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Extreme Climatic Events as Drivers of Ecosystem Change

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1. Introduction

It is difficult to stand in the cliff dwellings that lie in the shallow caves that line the canyon walls of Mesa Verde National Park in south-eastern Colorado and not be amazed. These impressive structures were built in the late 12th and early 13th centuries by pre-Columbian native American Anasazi people, who, at that time, occupied much of the Four Corners region of south-western USA. Some cliff dwellings were of exceptional size, containing over 150 rooms and lodging 100 or more people, and were supported by the farming of maize on the surrounding semi-arid mesa tops (Benson *et al.* 2007a) which today are covered in forests of piñon pine and juniper. Perhaps more interesting, however, is that this phase of occupation represented just one stage in the development and decline of Anasazi culture in the southwest. Anasazi populations waxed and waned repeatedly over time, and most of the even bigger, multi-storey stone houses (great houses) located across the central San Juan Basin, for example, were abandoned in the mid 12th century (Benson *et al.* 2007a,b). Construction activity in the wetter, more favourable northern San Juan Basin then increased (Lekson & Cameron 1995; Benson *et al.* 2007a), but by the late 13th century the Mesa Verde cliff dwellings, along with other Anasazi population centres in the Four Corners region, had also been abandoned for areas closer to the Northern Rio Grande region of New Mexico (Ahlstrom *et al.* 1995).

What caused these large scale human migrations? The most likely scenario is that Anasazi populations, which over time had become increasingly sedentary and dependent on maize for provision of dietary needs (Benson *et al.* 2007b), were primarily responding to movement of the climatic niche in which maize could be grown (Petersen 1994). Reconstructed climate data suggest that between AD 900 and AD 1300 the south-western United States was affected by elevated aridity and protracted drought that exceeded in severity anything that has been observed in the centuries since (Cook *et al.* 2004; Stahle *et al.* 2007), and particularly severe multi-decadal drought, apparently linked to changes in the Pacific Decadal Oscillation (MacDonald & Case 2005), occurred during AD 1135-1170 and AD 1276-1297. Around this time the central and northern San Juan Basin Anasazi cultures, respectively, declined (Benson *et al.* 2007a), and it is likely that agricultural collapse (Benson *et al.* 2007a), coupled with breakdown in societal structure (Benson *et al.* 2007b), ultimately led to the depopulation of the entire region.

This and other historical examples in which drought has played a pivotal role in socioeconomic and cultural decline (e.g., Weiss & Bradley 2001; Acuna-Soto *et al.* 2002, 2005; Endfield *et al.* 2004; Hodell *et al.* 2005) underscore the capacity for extreme climatic events to threaten the very fabric of society. Modern agricultural systems are not immune from similar pressures; recently the severe 1997-2009 “Millennium Drought” in south-eastern Australia (Whitaker 2006; Bond *et al.* 2008) caused massive agricultural decline (Pook *et al.* 2009), extensive job losses (Mpelasoka *et al.* 2008), and real declines in household consumption, wages, and gross regional product (Horridge *et al.* 2005). What makes these cases of added importance is that the frequency of extreme events is expected to increase under anthropogenic climate change (Tebaldi *et al.* 2006; Planton *et al.* 2008), and changes in precipitation and temperature extremes are already being observed around the world (e.g., Collins *et al.* 2000; Easterling *et al.* 2000; Goswami *et al.* 2006). Significant impacts on human societies and the natural world are expected if such trends continue (Easterling *et al.* 2000).

Recently, there has been a significant increase in research focusing on the impact of extreme climatic events, and, more broadly of climate change, on natural and agro-ecosystems (e.g., Easterling *et al.* 2000; Meehl *et al.* 2000; Walther *et al.* 2002; Tubiello *et al.* 2007). Extreme events can have severe and often disproportional effects (Gutschick & BissiriRad 2003) on a wide range of animal and plant groups (e.g., Dudley *et al.* 2001; Morecroft *et al.* 2002; Martinho *et al.* 2007), with population-level changes to extinction rates, range movement, behaviour and reproduction observed in a range of different ecosystems (reviewed in Easterling *et al.* 2000; Parmesan *et al.* 2000). However, such examples raise further questions, to which we at present only have a rudimentary and fragmented understanding. For example, which ecosystems are most sensitive to extreme climatic events, and to what type of events? How extreme, and over what timeframes, do climatic conditions have to be to cause significant mortality among plant species? Over what timeframes can community-level compositional change occur? Most importantly, can we predict the nature and magnitude of change in plant communities that are affected by different kinds of extreme events? These questions are more than just academic: the ecosystem services that plant communities provide underpin both human societies and biodiversity alike.

The objectives of this chapter are twofold. First, by drawing on a range of case studies, I assess the conditions under which extreme climatic events are likely to rapidly alter the structure and composition of natural plant communities. I focus specifically on the impacts of extreme drought and heatwaves, since both are expected to increase in severity in coming decades as climate change alters the probability distribution of temperature- and precipitation-related climatic variables (Meehl *et al.* 2000; Hennessy *et al.* 2008; Planton *et al.* 2008); the impacts of other extreme events are discussed elsewhere (see Easterling *et al.* 2000; Parmesan *et al.* 2000; Holmgren *et al.* 2006). I then test some of these ideas by reporting the results of a field study which compares the demographic responses of three semi-arid Australian grassland species to drought, with a specific focus on using a better understanding of the specific roles of habitat heterogeneity, species characteristics, and drought severity to predict the likely impact of extreme events on plant communities under climate change.

2. Characterisation of extreme events

It is widely understood that ecological stresses often reflect statistical extremes rather than climatic means or variances (Gaines & Denny 1993), and the responses of individuals and

populations to stressful abiotic conditions is, in many cases, non-linear and sensitive to discrete thresholds (Easterling *et al.* 2000; Beniston & Stephenson 2004). As such, accurate quantification of the likelihood and intensity of extreme climatic events is essential. Unfortunately, this task is made difficult by the fact that no single definition of what constitutes an extreme event actually exists, and the impacts of unusual climatic situations on ecosystems have not traditionally been studied in a systematic manner (Gutschick & BassiriRad 2003; Smith 2011). As noted by Beniston & Stephenson (2004), extremes can be defined in terms of rarity, intensity or impact, although individually these definitions may fail to capture the critical features of climatic variability that impact on plant and animal populations. Smith (2011) suggests that an extreme climatic event should be defined as a rare or unusual climatic period that alters ecosystem structure and/or function well outside what is considered normal variability, and many of the studies discussed below inherently use this concept, despite the fact that the rarity of the climatic conditions being studied is often not formally described.

From a quantitative standpoint, a range of approaches are used to characterise extreme events. The Intergovernmental Panel on Climate Change (IPCC 2011) defines a climate extreme as “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” (p. 2). Indices derived using this approach usually quantify the duration or frequency of events which exceed a specific temperature or precipitation threshold, for example total number of frost days, growing season length, heat wave duration, and number of consecutive dry days (e.g., Tebaldi *et al.* 2006). Another commonly-used method is to define extreme events as those occurring within a certain percentile range (often the 5th, 10th, 90th or 95th percentiles) of a climatological distribution within a given timeframe (see Bell *et al.* 2004). Hennessey *et al.* (2008) define exceptional droughts as those of one year in duration and occurring, on average, once every 20 years (i.e., a 5% probability of occurring within a given year; Katz *et al.* 2005).

The standard statistical approach for quantifying climatic variation is to fit a probabilistic model to a given climatic data set and then to evaluate the likelihood (and severity) of specific climatic events based on the associated probability density function. In recent years a cohesive statistical theory of extreme events has emerged (Coles 2001). These techniques, and their application to ecological problems, have been discussed in detail elsewhere; readers are directed to Katz & Brown (1992), Gaines & Denny (1993), Katz *et al.* (2005), and Resnick (2007) for details. The basic statistical approach can be visualised in Fig. 1; for further discussion see Meehl *et al.* (2000) and IPCC (2011). Consider a normally-distributed climatic variable, such as temperature (Fig. 1a). For this probability density function (PDF), the top 5% of values, which may be classified as extreme, lie 1.65 standard deviation (σ) units above the mean (PDF I; Fig. 1a). A shift in climate alters the frequency and severity of extreme events, with the magnitude of change depending on the location and shape of the new distribution (Fig. 1b). In PDF II (Fig. 1b), the distribution undergoes only a mean shift with variability (σ ; the standard deviation) remaining constant, this results in an increase in the frequency of climatic events of a given magnitude (from 5% in PDF I to 26% in PDF II). Similarly, the incidence of extreme events at the other end of the distribution declines. A change in the shape of the distribution (increase in σ in PDF III, Fig. 1b) results in a further increase in the frequency of extreme events (PDF III, Fig. 1b), indeed more than an equivalent change in the mean (Katz & Brown 1992; Meehl *et al.* 2000).

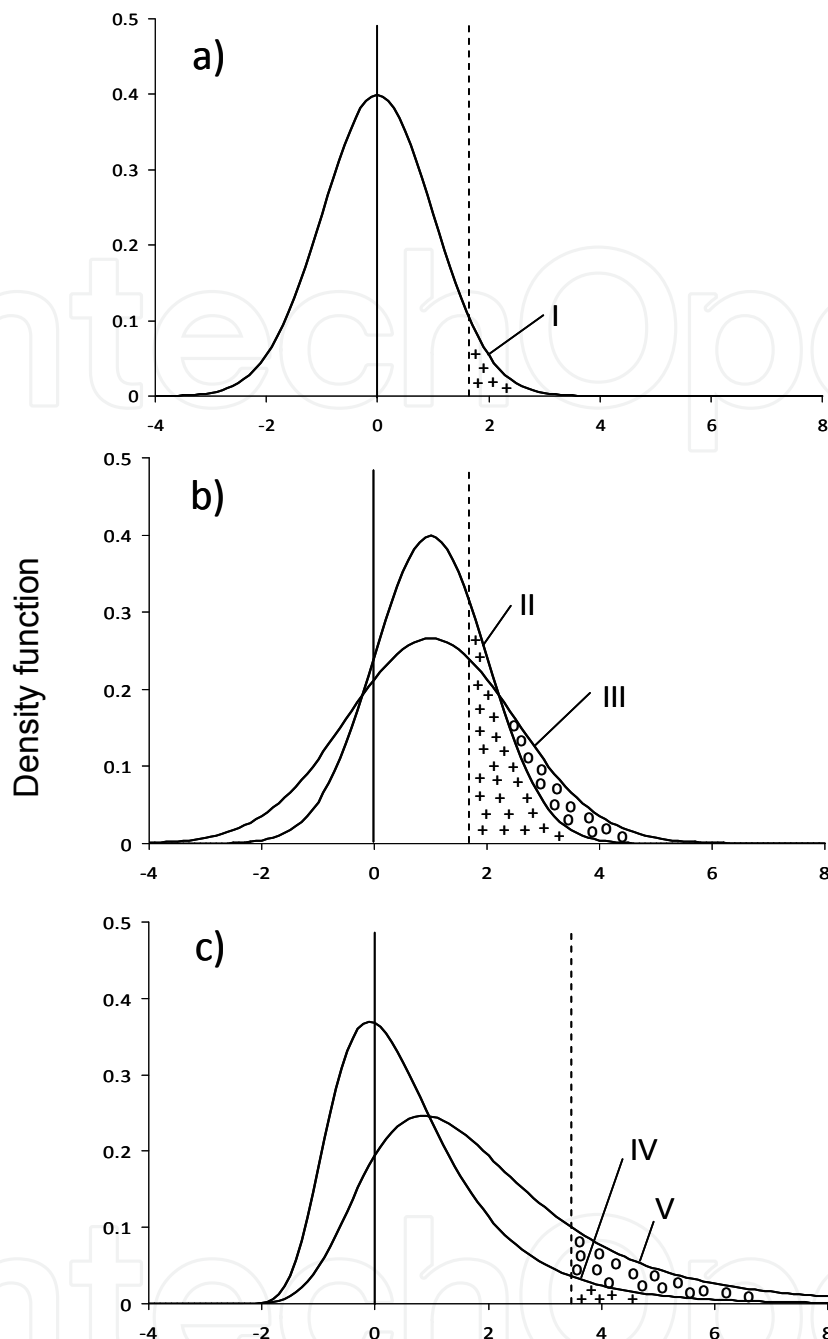


Fig. 1. Frequency of extreme events for a given hypothetical climatic variable showing variation in probability related to change in shape and location of the probability density function (PDF). a) normal distribution (PDF I; $\mu = 0$, $\sigma = 1$) with the 5% most extreme events occurring 1.65 or more standard deviation units from the mean (vertical dashed line). b) Increase in frequency of extreme events following increases in the climatic mean (PDF II; $\mu = 1$, $\sigma = 1$) and standard deviation (PDF III; $\mu = 1$, $\sigma = 1.5$). c) Generalised extreme value (GEV) distribution with location parameter (μ) = 0, scale parameter (σ) = 1, and shape parameter (ξ) = 0.1 (PDF IV) showing the larger tail that characterises the GEV PDF, with the 5% most extreme events lying above the vertical dashed line. An increase in the parameter σ to 1.5 (PDF V) increases the spread of the distribution and the probability of extreme events that lie in the upper tail. The shape of the GEV function is determined by ξ (see Katz *et al.* 2005 for details).

While some climatic variables can be approximately normally distributed, many others have heavy tails with significant skew towards large values (Gaines & Denny 1993; Gutschick & BassiriRad 2003). For example, precipitation-related variables tend to be non-normal, and are often modelled using gamma (Watterson & Dix 2003) or lognormal (Cho *et al.* 2004) distributions. Model selection is critical, since the objective is to adequately characterise the distributional tails. One family of distributions widely used for modelling extreme values, especially maxima, is the generalised extreme value (GEV) probability density function, which produces light-, heavy- and bounded-tailed distributions (Katz *et al.* 2005). A typical heavy-tailed (Fréchet) GEV distribution is shown in Fig. 1c (PDF IV). Shifts in location (μ), scale (σ) and shape (ξ) parameters that define the GEV distribution all impact on the frequency and severity of extreme events (Fig. 1c, PDF V).

3. Extreme climatic events as ecosystem drivers: The evidence

3.1 Demographic change and plant mortality

Probably the most important mechanism by which extreme climatic events (ECEs) can drive rapid ecosystem change is by causing extensive mortality in dominant or keystone plant species. The loss of such species can result in rapid, cascading compositional change in plant communities, in turn affecting the population viability of faunal and floral community associates (Gitlin *et al.* 2006) and the ecosystem services that they provide (Walker *et al.* 1999; Kremen 2005). Unfortunately, ECEs are difficult to study within a pre-planned experimental and statistical framework (Buckland *et al.* 1997), and so little or no information exists on the responsiveness of most plant communities to ECEs of varying severity. However, a range of studies provide insight into the dramatic and persistent impacts of prolonged abiotic stress on plant community composition and structure.

The classic studies of Albertson and Weaver (1944, 1945) on prairie and woodland ecosystems in North America were among the first, and most comprehensive, to document the impacts of protracted, multi-year drought on plant communities. During the 1930-1940 “dustbowl” years, much of the central US experienced record- or near-record low rainfall, high temperatures, high evaporation, and declining soil moisture. In the most extreme years (e.g., 1934, 1936, 1939), rainfall was up to 40% below normal, summer maximum temperatures were 3-6°C above normal, evaporation exceeded that of non-drought years by up to 33%, and the water table fell by one metre or more (Albertson & Weaver 1945). This drought was one of the three most extreme to affect North America since 1900 (Cook *et al.* 2004), although not as severe as previous megadrought periods that occurred in the 12th to 16th centuries (Woodhouse & Overpeck 1998; Stahle *et al.* 2007).

The most striking effect of this drought was the high level of mortality that occurred in virtually all plant species across the landscape. Mortality of dominant and subordinate tree species (e.g., *Ulmus americana*, *Populus sargentii*, *Celtis occidentalis*, *Salix* spp.) exceeded 50% across a broad range of topographic habitats with distinctly different hydrological regimes, most notably in dry ravines and along intermittent creeks (Albertson & Weaver 1945). In prairie communities perennial grasses such as *Andropogon scoparius*, *Koeleria cristata* and *Poa pratensis* suffered up to 80-90% mortality, while subordinate grasses and forbs were almost eliminated (Albertson & Weaver 1944). The catastrophic loss of groundcover resulted in intense wind erosion, with dust accumulating to depths of 2 feet (60 cm) in sheltered

locations (Albertson & Weaver 1945). This dust exacerbated the severity of water stress experienced by plants during the drought by preventing rain infiltration into the soil, effectively blocking moisture from reaching the rhizosphere (Albertson & Weaver 1945). Insect attack also increased the impact of drought on tree populations (Albertson & Weaver 1945; Mattson & Haack 1987).

Other studies report similar effects during prolonged periods of exceptionally severe drought. Record dry conditions experienced during 2006-2007 at a semi-arid grassland site in south-eastern Australia resulted in 90% or higher mortality of the dominant grass species *Austrostipa aristiglumis* (Godfree *et al.* 2011). Here, the most acute period of rainfall deficiency occurred during the middle of a decade-long drought. Similarly, Edwards & Krockenberger (2006) reported 64% mortality among seedlings of rainforest species during the 2002 ENSO event in north-eastern Australia, during which rainfall at their study site was only 36% of average. On a much larger spatial scale, mortality of piñon pine (*Pinus edulis*) in western North America varied between 40% and >90% in response to drought during 2000-2003 (Breshears *et al.* 2005). The severity of this drought, which was among the three driest in the past century, was exacerbated by high temperatures (Breshears *et al.* 2005).

Similar levels of drought-induced mortality have been observed in Canadian aspen forests (Hogg *et al.* 2008), beech forests (Peterken & Mountford 1996), and in forests globally (for review see Allen *et al.* 2010). Indeed, forest mortality in response to drought and heatwaves is so common that Allen *et al.* (2010) concluded that no forest biome is invulnerable to climate change, even in systems that are not thought to be water-limited. However, while droughts do not have to be of unprecedented or record severity to cause significant mortality in plant communities, it is also clear that not all droughts result in high levels of plant mortality (e.g., Condit *et al.* 1995; Fensham and Holman 1999; references in Allen *et al.* 2010); and not all generate detrimental, lasting effects on plant populations (e.g., Morecroft *et al.* 2002; Yurkonis & Meiners 2006).

Briefly, other extreme climatic events can also have strong, direct impacts on ecosystems by inducing injury or mortality in plants. High temperatures, especially those exceeding 55°C, when Rubisco activity, electron transport and overall photochemical performance becomes impaired (Kappen 1981; Musil *et al.* 2009) are known to be detrimental to plants. Simulated heatwaves in which temperatures approach or exceed these temperatures have been shown to result in canopy decline and mortality of succulent plant species (Musil *et al.* 2005); in this study mortality in heated treatments ranged from 33-74% compared with 7-38% in controls that experienced 5.5°C cooler daytime temperatures. Such extremes are probably most likely to occur in arid and semi-arid systems where lower-canopy species lack cover, and may in part explain the loss of low-stature mesophyllic grasses and forbs following death of overstorey plants in drought-affected grasslands and woodlands (Albertson and Weaver 1944, 1945). Studies conducted in tundra environments have also resulted in physiological impairment and mortality in cold-adapted species (Marchand *et al.* 2006); numerous examples exist in other systems (e.g., Van Peer *et al.* 2001; Groom *et al.* 2004, Larcher *et al.* 2010).

3.2 Community composition and structure

During drought, a range of physiological, demographic and environmental factors interact to determine the impact of extreme water deficiencies on specific plant individuals and

species. McDowell *et al.* (2008) recently reviewed these mechanisms; briefly, the key drivers of plant mortality under moisture stress are thought to be carbon starvation, the activity of biotic agents, and hydraulic failure, with the relevance of each depending on the intensity and duration of stress. Plants adopt a range of mechanisms to tolerate or resist drought, with intraspecific and interspecific variation found in water use efficiency (Farquhar *et al.* 1989), dormancy (Oram 1983), dehydrin expression (Volaire *et al.* 2001), extraction of water at low soil water potential (Volaire and Lelièvre 2001), senescence of aerial tissue (Volaire *et al.* 1998; Bolger *et al.* 2005), root structure (Van Splunder *et al.* 1996) and resource allocation (Aronson *et al.* 1993) to name a few. Indeed, most species use different physiological and anatomical mechanisms to protect tissue during periods of moisture stress (Scott 2000).

Plant survival also depends strongly on spatial heterogeneity in the landscape. Variation in soil moisture occurs at a range of spatial scales (Buckland *et al.* 1997; Gitlin *et al.* 2006; Dobrowski 2011; Godfree *et al.* 2011), and because plant mortality is non-linearly related to soil moisture content, microscale variation in water availability can critically influence plant survival under extreme drought (Godfree *et al.* 2011). At larger spatial scales, hydrological variation and the frequency of soil drought is a key driver of species assortment and community composition (Oberbauer & Billings 1981; Buckland *et al.* 1997; Yurkonis & Meiners 2006), a process which reflects variation in the ability of species to recover from drought (e.g., Tilman & El Haddi 1992; Stampfli & Zieter 2004) as much, or more, than tolerance of drought itself (Gutschick & BassiriRad 2003).

Given these sources of variation, it is not surprising that plant species tend to show highly differential mortality when placed under extreme drought in natural settings. During drought in the 1930's, Albertson and Weaver (1944, 1945) observed that survival among tree species in ravine environments ranged from 64% (*Celtis occidentalis*) to only 30% (*Ulmus americana*), and drought hardy species, such as *Juniperus virginiana*, had much lower mortality (1-37%) than all other co-occurring species, even persisting as monospecific stands on the most xeric sites (Albertson & Weaver 1945). In prairie communities, all species were affected but some, including *Andropogon furcatus*, suffered much lower mortality than others (e.g., *Andropogon scoparius*, *Stipa spartea*) which experienced over 80% mortality. Survivorship was linked strongly to depth of the rooting system, since during the drought soil water deficiencies gradually moved lower in the soil profile (Albertson & Weaver 1944). Interestingly, over the entire drought period the composition of the prairie community was in constant flux (Albertson & Weaver 1944). Interspecific variation in mortality has also been observed in numerous other studies (Tilman & El Haddi 1992; Condit *et al.* 1995; Gitlin *et al.* 2006), and in response to other climatic stressors (e.g., Stiles 1930; Barua *et al.* 2003; Henry & Molau 2003; Marchand *et al.* 2006; many others).

Under extreme, prolonged drought, rapid changes in vegetation composition can be persistent or effectively permanent. Perhaps the best documented example occurred during extreme drought in the 1950's, when the ecotone separating *Pinus ponderosa* forest from *Pinus edulis-Juniperus monosperma* woodland moved by 2 km or more within only five years. This change has persisted for at least 40 years (Allen & Breshears 1998). One of the most significant persistent changes observed by Albertson & Weaver (1944) was the expansion of wheat grass (*Agropyron smithii*), which was favoured by moist springs and dry summers, at the expense of other species such as *Andropogon furcatus*. Elsewhere, Gitlin *et al.* (2006)

showed that continuation of extreme drought conditions in the southwestern United States experienced during 2002 would likely result in significant change to the composition and structure of entire plant communities and ecosystems. Similarly, Tilman & El Haddi (1992), in a controlled experiment, showed that post-drought recovery of grassland vegetation was not accompanied by a significant recovery in species richness, and suggested that post-drought recruitment limitation may determine the richness of prairie plant communities. Here, drought with a return interval of approximately 50 years was sufficient to significantly alter local species richness (Tilman & El Haddi 1992). Drought can also alter competitive relationships among species, resulting in stratification of plant communities along hydrological gradients (Buckland *et al.* 1997) or promotion of invasion by fast-growing annuals (White *et al.* 2001).

4. Case study: Change in composition of an Australian semi-arid grassland during and following extreme drought

The case studies above provide overwhelming evidence that extreme climatic events, and especially drought, can drive rapid changes in plant community composition by causing differential rates of mortality and recovery among plant species. A central remaining challenge to ecologists, however, is to understand when, and under what threshold conditions, abiotic stress will lead to changes of large magnitude (McDowell *et al.* 2008), knowledge that will be essential if we are to accurately predict the impact of climate change on natural vegetation globally. In this section I aim to improve our understanding of such processes by drawing conclusions from a study in which I investigate the impact of a multi-year period of exceptional drought on a semi-arid Australian grassland ecosystem.

4.1 Background: The “Millenium Drought” in Australia

Between 1997 and 2009 much of south-eastern Australia was affected by an extremely severe and protracted drought known as the “Millennium Drought” (Whitaker 2006; Bond *et al.* 2008). During this period, annual rainfall was well below average, especially during autumn (March-May), while maximum and minimum temperatures were at or near record highs (Murphy & Timbal 2008). Over the past half century mean maximum and minimum atmospheric temperatures have increased over most of Australia (Nicholls *et al.* 2004; Nicholls 2006) and extreme temperature events have become more frequent (Collins *et al.* 2000). Recent droughts also may have become more severe due to increased evaporation associated with warmer temperatures (Nicholls 2004; Cai & Cowan 2008). Severe drought is a regular phenomenon in Australia (Ummenhofer *et al.* 2009), and there is a strong suggestion that rising atmospheric greenhouse gas concentrations have played a role in the development of rainfall deficiencies and elevated temperatures across southern parts of Australia in recent decades (Timbal *et al.* 2006; Murphy & Timbal 2008).

The most extreme droughts in Australia impact on regional agriculture, hydrology, ecosystem function, and the population dynamics of flora and fauna. The 1997-2009 drought was no exception: extreme low rainfall and high temperatures (Cai & Cowan 2008) during the drought resulted in the near total loss of surface water and a persistent decline of

groundwater (Leblanc *et al.* 2009), which in turn reduced agricultural productivity significantly (Horridge *et al.* 2005; Pook *et al.* 2009). Large impacts were observed on aquatic flora and fauna (Bond *et al.* 2008; references therein), with extensive tracts of the key riparian tree species *Eucalyptus camaldulensis* dying in the lower Murray-Darling Basin (Cunningham *et al.* 2009). While Australian ecosystems are commonly perceived to be resilient to drought (e.g., Bond *et al.* 2008), their ability to recover from events of this severity and duration, or the increasingly extreme events of the future (Mpelasoka *et al.* 2008), remains open to question (Godfree *et al.* 2011).

4.2 Study objectives

The objective of this study was to improve understanding of the role of extreme climatic events as drivers of rapid ecosystem change by comparing the landscape-level responses of different plant species to drought across multiple grassland habitats, and investigate whether the observed phytosociological changes could be explained by simple predictors including statistical quantification of drought severity, topography, and knowledge of the broader range distributions and habitat affinities of the study species. I specifically addressed the following hypotheses:

1. prolonged drought of unprecedented severity will result in high mortality across a range of grassland plant species;
2. mortality will be highest in the most xeric sites and mesic low-lying habitats will act as refugia during drought;
3. post-drought recruitment and recovery will be the primary drivers of post-drought community composition and structure; and
4. species with ranges that extend further into drier regions will have higher survival and recruitment than species with more mesic distributions.

Evidence supporting these hypotheses might indicate that at least some basic principles could be generally applied to the study of extreme events to improve prediction of their impacts on vegetation systems.

4.3 The study system

The study was conducted in a high quality remnant semi-arid grassland located approximately 30 km to the east of West Wyalong in central NSW (Fig. 2). The choice of a semi-arid biome reflects the general view that these ecosystems are highly susceptible to shifts in climate (Allen & Breshears 1998; Holmgren *et al.* 2006). The topography of the 34 hectare site is mainly flat with extensive treeless plains dissected by a series of small creeks that incise up to 2-3 m below the surrounding terrain. While low, this topographic heterogeneity does generate a range of habitat types characterised by different floral assemblages (illustrated in Fig. 2). Prior to 2006, grasslands dominated by the tussock grass *Austrostipa aristiglumis* (F.Muell.) S.W.L.Jacobs & J.Everett (plains grass) and *Panicum prolatum* F.Muell [= *Walwhalleya proluta* (F.Muell.) Wills & J.J.Bruhl] (rigid panic) occurred on flat and mesic low-lying terraces and gullies, while xeric, sloping terrain was dominated by the small perennial shrub *Leiocarpa panaetioides* (DC.) Paul G. Wilson (woolly buttons). Natural grasslands and grassy woodlands dominated by *A. aristiglumis* and other grassland

species once occurred widely across inland NSW (Benson *et al.* 1997), but unfortunately most have been degraded by overgrazing, cultivation, and weed invasion and the remaining areas have now been listed as critically endangered under the *Environment Protection and Biodiversity Act 1999* (Threatened Species Scientific Committee 2008). *A. aristiglumis*, *P. prolutum* and *L. panaetioides* all grow on the western slopes and plains regions of NSW, Queensland and Victoria, but *P. prolutum* and *L. panaetioides* extend further into the drier, semi-arid zone than *A. aristiglumis*, and *L. panaetioides* occurs in arid habitats in far western NSW (Fig. 3).

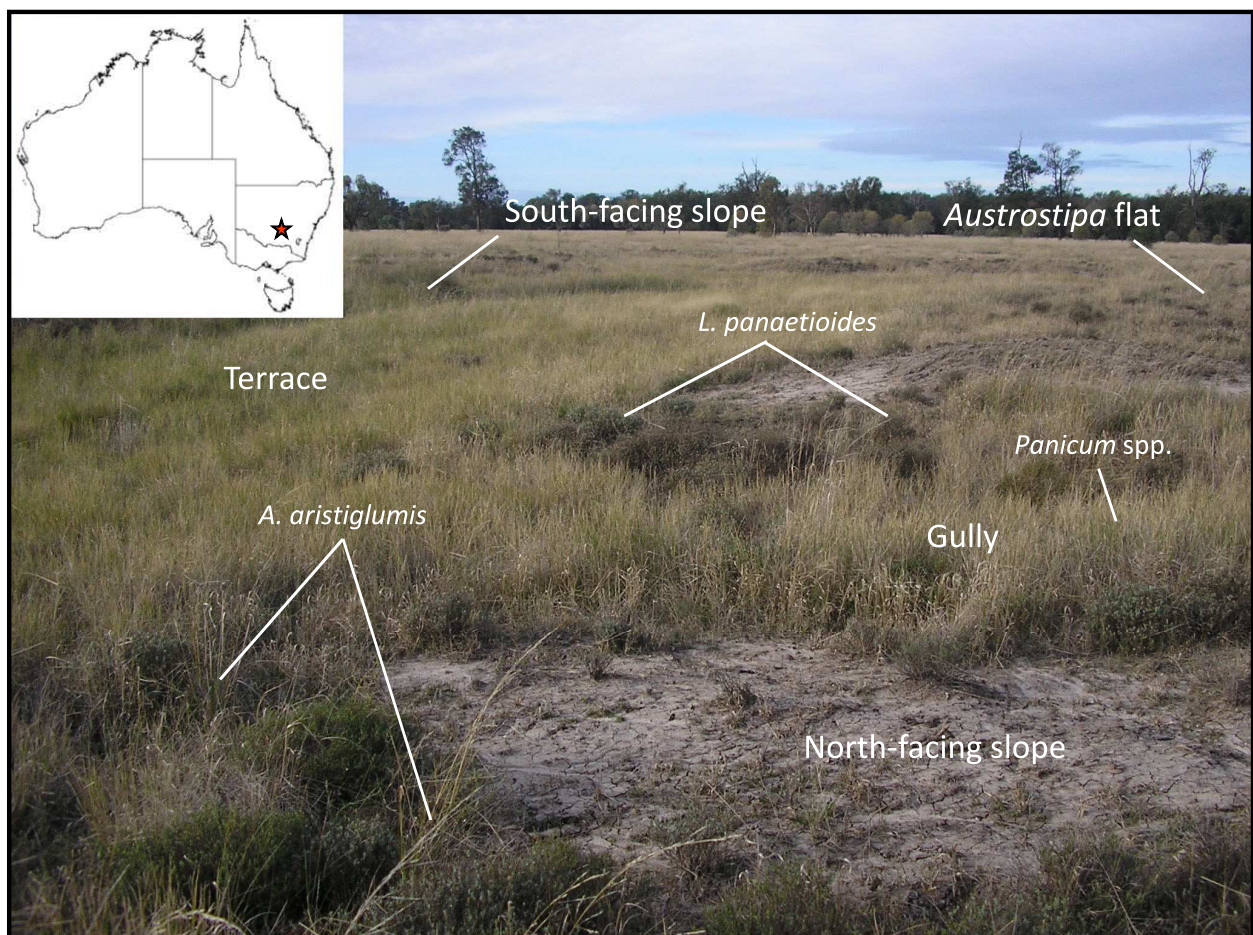


Fig. 2. Location and characteristics of the semi-arid grassland study site in south-central NSW, Australia. The location of the site is shown in the inset as a red star. The main habitat types along with the study species *Leiocarpa panaetioides*, *Austrostipa aristiglumis* and *Panicum* spp. (mainly *P. prolutum* with some *P. decompositum*) are labelled on the photograph taken looking north-east near the centre of the study site. The terrace habitat lies around 2 m in elevation below the *Austrostipa* flat.

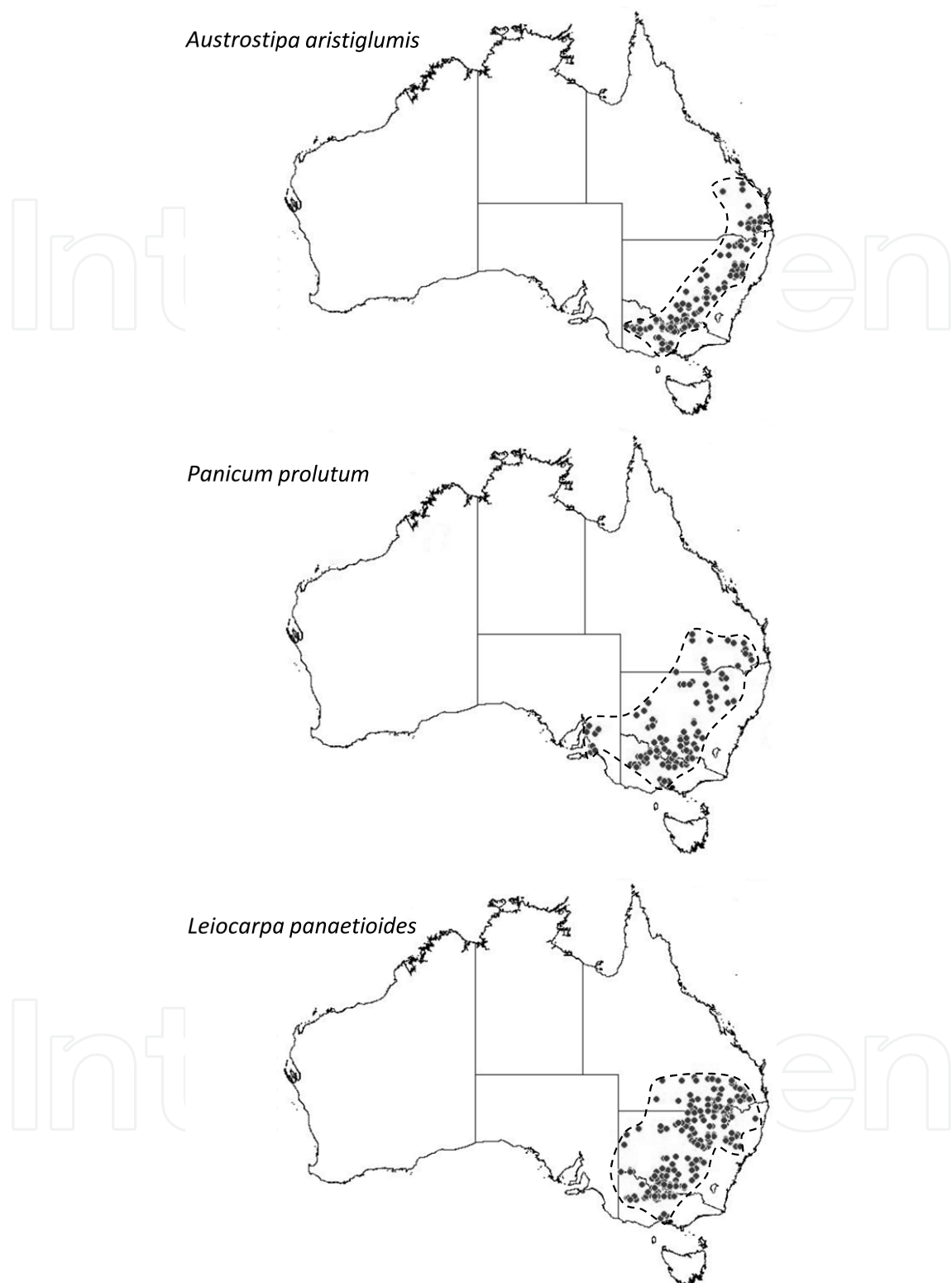


Fig. 3. Approximate distribution of the three study species in Australia. Dots represent locations where herbarium records exist for each species (some incorrect records or those representing adventive occurrences have been removed). Data derived from Australia's Virtual Herbarium, Council of Heads of Australasian Herbaria Inc. (http://chah.gov.au/avh/public_query.jsp)

4.4 Climatic conditions during 2006-2007

Like most of south-eastern Australia, the study site was affected by chronic drought between 2001 and 2009, with particularly severe conditions occurring during 2006 and 2007. At Wyalong Post Office (S 33.93°, E 147.24°), the nearest high quality meteorological station to the study site, only 181 mm of rain fell in 2006 – easily the driest year since at least 1900 and 62% below the 1900 to 2009 average of 474 mm (Fig. 4a). Rainfall was also low during 2007 (356

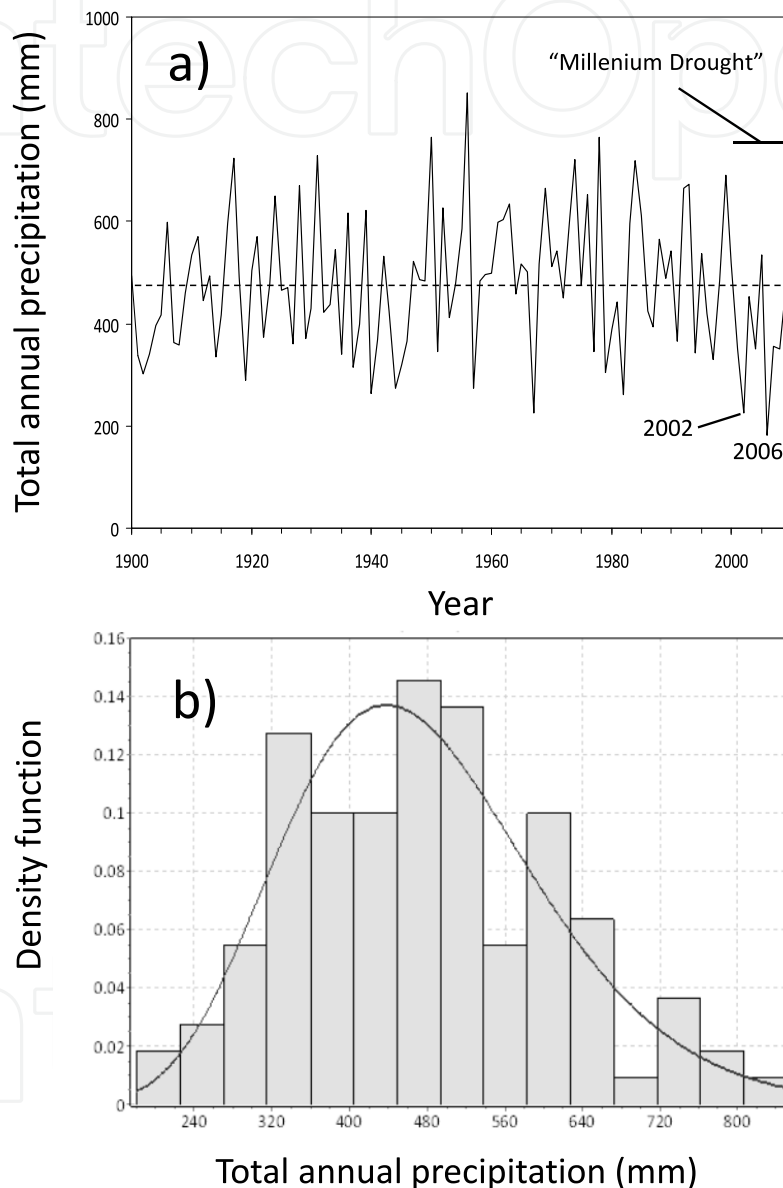


Fig. 4. a) Total annual rainfall at Wyalong Post Office, NSW, Australia, 1900-2009. The extreme drought years of 2006 and 2002 are indicated, along with the timeframe of the “Millennium Drought”, a protracted period of rainfall deficiencies experienced across much of south-eastern Australia. b) Total annual rainfall fit with gamma distribution ($\alpha = 12.50$, $\beta = 38.08$). Annual rainfall data were obtained from the Australian Bureau of Meteorology’s Patched Point Dataset (available at <http://www.longpaddock.qld.gov.au/silo/>). Approximately 87% of data were station data with the remaining being interpolated daily observations (mainly pre-1950).

mm) and 2008 (350 mm), and collectively over the period 2001-2009, annual rainfall averaged only 362 mm, 24% below the long term average (Fig. 4a). Temperatures during this period were also at or near record levels (see below), which exacerbated drought severity (see Nicholls 2004).

4.5 Field surveys

The exceptionally dry conditions of 2006 and 2007 presented an ideal opportunity to quantify the responses of *A. aristiglumis*, *P. prolutum* and *L. panaetioides* to acute water deficiencies in different habitat types across the study site. For each species, I quantified rates of population mortality and recruitment across six different topographic habitat types (for detailed description of habitat types see Godfree *et al.* 2011; Fig. 2) based on surveys conducted in three representative transects which spanned the study site. I estimated mortality rates based on counts of dead and live adult plants, and recruitment rates based on counts of juvenile plants that had established in 2007. Further details (for *A. aristiglumis*), along with soil water data documenting the severity of the drought, are provided in Godfree *et al.* (2011).

Survey data were used to estimate pre-drought population densities of each species in each habitat type (based on adult plant density), while the post-drought population density was determined based on total counts of surviving adult and juvenile plants. Species survival rates were determined based on estimated pre- and post-drought adult plant densities, and adult plant replacement rates were calculated as the number of recruits per number of dead plants recorded at the time of the survey. The areal contribution of each habitat type to the total site area was determined based on the total intercepted length (m) of each habitat across all three transects.

4.6 Demographic change in response to drought

Prior to the major mortality event that occurred in late 2006, *A. aristiglumis* dominated the more mesic and flat habitats at the study site, while *P. prolutum* was most abundant in the *Panicum* flats habitat (Fig. 5a). In drier habitats (south- and north-facing slopes) both grasses had much lower densities, being largely replaced by the more xerophytic shrub *L. panaetioides* (Fig. 5a). By late 2007, however, the population density of *A. aristiglumis* and *P. prolutum* had changed considerably (Fig. 5b), reflecting drought-induced mortality followed by a major recruitment event in autumn and winter 2007.

During the most extreme phase of the drought mortality of *A. aristiglumis* and *P. prolutum* occurred in all habitats, with populations in the more xeric, sloping habitats suffering losses of 90% or more (Fig. 6a). *P. prolutum* suffered >65% mortality in all habitats and was eliminated from north-facing slopes (the most xeric habitat), while *A. aristiglumis* survival exceeded 30% only in the most mesic terrace environments (Fig. 6a). In contrast, *L. panaetioides* survival was at least 70% in all but one habitat (north-facing slopes) and no plants died in the terrace and gully habitats (although density was low to start with). Mean site survival, averaged across habitat types, was 21% for *A. aristiglumis*, 17% for *P. prolutum*, but 79% for *L. panaetioides*.

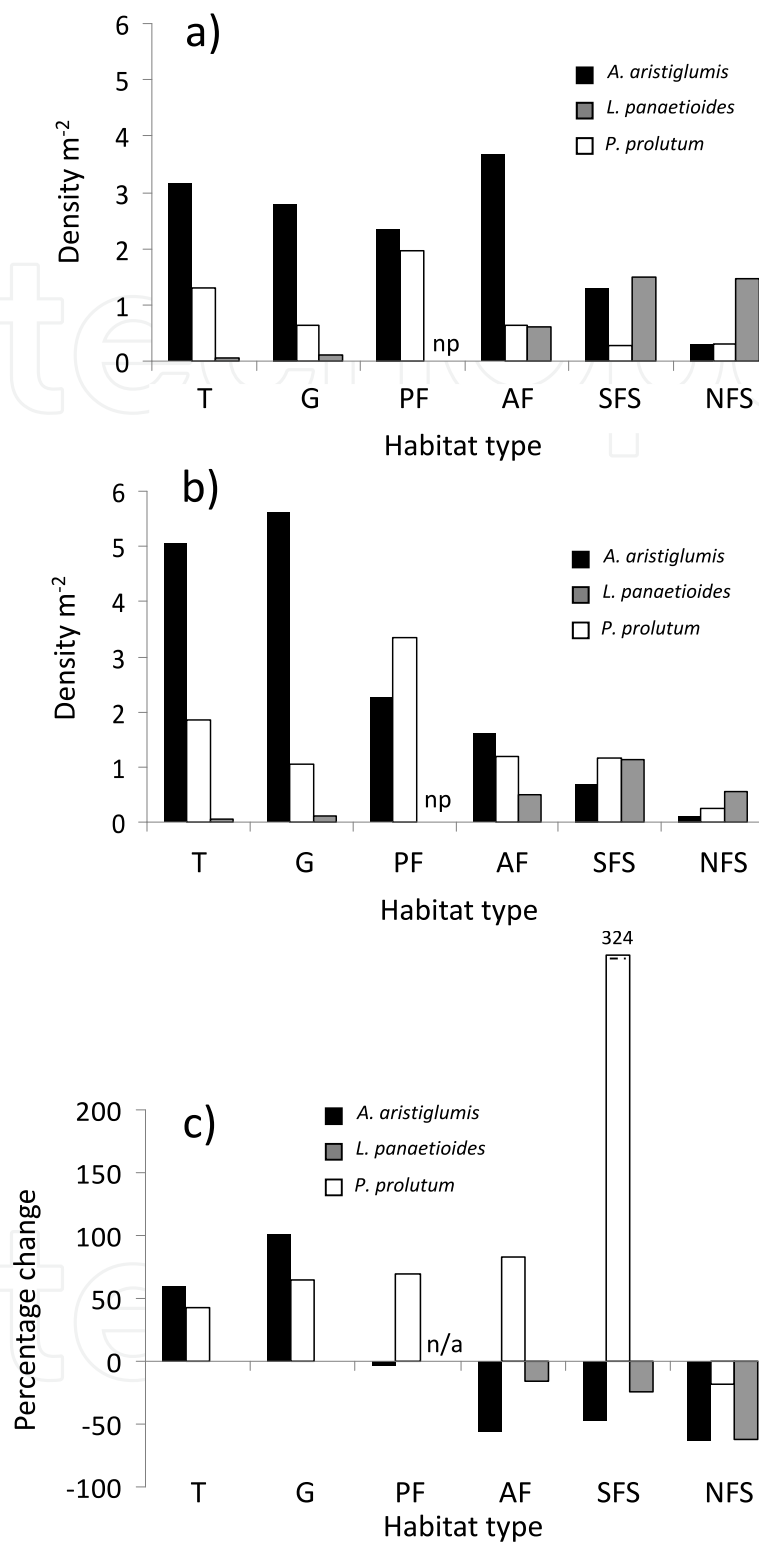


Fig. 5. Demographic changes observed across the study site July 2006-December 2007. a) Estimated pre-drought population density (July 2006). b) Post-drought population density (December 2007). c) Percentage change in density July 2006 to December 2007. T = terrace, G = gully, PF = *Panicum* flat, AF = *Austrostipa* flat, SFS = south-facing slope, NFS = north-facing slope. Habitat types are arranged from most mesic (terraces) to most xeric (north-facing slopes). np = species not present in the habitat type; n/a = not applicable.

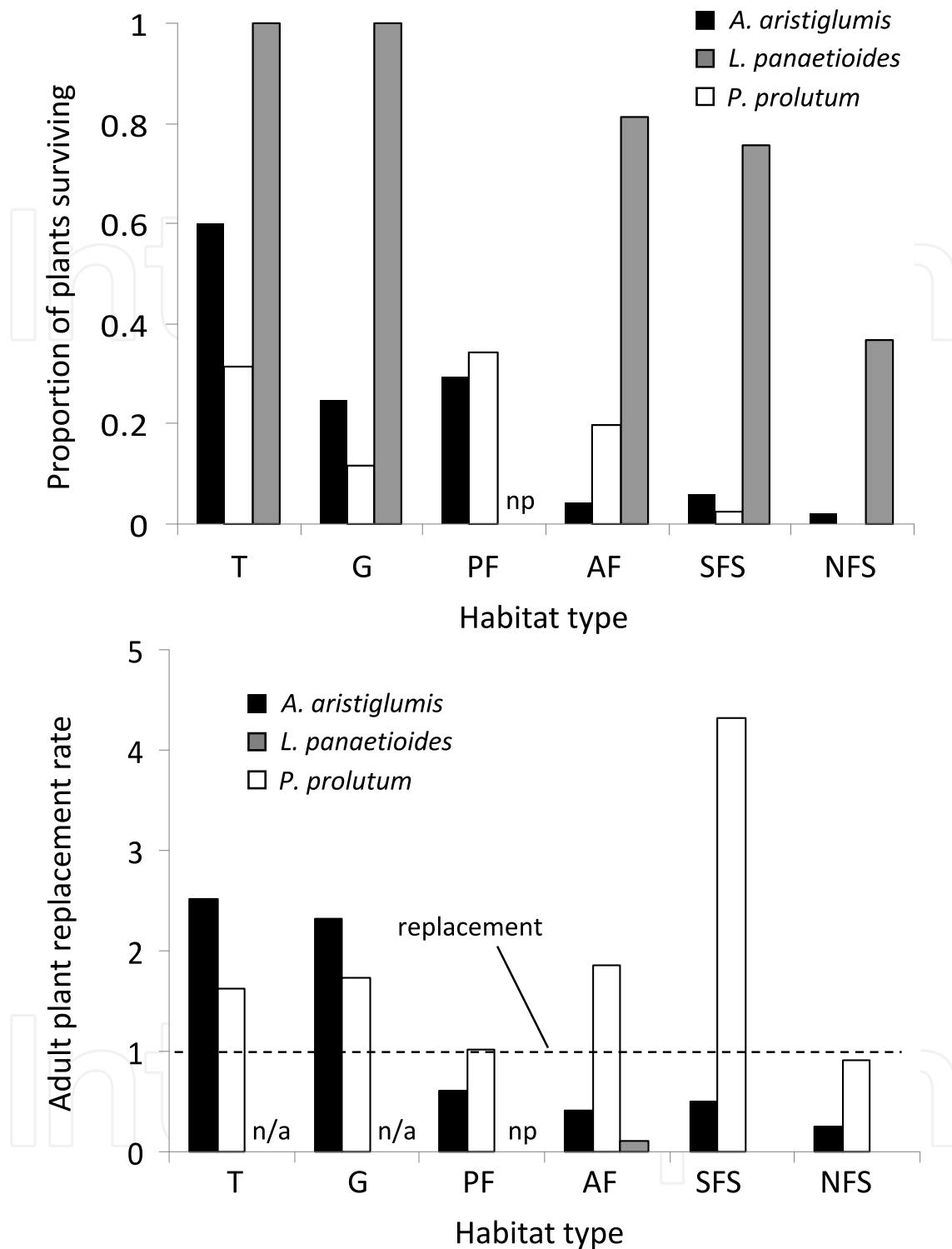


Fig. 6. Survival and recovery of plant populations observed across the study site July 2006-December 2007. a) Survival rate of adult plants present in July 2006. b) Rate of replacement of dead adult plants by recruits. The dotted line indicates the replacement rate (1) where numbers of new recruits exactly equals that of dead adult plants. T = terrace, G = gully, PF = *Panicum* flat, AF = *Austrostipa* flat, SFS = south-facing slope, NFS = north-facing slope. Habitat types are arranged from most mesic (terraces) to most xeric (north-facing slopes). np = species not present in the habitat type; n/a = not applicable.

Spatially, each of the habitats accounted for a different proportion of the area of the study site, and the impact of the drought on the total population size of each species reflected both mortality rate and the spatial extent of each habitat in which it occurred. For *A. aristiglumis*, only 16% of all plants at the site survived the drought, since high mortality (96%) was observed in the extensive *Austrostipa* flats habitat. *P. prolutum* survival was highest (34%) in habitats where its original density was also highest (2.0 m⁻²), and so overall survival (27%) exceeded that of *A. aristiglumis*. The relatively high total survivorship of *L. panaetioides* (73%) also strongly reflected generally high survivorship across habitat types.

Following rain in autumn 2007, significant recruitment of *A. aristiglumis* and *P. prolutum*, but not *L. panaetioides*, occurred across the study site. Recruits exceeded the number of drought-killed plants in gullies and terraces (*A. aristiglumis*) and gullies, terraces, *Austrostipa* flats and south-facing slopes (*P. prolutum*). Recruitment was minimal in *L. panaetioides*, and in no habitats did recruits fully replace plants that succumbed to the drought (i.e., adult plant replacement rate < 1; Fig. 6b). These differences in mortality and recruitment over the 2006-2007 study period resulted in a significant spatial redistribution of plant species across the study site, and a landscape-level change in community composition. By late 2007, *A. aristiglumis* was predominantly restricted to terrace and gully habitats, where post-drought populations were actually larger than pre-drought populations (Fig. 5b), and was virtually absent from xeric habitats (Fig. 5b). *P. prolutum*, in contrast, increased in abundance in most habitats, and became co-dominant with *A. aristiglumis* in *Austrostipa* flat and south-facing slopes habitats, and increased its dominance in the *Panicum* flats habitat (Fig. 5b). *L. panaetioides* declined in all habitats, but maintained dominance on the most xeric north-facing slope environments (Fig. 5c). In reality, however, the decline of all species in this habitat (Fig. 5c) left it essentially bare (Fig. 2), a condition which has been largely maintained for at least 3 years since (R. Godfree, personal observation).

4.7 Implications for predicting the impacts of extreme events

The results of this work, and those published previously (Godfree *et al.* 2011), support the hypothesis that extreme climatic events can significantly reconfigure landscape-scale vegetation mosaics within relatively short timeframes via direct mortality of established plants. While other studies have reported very high plant mortality during extreme drought (e.g., Albertson and Weaver 1944, 1945; Allen & Breshears 1998; Breshears *et al.* 2005; Gitlin *et al.* 2006; Edwards & Krockenberger 2006), the >90% mortality rates observed in this study in two community dominant species do appear to be unusually high. Perhaps this ultimately reflects the magnitude of rainfall deficiencies observed at the study site – 2006 was the driest year in at least a century, and, surprisingly, 20% drier than the next driest year (2002). Heavy mortality can have a range of important demographic and genetic consequences for the long-term fitness of plant populations and species, and if the frequency of events such as the one described here increase under projected climatic change (Meehl *et al.* 2000; Hennessy *et al.* 2008; Planton *et al.* 2008), the consequences for the conservation of native vegetation are likely to be significant.

As a result of the 2006-2007 drought, populations of two of the three study species (*A. aristiglumis* and *L. panaetioides*) shifted lower in the landscape, with the dominance of *A. aristiglumis* declining in all but the most mesic terraces and gully environments. Consistent with hypothesis 2, all three species suffered the greatest mortality in the more xeric

environments, and at the height of the drought, live plants were restricted almost entirely to mesic refugial habitats (with the exception of *L. panaetioides*, which although completely defoliated, did survive in modest numbers in drier areas). Interestingly, however, there was also some evidence that pre-drought habitat suitability was not a good predictor of drought survival or post-drought recruitment. For example, *Austrostipa* and *Leiocarpa* both declined most in the habitats in which their pre-drought populations were most dense (Figs. 5a, 6a), and recruitment of *P. prolutum* was poorer in the *Panicum* flats habitat than in most other habitats. In the case of *A. aristiglumis* and *P. prolutum* it is possible that terrace habitats were actually more suitable for these species (the plants present, although of lower density, were much larger than in drier habitats). This did not seem to apply to *L. panaetioides* - plants were large and abundant on the most xeric sites. Perhaps *L. panaetioides* is competitively excluded from mesic habitats by *A. aristiglumis* and *P. prolutum* and drought alters this competitive hierarchy, a pattern that has been observed elsewhere (White *et al.* 2001). Regardless, mesic refugia, albeit small in spatial scale (Godfree *et al.* 2011) clearly play a key role in ensuring survival of a range of species in a given plant community during extreme drought, including those that are adapted to drier conditions.

The pattern of change among species observed at the study site did not support the hypothesis that post-drought recruitment and recovery are the primary drivers of post-drought community composition for all species, the demographic responses of which were highly idiosyncratic. The final distribution of *P. prolutum* mainly reflected strong post-drought recruitment across multiple habitats, but *A. aristiglumis* was most abundant in terrace habitats due to significant post drought recruitment and high mortality. *Leiocarpa* density depended almost solely on high drought survivorship, and the final composition of the vegetation found in the more xeric habitats primarily reflected the drought hardy nature of this species. The presence of such complex patterns is perhaps not surprising given the diversity of strategies displayed by plants for ensuring survival through drought and other abiotic stresses (e.g., Barrett 1998; Mal & Lovett-Doust 2005; McDowell *et al.* 2008) but it does indicate that post-drought community composition jointly reflects the processes of mortality and recovery in heterogeneous environments.

Finally, from a practical point of view, the species-level responses observed here do partly support the hypothesis that population behaviour in response to drought can be predicted by their broad climatic envelopes (see McDowell *et al.* 2008; references therein). Drought survival of *A. aristiglumis* was much lower than that of the more arid-adapted (see Fig. 3) *L. panaetioides* in all habitats, with differences in survivorship between the two species being greatest in the more xeric, sloping habitat types (Fig. 6a). Differences between *A. aristiglumis* and *P. prolutum* were not as clear, since survival of *A. aristiglumis* was actually higher than that of *P. prolutum* in three habitats (terraces, gullies and north-facing slopes; Fig. 6a), which does not appear to be consistent with the fact that *P. prolutum* is capable of surviving in much drier regions than *A. aristiglumis* (Fig. 3). On the other hand, *P. prolutum* populations did perform better overall than *A. aristiglumis*, mainly as a result of a higher rate of post-drought recruitment from the seedbank (Fig. 6b). Perhaps the presence of a large persistent seedbank, rather than high drought survivorship, explains why *P. prolutum* grows in areas that are considerably drier than *A. aristiglumis* can tolerate (e.g., far western NSW and Queensland; Fig. 3). Such traits are known to be linked to population fitness and reproductive assurance in arid environments (Auld *et al.* 1995; Facelli *et al.* 2005).

4.8 Drought severity and species responses

This study has shown that extreme drought drives changes to ecosystem structure and composition by impacting on mortality and recruitment of plant populations, and that these processes may be broadly predictable given an understanding of drought severity and community composition. But this observation begs the questions: how extreme do droughts need to be to result in changes of this magnitude, and how much might drought severity increase under anthropogenic global warming?

Let us return to the study system at hand. As mentioned, drought conditions at the study site during 2006, when only 181 mm of rain fell, can reasonably be described as being of unprecedented severity with respect to the 1900-2009 instrumental record (Fig. 4a). Based on historical annual rainfall data for Wyalong, NSW, fit with a gamma probability distribution (Fig. 4b), an annual rainfall of 181 mm has a predicted return interval of 453 years, and although care needs to be taken when such low probabilities are involved, it is obviously an exceptionally rare occurrence indeed. As noted previously, the mortality rates observed in this study are consistent with the impacts of exceptional drought observed in other systems. But an event like 2006 is highly unusual, and somewhat less extreme events are much more likely to occur, even under climate change. Unfortunately, we have little evidence beyond anecdotal sources whether less severe droughts have had similar effects on this grassland vegetation.

In 2002, when 225 mm of rain fell at Wyalong (the second driest year on record, return interval = 84 years) I observed mortality of around 50% of *A. aristiglumis* at a nearby grassland site, but mortality was lower in wetter, low-lying sites. This might, however, reflect the fact that 2006 occurred after many years of drought, in contrast to 2002. During 2002-2009 significant tree death occurred in central NSW, including around the study area, but similar events have been observed previously in NSW, for example during the 1896-1902 drought (McKeon *et al.* 2004). We simply do not understand the exact conditions that resulted in the observed changes at the study site, beyond the fact that many weeks of dry weather occurred during spring and summer at the end of a very dry year in the middle of a decade-long drought. Perhaps we can at best speculate that substantial mortality of natural, minimally disturbed grassland in the study region is most likely to occur when extremely dry years (roughly 250 mm, around 50% of average; return interval 40 years) occur during an extended period of below-average rainfall. There might have been as many as 3 to 5 instances of such conditions over the past 110 years (Fig. 4a). However, it may require extremely rare events, like 2006, to generate the high levels of mortality observed in this study.

A further complication is that the actual level of water stress experienced by a plant population is a function of evapotranspirational demand relative to water availability. The extremely dry conditions experienced in central NSW during the Millennium Drought were exacerbated by high temperatures (Cai & Cowan 2008), which suggests that consideration of rainfall deficiencies alone would underestimate the severity of the drought. Data from Wagga Wagga AMO (S 35.16°, E 147.46°; Fig. 7), the nearest station with suitable observations for estimating potential evapotranspiration (ET_o), show the severity of 2006 in terms of low rainfall (Fig. 7a), high ET_o (Fig. 7b), and very low atmospheric water balance (AWB; calculated here as annual rainfall - ET_o). Indeed, the AWB was considerably lower in 2006 than any year since at least 1970 (Fig. 7c). Given that 2006 was drier at Wyalong than at Wagga Wagga compared with other years, these data support the contention that moisture stress experienced at the study site during 2006 was the most extreme in many decades, if not the last century.

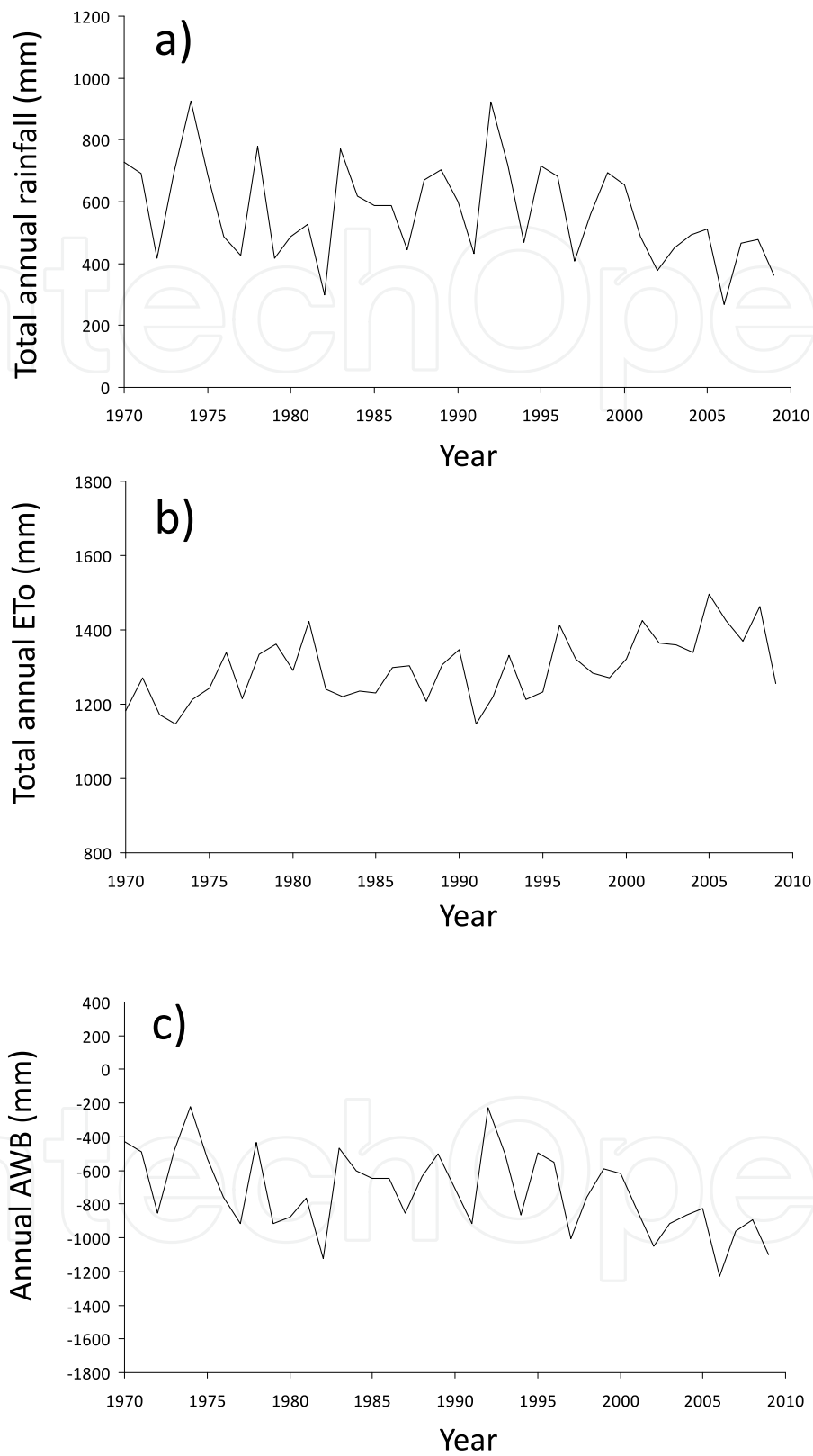


Fig. 7. Climatic conditions experienced at Wagga Wagga, NSW. a) Total annual rainfall (R) 1970-2009. b) Estimated total annual potential evapotranspiration (ETo). c) Annual atmospheric water balance (AWB), determined as $AWB = R - ETo$. Based on these data, AWB during 2006 was the lowest since at least 1970.

4.9 Predictions under climate change

We may conclude this study by making some very rough guesses as to the possible impacts of drought on grassland vegetation at the study site under climate change. First, we can estimate changes in drought severity at the study site based on the projections of global circulation models (here I use 50th percentile, medium emissions projections; see www.climatechangeinaustralia.gov.au). Current estimates for changes in precipitation in the study region by the year 2070, relative to the 1980-1990 baseline period, are for declines of 0%, 3.5%, 15%, and 15% for summer, autumn, winter and spring respectively, with changes in ETo of 6%, 10%, 14%, and 3%. Historically, mean annual AWB at Wagga Wagga (1970-2009) is -720 mm (Fig. 7c). If we use the extremely simple approach of modifying the observed 1970-2009 data according to these projections, we obtain a 2070 estimate for annual AWB of -860 mm, a 19% increase. Under the current climate regime (1970-2009) a year like 2006 (AWB = -1229 mm) has a return interval of 62 years, but by 2070, the return interval becomes 19 years. This suggests that, if a similar condition holds at Wyalong, the frequency of years in which significant mortality might occur in native plant communities could increase by around three-fold, possibly resulting in persistent shifts in vegetation composition similar to those observed in this study. However, given the low mortality of the three study species in terrace habitats even under the conditions experienced during 2006, their long-term persistence at the study site, albeit in a possibly restricted manner, seems virtually certain.

A final line of evidence supports this prediction. Nyngan, NSW, which lies approximately 450 km north of Wyalong, is an approximate 2070 climate analogue for the study site. All three study species occur at, or near Nyngan (although *A. aristiglumis* is restricted to very mesic riverine habitats), and *P. prolutum* and *L. panaetioides* occur much further west in drier areas. As mentioned, however, it is exceedingly difficult to make accurate predictions of this kind, and to account for mitigating factors such as atmospheric CO₂ enrichment (Koch *et al.* 2004), population-level evolution for drought tolerance, competition (White *et al.* 2001) or many other potentially important factors (see Godfree *et al.* 2011) that are known to affect the response of plant species to drought.

5. Conclusions

Understanding the role of extreme climatic events as drivers of contemporary and future vegetation change is one of the greatest challenges that ecologists face today. Extreme events are difficult to study, and the responses of plants, species and communities to abiotic stress are contingent on a broad array of physiological, demographic and landscape-scale processes that are often nonlinear in nature. In this paper I have provided evidence that extreme climatic events, and especially drought, have the capacity to rapidly alter the structure and composition of plant communities, with the magnitude of change roughly reflecting the statistical severity of the conditions. The majority of droughts that cause the highest rates of mortality among extant plant populations seem to be exceptionally rare events, occurring only on multi-decadal or century timescales, although quantifying the exact relationship between drought severity and plant mortality clearly needs further research.

The results of surveys conducted in a semi-arid grassland site in Australia suggest that changes in community structure and composition following drought reflect the processes of both mortality and post-drought recruitment and recovery, and that the demographic responses of species to extreme water stress are highly idiosyncratic. Nonetheless, drought

performance of individual species does appear to be at least partly predictable based on the nature of their climatic envelopes. The data also suggest that, if drought is severe enough, topographic refugia are crucial for the survival of a broad suite of species, not just those that favour mesic habitats. Finally, quantification of the statistical distribution of rainfall and atmospheric water balance in the semi-arid study region suggests that relatively modest changes in rainfall and evaporation could lead to large changes in the frequency and severity of extreme drought in coming centuries.

Much remains to be understood about the mechanisms and conditions under which extreme climatic events act as drivers of vegetation mortality, and the specific characteristics of populations, species and communities that predispose them to rapid abiotically-driven change. The overall objective of ecology is to develop theory that usefully predicts phenomena in nature, and working towards development of a theory that improves our understanding of the relationship between extreme climatic events and vegetation change is certain to be a fruitful area of ongoing ecological research.

6. Acknowledgments

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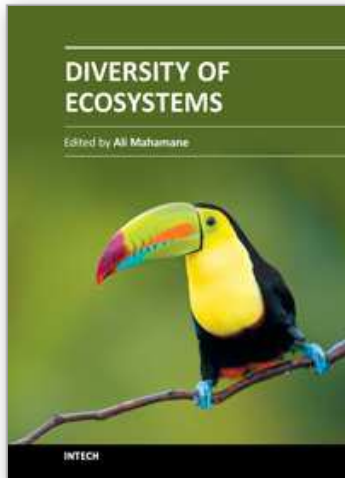
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The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

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