennium Drought. Dieback was observed in river red gum populations across much of south-eastern Australia during the drought as a result of extremely low rainfall combined with water extraction for human use. [Courtesy of Robert C. Godfree]

They also noted that the impact of the Millennium Drought exceeded that of drought periods in the past, probably due to record high temperatures, low rainfall, a reduction in water-table depth, and the increasing removal of water from the Murray River for irrigation (Horner et al. 2009).

The impact of these extreme flow regimes on *Juncus ingens* (giant rush; Fig. 10a) in the BMF also demonstrates the role that extreme events can play in maintaining vegetation composition, and the changes that can occur following river regulation. *J. ingens* is a very tall (2–3 m) native rush which has expanded to form extensive near-monospecific stands across much of the BMF, where it is considered a key cause of degradation of treeless floodplains dominated by *Pseudoraphis spinescens* (Moir grass). *J. ingens* is intolerant of sustained submergence during deep winter/spring floods, and so has increased dramatically in distribution and abundance following river regulation (Vivian et al. 2014b).

During the latter stages of the Millennium Drought, soil water deficits were so severe on some floodplains that death of mature *J. ingens* was observed (Mayence et al. 2010; Fig. 10a) and at least some invasive populations suffered significant declines in stem density. Even more dramatic impacts were observed during and after the 2010–2012 floods, when extensive stem death of *J. ingens* was recorded in lakes and open plains across much of the forest. Stem mortality was greater, and post-flood recovery lower, in areas that experienced deeper floods, such as along the edge of Barmah Lake (Fig. 10a): as shown in Fig. 10b, recovery of *J. ingens* was negligible in areas submerged by more than 2.5 m of water.

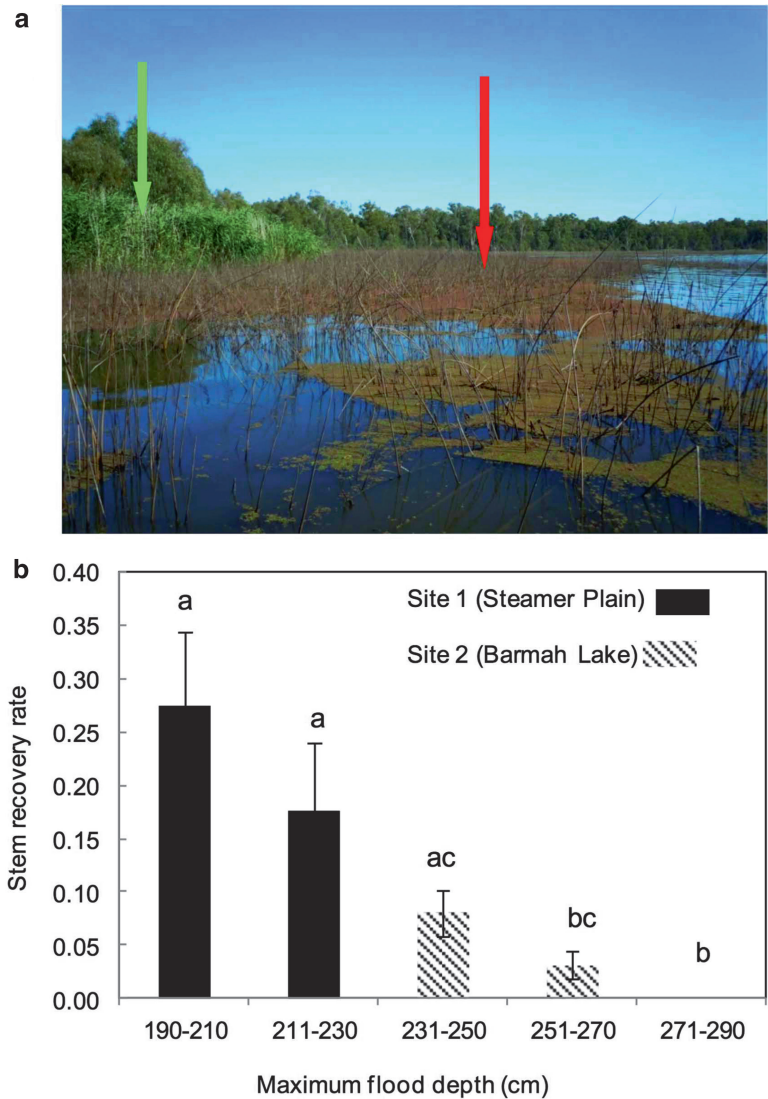


Fig. 10 Impact of flood depth on *Juncus ingens* survival and recovery at Barmah-Millewa Forest during the 2010–2012 floods. Deeper floods result in stems more likely being submerged for longer periods. **(a)** Stem die back (*red arrow*) following prolonged submergence. This site is along the edge of Barmah Lake where *J. ingens* has encroached over several decades to become invasive. Taller species such as *Phragmites australis* (*green arrow*) have remained emergent above flood water depths and have survived the extreme flooding. **(b)** Comparison of stem recovery rates ((new stems + surviving stems)/old stems) in response to different flood depths. Bars with *different letters* are significantly different (ANOVA). [Courtesy of Lyndsey M. Vivian]

The results of this study demonstrate that extreme events can play a critical role in determining the structure and composition of aquatic vegetation, and may even be essential for maintaining ecosystem health. The impact of flooding and drought on *J. ingens* populations strongly suggest that periods of extremes in river flow, especially deep floods, historically limited the invasive potential of this species. These constraints were reduced by river regulation, with events of sufficient extremity to halt the invasion of *J. ingens* now occurring only occasionally.

ECES and the Response of Plant Populations to Climate Change

The case studies above demonstrate that climate extremes have the potential to profoundly affect wild plant populations in both terrestrial and aquatic environments. Demographic changes induced by abiotic stress often occur in a rapid, non-linear manner, and involve persistent shifts in vegetation structure and composition that manifest at plant community to ecosystem scales. However, while the case studies above primarily involve the impact of short-term extreme events which are followed by a return to prior, more favourable conditions, recent developments in our understanding of the nature of anthropogenic climate change has seen an increased focus among ecologists and evolutionary biologists on the role of ECEs in changing climates.

Most plant species have a geographic range that is delineated at least in part by their physiological ability to tolerate climatic stress, known as their climatic envelope. As discussed previously, when climatic extremes move plant populations outside of this envelope, fitness declines and populations may contract. However, because climate varies across a species' range, populations from different parts of that range experience different levels of abiotic stress which may or may not lead to demographic change. Consider, for example, a plant species that occurs within a climatic envelope delineated by upper and lower thresholds for a specific climatic variable, such as rainfall, as shown in the diagram in Fig. 11a. In this very simple, stylised model, populations persist within the geographic region that experiences climatic conditions that lie within these thresholds (populations A–C, Fig. 11a) for a proportion of the time sufficient to maintain stable or positive population growth.

Fig. 11 (continued) C becomes range-core, and a new population could become established at D via migration. However, population B faces extinction if it cannot adapt. (c) Climatic conditions experience by a range-core population with stable long-term climate. Even extreme events (marked by the *arrow*) may not fall outside the physiological limits of the population. (d) Climatic conditions experienced by a range-edge population, with extreme events (*arrows*) potentially exceeding the population's physiological limits. (e) Potential scenario for a range core population able to persist even in the presence of climate change. (f) Potential scenario for a range edge population which faces an increasing number of damaging climatic events and possible extinction

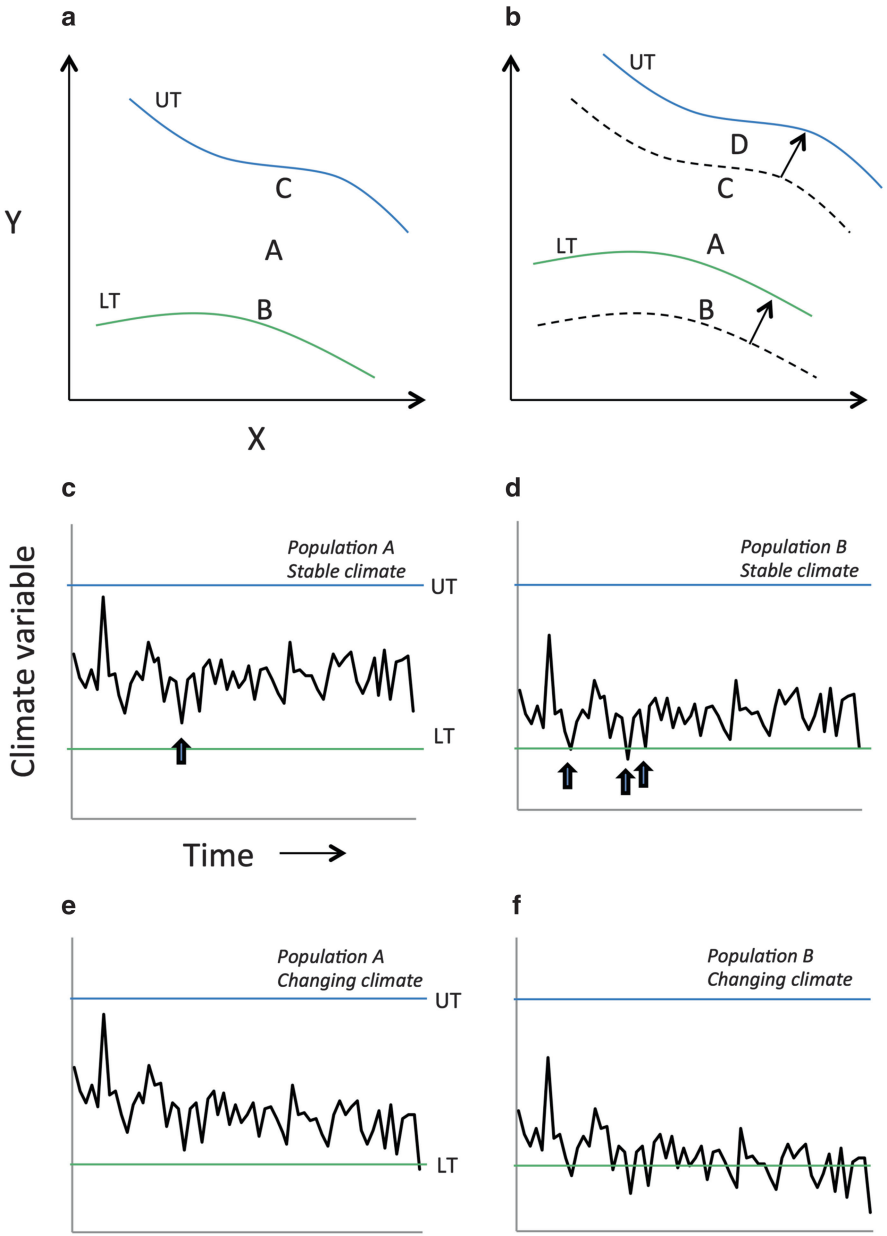


Fig. 11 Scenarios faced by populations of a plant species under climate change. (a) Simple representation of a situation where the range of a species is determined by a single climate variable. The range is shown in two spatial dimensions (X and Y) and is bounded by the species' upper and lower climate thresholds (UT and LT). Population A exists in the core of the species range, while B and C exist towards the range edge. (b) Scenario in which the species' climatic envelope moves in space, shown by the arrows. Population A now lies near the edge of the climatic envelope,

Towards the centre of their species range, populations (A in Fig. 11a) generally experience favourable climatic conditions which rarely, if ever, exceed the stress tolerance characteristic of the population (Fig. 11c). Extreme events, while a statistical phenomenon (Fig. 11c), are less likely to be of sufficient severity to affect the demography of resident populations, especially in a catastrophic manner. In contrast, environmental conditions in range - edge areas (B and C in Fig. 11a) are more marginal, and populations tend to be subjected to a higher frequency of events that are near to or exceed their physiological stress thresholds (Fig. 11d). Although populations can to a certain degree adapt to these conditions by means of life history avoidance strategies (e.g., the production of a persistent seedbank) and the ability to alter phenotype in response to environmental cues (phenotypic plasticity), at a certain point adaptive limits are reached, populations fail to maintain positive growth rates, and ultimately go extinct.

There are good reasons to think that a high frequency of ECEs and associated episodes of extensive plant mortality (c.f., Tigerstedt 1994) play a particularly important role in the evolutionary dynamics and viability of range-edge plant populations. As discussed above, many of the best examples of rapid vegetation mortality and change associated with ECEs do come from range-edge environments (e.g., Albertson and Weaver 1945; Allen and Breshears 1998), although it should be noted that there are certainly exceptions (e.g., Godfree et al. 2011). Due to their typically small size, fragmented distribution and low fecundity (Bridle and Vines 2007), range-edge populations are more likely to suffer adverse evolutionary consequences of ECE-induced bottlenecks, and in particular the deleterious effects of inbreeding depression, genetic drift, and Allee effects (Bridle and Vines 2007). Indeed, these processes, and the associated dynamics of migration-selection balance in which adaptive potential is maintained without swamping of advantageous alleles (Phillips 1996; Bridle and Vines 2007), are often invoked to explain the presence of relatively stable range limits that are observed in many plant species globally (Hoffmann and Hercus 2000).

In a changing climate, many plant populations face the likelihood of being exposed to increasing abiotic stress as their climate envelope undergoes geographic movement (Fig. 11b). For some populations (e.g., population C in Fig. 11a, b), climatic conditions may become more favourable, even leading to the establishment of new founder populations in areas previously located outside the species range (e.g., population D in Fig. 11b). Others, especially those with broad climatic envelopes which encompass past and future climate regimes, may be relatively unaffected by the changing climate, at least temporarily (e.g., Fig. 11e). These populations may adapt via expression of advantageous plastic phenotypes, although the behaviour of plasticity traits in truly novel climates may be disrupted by climatic extremes and remains poorly understood (Chevin et al. 2010). So-called rear or trailing edge populations (B in Fig. 11a, b) face exposure to climatic conditions that lie outside their physiological limits (Fig. 11f), and for these populations evolutionary adaptation becomes necessary if extinction is to be avoided (Kuparinen et al. 2010).

The extent to which evolutionary processes are likely to allow rear-edge plant populations to track climatic change remains a contentious issue (Kuparinen et al.

2010). On the one hand, there is abundant evidence that ongoing physical stress can shift the means of adaptive traits by means of directional selection (Reznick and Ghalambor 2001), even if the intensity of selection is not high (Hoffmann and Hercus 2000). On the other hand, clear evidence for a dominant role of evolution in species responses to past episodes of climate change remains lacking (Gienapp et al. 2008); most species appear to track their climatic envelopes closely during periods of climatic change. Evidence from invasion biology also suggests that invasions rarely occur in the absence of pre-adaptation of genotypes to newly encountered climatic regimes (Bridle and Vines 2007). Nevertheless, there are good reasons to once again expect that ECEs will play a significant role in the evolution of plant genomes under changing climatic conditions.

First, there is evidence that populations subjected to periodic disturbance and episodes of high mortality, such as occur during ECEs, might adapt most rapidly to climate change, since low mortality in established cohorts can slow the production and establishment of better adapted juvenile genotypes. This process has been modelled for populations of the tree species *Pinus sylvestris* and *Betula pendula*, where an adaptive lag in response to climate change was reduced by high adult mortality (Kuparinen et al. 2010). Second, stressful events can trigger the expression of new phenotypes within a population, which may then increase in frequency and maintain expression even under ameliorated growing conditions (Hoffmann and Hercus 2000). Such events may even increase mutation and recombination rates and hence the production of entirely new genotypes, and may also affect the heritability of traits under selection (Hoffmann and Merilä 1999). Finally, since population differentiation is also facilitated by low rates of outcrossing, ECEs may play an important role in local adaptation by reducing fecundity and hence the introgression of maladaptive alleles into the genomes of range-edge plant populations.

However, periods of elevated physiological stress that lead to high plant mortality may also hinder the optimal tracking of phenotypes to prevailing climatic conditions. First, small population sizes reduce the likelihood of *in situ* generation of better-adapted genotypes (Sgrò et al. 2011), and in general evolutionary change seems to primarily reflect the selective pressures that occur in environments that are experienced by the majority of individuals in a population (Bridle and Vines 2007). Second, extreme events may cause selective sweeps that reduce the diversity of genetic traits that mediate the organismal response to changes in climate, resulting in elevated rates of inbreeding and reduced fitness. Such effects are likely to be most severe in rear-edge populations, where extreme events are likely to have the biggest demographic impact on populations. Third, extreme events may drive rapid selection for traits that are adaptive under stressful conditions but maladaptive once favourable growing conditions return and other drivers such as disease and competition become more important. Finally, the evolvability of traits under climatic change is contingent on the presence of heritable genetic variation, and past extreme events may have already driven advantageous alleles to fixation in range-edge populations, thus reducing the capacity for further adaptive change (Davis et al. 2005).

As discussed above, a critical feature of ECEs is that they tend to affect populations in a nonlinear manner, with mortality rates increasing rapidly once certain

physiological thresholds have been exceeded. This may have important implications for plant evolution under climate change, because it suggests that topoedaphic factors that alter the immediate abiotic environment experienced by individual plants can have an immense impact on plant survival during extreme events. Indeed, in a heterogeneous environment we might expect ECEs to select plants that survive not by virtue of being better adapted to climatic extremes, but simply because they grow in a marginally more favourable environment. This was observed in the *Austrostipa aristiglumis* populations studied by Godfree et al. (2011), where minor differences in soil water availability was the dominant predictor of plant survival during a period of extreme drought, and where no increase in drought tolerance was observed among drought survivors. Under such circumstances, which are probably common, ECEs may act more as an agent of random rather than selective mortality.

A Role for Genomics in the Study of the Past and Future Behaviour of Climatic Extremes

Genomics can inform how ECEs have effected past demographic and evolutionary history of plant populations. Indeed, both selection and demography history should be considered jointly when inferring the history of a population based on observed genetic variation (Siol et al. 2010). Past demographic and selection events can result in similar signals and, until recently, it has been difficult to tease apart competing hypotheses. The primary difference is that demographic events should affect neutral variation across the genomic in a similar manner, while selective forces will only affect genes under selection. Genomics provides an opportunity to tease apart competing hypotheses by providing large datasets in which to explore patterns of variation across the genome. Specifically, by sampling a large number of unlinked genes from across genome, it is possible to identify patterns that likely result from selection pressures versus demographic events (Akey et al. 2004).

Demographic History

Genomic data can be DNA sequences or, commonly, single nucleotide polymorphisms (SNPs). Genomics allows the identification of a large number (100s–1000s) of SNPs from across the genome. SNPs allow more precise estimates of population history, compared to microsatellite markers, due to more predictable mutation rates (Brumfield et al. 2003). SNPs however can suffer from ascertainment bias that can be avoided by using DNA sequence data directly.

Large amounts of genome-wide data allows for estimating several parameters associated with more complex models of population history, including migration rates, timing and strength of bottlenecks, and expansions (Stoneking and Krause 2011).

The application of coalescent theory, or patterns of common ancestry (Kuhner 2009), to genomic datasets allows a more accurate picture of population history as there is typically variation among gene trees and the more unlinked genes examined allows for a more complete picture of population history.

The application of coalescent theory to many nuclear genes has been limited by computational challenges. Recent methods, such as pairwise sequentially Markovian coalescent (PSMC) modelling have shed light on complex human demographic history (Li and Durbin 2011). Similar methods applied to polar bears have informed past fluctuations in effective population size (N_E) in relation to past climatic events (Miller et al. 2012). More commonly, Bayesian and Approximate Bayesian (ABC) approaches are used to fit demographic models to genomic data. For example, Ross-Ibarra et al. (2008) reveal past fluctuations in effective population size in populations of *Arabidopsis lyrata* in relation to past glacial cycles.

Evolutionary History

Importantly, fitting demographic models to genomic data provide the necessary backdrop to explore signals of adaptation (Ross-Ibarra et al. 2008; Siol et al. 2010). Siol et al. (2010) provide a summary of plant studies that have used a coalescent approach to fitting demographic models to study selection.

Genomics can provide insights into past extreme events that have resulted in directional selection on a gene with a relatively large effect. A primary approach for identifying genes under selection is ‘outlier’ tests which identify loci that are out of the range of expected divergence (often F_{ST} based). Expected divergence of neutral variation is heavily dependent on demographic history and therefore the use of demographic models in conjunction with outlier test is an important advance in understanding both demographic and evolutionary history of a population. Genome wide association studies (GWAS) take this a step further and look for correlations among ‘outlier’ loci purportedly under selection and certain traits such as drought tolerance. GWAS have had a major impact on human medical research and other research areas, including plant studies, have been quick to follow. However, it is important to note that some genes may be adaptive under certain environmental conditions and neutral under other conditions (genotype \times environment interactions). Therefore, signals of past adaptive change due to one ECE may not convey adaptive traits to a future ECE. Additionally, phenotypes are often the product of many genes of small effects and signals of selection on these traits can be much harder to detect.

Phenotypic plasticity is yet another way in which plants can temporarily respond to ECEs. While phenotypic plasticity can be heritable, little is still known about the genetic basis (Anderson et al. 2011). Transcriptomics is allowing us to understand more about gene expression, and the effect of differing gene expression on phenotypes. In order to inform ECEs, transcriptomics requires the sequencing of RNA during the extreme event, ideally from the same individual, to provide insight

into how expression may help plants survive. This may be feasible to simulate in a laboratory setting/common garden experiment once regions of the genome hypothesized to be responsible for potential adaptive phenotypes have been identified.

Future Directions and Challenges

The study of climatic extremes has yielded profound insights into the way in which plant populations survive in unpredictable and hostile environments. In many ways, however, this field of research is still in its infancy, and many of the potential impacts of ECEs on the demography and evolution of plant populations remain poorly understood. Some key questions that have yet to be resolved include:

1. *Which plant species, communities and ecosystems are most resilient to demographic change during climatic extremes?* Although an appraisal of the available literature suggests that certain biomes are particularly susceptible to ECEs, or even require them to maintain structure or composition, such as some aquatic ecosystems, few comparative studies have addressed this fundamental question. This is largely due to the difficulties in conducting experiments that simulate ECEs, and so further development of cost-effective techniques for performing such experiments in natural plant communities is urgently required.
2. *What are the ecological and evolutionary dynamics of plant populations following ECEs and when does recovery fail?* The majority of studies that have comprehensively documented the impact of climatic extremes on the demography of wild plant populations have focused on their immediate impact on plant performance and mortality. There is a need to better understand the factors that limit the fitness of population under more favourable conditions that follow ECEs, such as disease, competition and predation. These factors may be at least as important as the direct impacts of the original climatic event itself.
3. *What is the role of ECEs as drivers of evolutionary change?* The evolutionary consequences of ECEs remain virtually unstudied for most groups of organisms. In particular, little is known about the amount and heritability of genetic diversity that exists for climate-sensitive traits in range-core and range-edge plant populations, nor how these are affected by episodes of climate-induced mortality. Lessons can probably best be learnt from studying organisms present in ecosystems which are already exposed to frequent ECEs.
4. *How will the nature of complex ECEs evolve under anthropogenic climate change, and what will the impacts be on plant communities?* Resolving this question is one of the most significant ecological challenges of our time. While many climatic extremes are expected to increase in frequency and severity under climate change, their impact on plant communities often depend not only on climate but on other phytosociological, biophysical and anthropogenic factors. As outlined above, the degree to which drought affects plant populations can be affected by absolute rainfall deficiencies, atmospheric temperatures,

plant population structure and density, soil composition, topography, the activities of grazing animals, disease, and atmospheric CO₂ concentration. Resolving questions of this kind will require an increasingly integrative approach involving a range of disciplines associated with the broader study of global change in general.

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