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16 Will Alien Plant Invaders Be Advantaged Under Future Climates?

16.1 Introduction

Alien plants have successfully invaded a wide variety of habitats around the globe. There has been considerable research attention, policy, and management action directed at alien invasive plants due to their significant negative impact on terrestrial biodiversity, agricultural systems, and human health (Bridges, 1994; Pimentel *et al.*, 2005; Pyšek & Richardson, 2010). There is now increasing focus on how alien invasive plants may be affected by climate change, including changes in agricultural weed assemblages (McDonald *et al.*, 2009); responses of allergenic plants that impact human health (Ziska *et al.*, 2003; Shea *et al.*, 2008); and potential impacts of changes in the distribution, abundance, and impact of alien invasive plants on terrestrial biodiversity (Hellmann *et al.*, 2008; Beaumont *et al.*, 2009; Bradley *et al.*, 2010; Gallagher *et al.*, 2010; Bellard *et al.*, 2013).

There are a range of scales and mechanisms by which anthropogenic climate change may directly influence the distribution and abundance of alien plant species. This ranges from global-scale drivers such as elevated CO_2 resulting in changes in mean annual, minimum and maximum temperature and precipitation, to influences at regional and local scales such as increases in the frequency and severity of extreme events (e.g. floods, cyclones, and fires) (Stocker *et al.*, 2013). In addition, climate change may indirectly affect alien plant species' abundance and distribution via changes in competitive interactions, mutualisms such as pollination and seed dispersal, rates of herbivory, and seed predation (Smith *et al.*, 2000; Byers, 2002; Ward & Masters, 2007; Schweiger *et al.*, 2010). All plant species are likely to respond to these alterations in climate, but the critical question is whether alien invasive plant species are more likely to be favoured by climate change than co-occurring native plant species.

Several ideas have been proposed for why alien invasive plants are likely to be favoured by climate change (Hellmann *et al.*, 2008; Bradley *et al.*, 2010). For instance, alien invasive plant species typically possess mechanisms for long-distance dispersal and a superior ability to colonise a wide range of environments, which may allow them to move to areas of suitable climate and to colonise gaps caused by disturbance or mortality (Chown *et al.*, 2012). Alien plant species generally have large native geographic ranges (Gravuer *et al.*, 2008) and broad environmental tolerance (Gallagher *et al.*, 2011), and consequently are likely to be able to cope with a wide range of environmental variability. Finally, alien invasive plant species tend to be phenotypically plastic (Davidson *et al.*, 2011) and many are capable of rapid genetic change (Prentis *et al.*, 2008; Clements & Ditommaso, 2011), leading to high adaptive capacity that may enable persistence and responsiveness to changes in environmental conditions (e.g. Willis *et al.*, 2010).

Both experimental manipulations and functional trait approaches have shown how invaders may become more dominant under future climates. Functional traits such as specific leaf area, seed mass, or wood density are the morphological, phenological, chemical or physical attributes that relate to ecological performance of a species (McGill *et al.*, 2006). Sandel and Dangremond (2012) combined functional trait information with spatial analysis to show how warmer temperatures are likely to lead to increased dominance of exotic plant species in California's grassland flora. Experimental studies have typically found stronger biomass and reproduction responses of alien invasive compared to native plant species, suggesting a potential shift to increasing dominance by alien invasive plant species (e.g. Smith *et al.*, 2000; Tooth & Leishman, 2014).

This chapter focuses on terrestrial alien invasive plants and their potential impact on biodiversity under climate change. We first examine how climate change may influence the abundance and distribution of alien plant species, using the framework of the naturalization-invasion continuum concept (Richardson & Pysek, 2006). We go on to review evidence for the direct and indirect effects of climate change favouring alien invasive plants compared to native species. In light of this evidence, we assess the major drivers of climate change on vegetation to determine whether a shift to alien-dominated vegetation assemblages is likely under future climates. Finally, we discuss issues of management of invasive plant species under climate change and highlight knowledge gaps and potential research directions.

16.2 The Naturalization-invasion Continuum as a Framework for Understanding Potential Climate Change Influences on Alien Plants

Our understanding of the processes of alien plant arrival, persistence, and spread has been greatly influenced by the development of frameworks such as the naturalization-invasion continuum (Richardson & Pyšek, 2006; see also Catford *et al.*, 2009; Blackburn *et al.*, 2011) (Figure 16.1). The naturalization-invasion continuum conceptualises the environmental and biotic barriers that an alien species must overcome in order to become established, persist, and spread in a new environment. Several previous reviews have used this framework to consider how climate change may influence these environmental and biotic barriers (e.g. for alien species generally Hellmann *et al.*, 2008, Walther *et al.*, 2009; for invasive species in freshwater ecosystems Rahel & Olden, 2008). These reviews have resulted in a significant increase in research focus on the effect of climate change on alien invasive species. In this chapter we assess the total body of evidence, focusing particularly on differential responses of native and alien plant species, which will be crucial in determining whether shifts to alien-dominated vegetation assemblages occur under climate change.

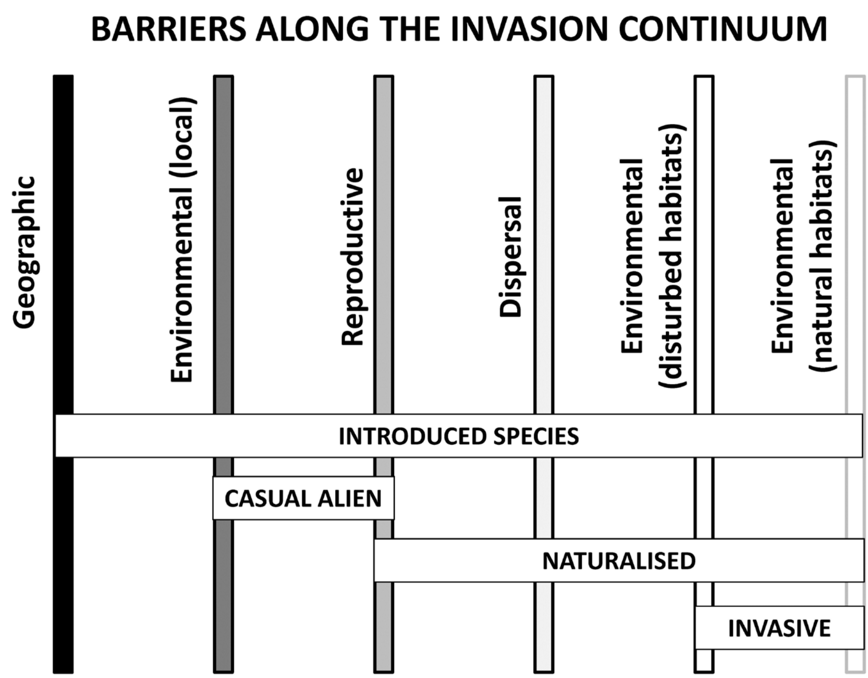

Fig. 16.1: The naturalization-invasion continuum. A schematic representation of major barriers limiting the spread of introduced plants. Climate change may affect plant invasion dynamics at each or all of these barriers. Adapted from Richardson *et al*. (2000).

16.2.1 Arrival of Propagules to New Areas

The first barriers that an alien species must overcome are those restricting the arrival of propagules into a new area. Climate change may increase the likelihood of propagule arrival (or introduction) of alien species by three main pathways. Firstly, changes in climate may result in a desire for new agricultural and horticultural species that can better cope with new climate conditions (Hellmann *et al*., 2008; Bradley *et al*., 2012). For example, drought-tolerant plants with low water requirements, such as desert grasses, are often promoted for garden plantings in areas experiencing reductions in rainfall. This push to plant hardier alien species and varieties may be problematic given that deliberate introductions of agricultural and horticultural species have been the largest source of alien invasive plants in many parts of the world (e.g. Australia (Groves *et al.*, 2005); United States (Reichard & White, 2001)). Secondly, increases in extreme climatic events such as floods and cyclones may result in increased propagule dispersal of alien plants (Florentine & Westbrooke, 2005; Murphy *et al.*, 2008; Diez *et al.*, 2012). Floods may carry propagules or stem fragments large distances, extending the invasion front of alien species (Sainty *et al.*, 1997; Florentine & Westbrooke, 2005) (Figure 16.2). For example, athel pine (*Tamarix aphylla*) was able to establish and spread along the Finke River system in central Australia after major floods in 1974, and is now considered one of Australia's worst weeds (Low, 2008). Thirdly, assisted colonization of native species to new areas outside their current range as a conservation action to increase a species' resilience to climate change will result in deliberate introductions of species to new areas (Mueller & Hellmann, 2008; Gallagher *et al.*, 2015). Of the three pathways, new introductions from commercial enterprises are likely to be the most important, but these have the potential to be effectively contained by Weed Risk Assessment and quarantine operations. Extreme climate events are just as likely to affect both native and alien plant species, although the superior dispersal and colonization ability of many alien invasive species may result in an advantage. Furthermore, extreme climatic events that create disturbance may be instrumental in allowing 'sleeper weeds' to transition from naturalized to invasive. Finally, assisted colonisation, whilst not likely to lead to a large number of new invaders, does have important consequences for how people perceive native, alien, and invasive plant species (see section 16.4 Issues of Management of Invasive Plants under Climate Change).

16.2.2 Establishment, Increased Abundance and Spread

Once a species has been introduced to a new area, it must overcome barriers to establishment in order to form self-sustaining populations and become naturalized. To transition from naturalized to invasive, populations must increase in abundance and spread successfully across the landscape (Richardson & Pyšek, 2006). Climate change and its drivers (e.g. elevated atmospheric CO_2 concentrations) will influence the likelihood of establishment, population growth, and spread via direct and indirect effects on demographic processes, such as seed bank persistence, seedling survival, growth rate, and reproductive output (Leishman *et al.*, 2000; Williams *et al.*, 2007). However, as native plant species will also be affected by changing climate, it is crucial to understand whether differential responses to increases in temperature and CO_2 and altered rainfall patterns will benefit invaders more than co-occurring natives. Below, we outline the evidence for the direct and indirect effect of a range of climate change factors on demographic processes of alien invasive compared to native plant species, and resultant community outcomes.

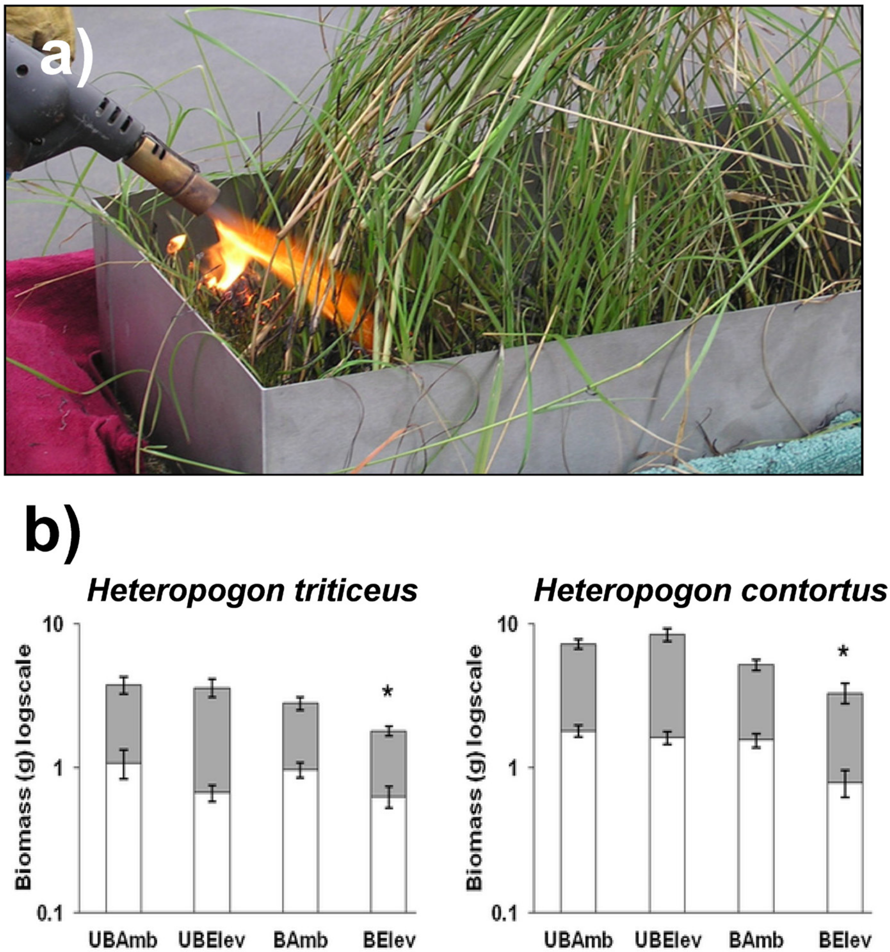

Fig. 16.2: Effects of invasion of *Nicotiana glauca* R. Graham (Solanaceae) following an extreme flooding event in early 1997 in western New South Wales, Australia. Extreme weather events of this nature are projected to increase under future climate scenarios in some regions of the globe. (a) Thick infestation of adult *N. glauca* plants (b) flower heads (c) emergence of new seedlings after flood water starts to recedes (d) mortality in co-occurring extant vegetation (e) seedling emergence. Images courtesy of S. K. Florentine (Federation University, Australia).

16.2.2.1 Elevated CO_2

Atmospheric concentrations of CO_2 have been rising steadily since the Industrial Revolution, from a concentration of ~270 ppm to current levels of ~400 ppm, and this increase is predicted to continue under a range of emission scenarios (Stocker *et al.*, 2013). It has been suggested that alien invasive species are likely to be more responsive than native species to elevated CO_2 as they tend to be capable of rapid growth when resources are not limiting due to traits such as high specific leaf area, high leaf nitrogen content, and high photosynthetic capacity (Grotkopp & Rejmanek, 2007; Leishman *et al.*, 2007; Leishman *et al.*, 2010). The ability to grow rapidly whilst exhibiting less conservative water use strategies may allow alien invasive species to benefit from both carbon fertilization and water savings under elevated CO_2 (Blumenthal *et al.*, 2013). A range of studies in growth chambers, glasshouses, open-top chambers, and FACE experiments have provided support for this (Baruch & Goldstein, 1999; Huxman *et al.*, 1999; Smith *et al.*, 2000; Belote *et al.*, 2004; Hättenschwiler & Körner, 2003; Ziska *et al.*, 2005; Dukes *et al.*, 2011; Manea & Leishman, 2011; Blumenthal *et al.*, 2013). In a meta-analysis of the responses of native and non-native species, Sorte *et al.* (2013) showed that non-native species were more responsive to elevated CO_2, although the difference was relatively weak. Therefore, whilst studies of direct fertilisation effects of elevated CO_2 on invaders show they tend to respond more strongly than native species, the difference in response between the two plant groups may not be substantial and will vary with environmental conditions.

Importantly, the influence of elevated CO_2 on alien invasive plants is likely to be the outcome of indirect effects via changes in competitive outcomes, and interactions with other drivers such as fire. For example, experiments investigating the effect of elevated CO_2 on competitive interactions between native and alien invasive plants have shown that native species became less competitive compared to invaders (Manea & Leishman, 2011). Similarly, Dukes *et al.* (2011) showed that the invasive *Centaurea solstitialis* in grassland plots responded strongly to elevated CO_2 compared to the resident native species, which responded much more weakly or not at all. In an arid system, Smith *et al.* (2001) found that aboveground biomass and seed rain of the invader *Bromus tectorum* increased much more strongly under elevated CO_2 compared to co-occurring native species. Thus it is the *relative* response of co-occurring native and alien invasive species, particularly in relation to competitive interactions, that matters.

Only a small number of experiments have examined the interaction of CO_2 with other climate change drivers, although this is an area of increasing research focus. However, from the few studies that have been conducted, the evidence is equivocal. Dukes *et al.* (2011) found no interactive effects on plant growth between CO_2 and enhanced warming, precipitation, or nitrate. Similarly, Tooth and Leishman (2013) found no consistent difference between native and alien invasive species in their re-sprouting response after fire in a temperate grassland system. However, in a similar experiment for a tropical savanna system, they found that native species' re-sprouting response was reduced under elevated CO_2, resulting in a shift to a more alien invasive-dominated community (Tooth & Leishman, 2014) (Figure 16.3). Similarly, Manea and Leishman (2014) grew mesocosms of mixed native and alien invasive grasses under ambient and elevated CO_2 combined with repeated extreme drought events and found that the alien invasive grasses were less influenced by extreme drought than native grasses under elevated CO_2. Thus, it seems that elevated CO_2 can shift the balance of plant assemblages towards greater abundance of alien invasive species, but this is strongly dependent on environmental conditions, with resource availability likely to be critical. There is clearly a need for further research in this area.

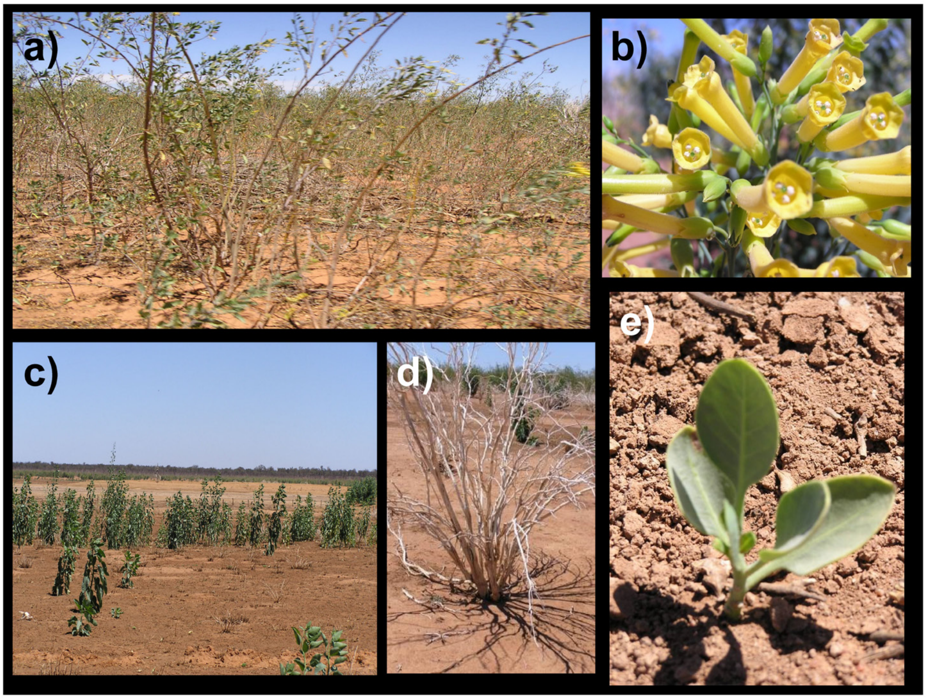

Fig. 16.3: Experimental manipulations of the interaction between fire and elevated CO_2 on native and exotic grasses. (a) Burning of competitive mixtures of native and invasive savanna grasses grown in mesocosms under glasshouse conditions of ambient and elevated CO_2 concentrations. Species in mixtures were three invasive exotic C4 grasses (Andropogon gayanus Kunth, *Cenchrus polystachios* (L.) Morrone, *Cenchrus ciliaris* L.), and three native C4 grasses (*Heteropogon triticeus* (R. Brown) Stapf ex Craib, *Heteropogon contortus* (L.) Beauv. ex Roem. & Schult., *Eriachne triseta* Steud.). (b) Graph showing total biomass (grey bars = aboveground, white bars = belowground) for two native grasses (*H. triticeus* and *H. contortus*) grown in mixed invasive and native species mesocosms under ambient and elevated CO_2. At day 154, half of the mesocosms in each glasshouse were burnt (B) and half were left unburnt (UB). These two native species had significantly less biomass under elevated compared with ambient CO_2 after burning, indicating an effect of elevated CO_2 on re-sprouting response when grown in competition with invaders. These results suggest that community composition and species interactions in this fire-prone community may alter in a high CO_2 world, shifting to a more exotic-dominated community and potentially resulting in an intensified fire frequency due to positive feedbacks. Images and graphs courtesy of I. Tooth (Royal Botanic Gardens, Sydney, Australia).

16.2.2.2 Changes in Temperature and Rainfall

Patterns of temperature and rainfall are shifting globally relative to baseline conditions. On average, combined global land and sea surface temperatures rose by 0.85°C [0.65 to 1.06] over the period from 1880 to 2012, and there have been both documented increases and declines in long-term average precipitation during this period (Stocker *et al.*, 2013). There is high confidence that the number of cold days and nights has decreased, whilst the number of warm days and nights has increased globally (Stocker *et al.*, 2013). In addition to changes in average conditions, the frequency and intensity of extreme weather events (e.g. heat-waves) has increased in some regions (Australia, Asia, Europe) and is projected to continue to increase in coming decades (Stocker *et al.*, 2013).

At the macro scale, changes in temperature and rainfall are expected to drive shifts in plant species distributions, with contractions in ranges at the equator-side boundaries and range expansions polewards and to higher elevations (Thuiller *et al.*, 2005; Kelly & Goulden, 2008). The ability to shift range will be contingent on species' ability to disperse propagules and establish populations into new regions (Corlett & Westcott, 2013). There have been a number of studies that have used species distribution modelling (SDM) approaches to examine likely responses of native plant species in large regions, such as Europe (Thuiller *et al.*, 2005), California (Loarie *et al.*, 2008), South Africa, and Western Australia (Yates *et al.*, 2010a, b). These have generally shown the potential for large species' range contractions and substantial shifts in native species assemblages. The SDM approach has also been used to project changes in suitable habitat under climate change for individual invasive plant species (e.g. Bradley *et al.*, 2009; Beaumont *et al.*, 2009; Murray *et al.*, 2012) as well as for multiple invasive species in large regions (e.g. O'Donnell *et al.*, 2012; Gallagher *et al.*, 2013; Duursma *et al.*, 2013). Generally, these studies have not found an increase in the areas of suitable habitat for alien invasive species. Instead, SDM studies show that although there is some variability among regions and taxa, areas of suitable habitat under future climate generally decline in size and shift polewards for invaders, as for native plant species. This suggests that although alien invasive plants tend to have larger native distributions with associated broader climatic ranges than native species (Milbau & Stout, 2008; Gallagher *et al.*, 2011), this does not buffer them sufficiently against the scale of climate change predicted. Instead, we can expect to see substantial shifts in species assemblages and the emergence of new colonisation opportunities created by losses of marginal populations at the edges of range boundaries of both native and alien species.

At more local scales, changes in temperature and rainfall will affect demographic processes such as seed bank mortality, seedling survival, growth rates, and reproduction. The ability of seeds to persist in the soil may be altered, via effects such as dormancy release and germination responding to changes in environmental cues, and soil pathogen activity responding to changes in soil temperature and moisture (Walck *et al.*, 2011). There have been few empirical tests on the expected effects of climate change on seed banks (but see del Cacho *et al.*, 2012; Leishman *et al.*, 2000;

Ooi *et al.*, 2009), and none have directly tested for differences in response of native and alien invasive species. Earlier work by Blaney and Kotanen (2001) found no difference in seed bank mortality due to soil fungal pathogens between native and invasive species. Whilst these authors did not test explicitly for the potential effects of climate change on seed banks, it seems reasonable that this pattern would be maintained.

Studies comparing growth responses to increased temperatures between native and alien invasive species have shown contrasting results. For example, Hou *et al.* (2014) compared the effect of extreme temperatures on seedling germination and establishment of invasive and native Asteraceae species, and showed that the invasive species coped better with extremes. However, Verlinden *et al.* (2013) grew native-invasive species pairs in ambient and elevated (+3°C) conditions and found no effect of warming on the competitive balance within pairs. In a meta-analysis incorporating results from multiple studies, Sorte *et al.* (2013) assessed whether non-native and native species responded differently to climate change factors, including warming and changes in rainfall. These authors found that there was a positive effect of warming on native terrestrial species but not on non-natives (note that this included some invertebrate species in the analysis), but no differences between natives and non-natives in response to changes in rainfall. Thus, it is likely that the effect of changes in temperature and rainfall on key plant demographic processes will be species- and system-specific, and that alien invasive plant species will not always be advantaged under changed temperature and rainfall conditions.

16.2.2.3 Changes in Disturbance Regimes Including Extreme Climatic Events

Climate change is likely to cause significant changes in disturbance regimes, such as floods, cyclones, and fire, which underpin plant demographic processes (Field *et al.*, 2012). Altered disturbance frequencies may affect germination and establishment success, regeneration and mortality, but it is unclear whether alien invasive plants will be advantaged relative to native species. More generally, invasive plants are thought to respond positively to disturbance, including physical disturbance (Burke & Grime, 1996; Daehler, 2003; Hansen & Clevenger, 2005) and nutrient enrichment (Burns, 2008; Leishman & Thomson, 2005). The most likely positive effect of changes in disturbance regimes and increased frequency of extreme climatic events on alien invasive plants will be via increased propagule input and hence colonization opportunities, increased resource availability favouring fast-growing species (Leishman *et al.*, 2010) and through reduced competition due to mortality of individuals and reduced biomass (Diez *et al.*, 2012; also see section 16.3).

16.2.2.4 Interactions Between Macro- and Local-scale Climate Change Drivers

The abundance and distribution of species is generally the outcome of a complex interplay of multiple factors. Thus, we might expect that the combined effect of multiple climate change drivers may be more important in determining ecosystem change than the effect of individual drivers such as elevated CO_2, changed temperature or rainfall, or increased frequency of extreme climatic events in isolation. Experimental work that tests hypotheses on the effects of multiple drivers on mixed assemblages of native and alien invaders is now emerging (e.g. Dukes *et al*., 2011; Tooth & Leishman, 2013; Tooth & Leishman, 2014; Manea & Leishman, 2014). Sheppard *et al*. (2012) found that species introduced into experimental European meadow communities did not show responses to any of the combinations of warming and extreme drought or deluge consistent with their native/alien provenance. Similar results were found by Godfree *et al*. (2013), who compared responses of a native and alien grass species in Australia under ambient and simulated 2050 conditions of drought, temperature, and elevated CO_2, and by Tooth and Leishman (2013), who compared re-sprouting responses after fire under ambient and elevated CO_2 for mixed temperate grassland assemblages. However, other studies have found evidence for a shift towards more alien-dominated communities under combinations of increased CO_2 and fire or drought (Dukes *et al*., 2011; Tooth & Leishman, 2014; Manea & Leishman, 2014) (Figure 16.3). It seems likely that the effect of multiple climate change drivers on vegetation assemblages will not consistently favour alien invasive plants, but that the outcomes may be dependent on the response of key species (Thuiller *et al*., 2007) to specific combinations, such as elevated CO_2 and drought, or warming and increased fire frequency.

16.3 Will There Be a Shift to Alien-dominated Vegetation Assemblages under Climate Change?

So far we have examined the evidence for differences in the responses of native and alien invaders to the direct effects of climate change factors, either individually or in combination, in order to assess how likely it is that there will be a shift to aliendominated vegetation as climate change progresses. However, changes in plant species assemblages under climate change are likely to come about due to a combination of the following drivers: (1) species-level responses to changed climate conditions, such as temperature and rainfall; (2) changes in competitive interactions between species under changed conditions of CO_2, temperature, rainfall, extreme events, and disturbance regimes; (3) reduced biomass or mortality of individuals resulting in the creation of colonization opportunities; and (4) changes in interactions between plant species and enemies (including pathogens, herbivores, and seed predators) or mutualists (including mycorrhizae, pollinators, and seed dispersers). We assess the evidence for each driver below and explore the interactions between them.

For the first driver (species-level responses to changed climate conditions such as temperature and rainfall) it is apparent from SDM approaches that both native and alien invasive species will have shifts in areas of climatic suitability towards the poles and to higher elevations, associated for many species with substantial contractions in size or connectivity between populations. Critical determinants for how these shifts in climate suitability play out in terms of changes in species' distributions are the dispersal capacity of a species and interactions among newly arriving species and the recipient community (driver 2). Several glasshouse-based experimental studies have shown that competitive interactions between native and alien invasive plant species shift to increase the relative advantage of the alien invaders under conditions such as increased CO_2 (Manea & Leishman, 2011), increased temperature (Verlinden & Nijs, 2010, but see Verlinden *et al.*, 2013), and extreme temperature (Song *et al.*, 2010). Similarly, field-based experiments have shown that warming (Chuine *et al.*, 2012) and elevated CO_2 (Dukes *et al.*, 2011) result in increased abundance of the invader in a native-dominated recipient community. These results suggest that competitive interactions will be an important determinant of vegetation composition under climate change. Thus, alien plant invaders may become more dominant in the novel vegetation assemblages created by changing climatic conditions due to their greater competitive ability, in combination with their greater capacity to disperse long distances in order to keep up with their changing climate space.

The third driver of changes in plant assemblages (reduced biomass or mortality of individuals resulting in the creation of colonization opportunities) arises due to reduced population viability on species' range margins with climate change, as well as from increased frequency and intensity of extreme climatic events (Diez *et al.* 2012). These factors are likely to result in reduced resilience of vegetation assemblages. Alien invasive plants may be best able to take advantage of these colonisation and growth opportunities in low resilience communities due to their capacity for dispersal into new areas (Pyšek & Richardson, 2007) and for rapid growth when resources are not limiting (Grotkopp & Rejmanek, 2007; Leishman *et al.*, 2010). Thus the reduced competitive ability of natives under changed climate conditions and disturbance-induced mortality creating opportunities for colonisation and growth, in combination with the typical invader traits of long-distance dispersal and fast growth, may result in clear advantages for alien invaders and resultant shifts to more alien-dominated species assemblages under future climates.

Finally, the fourth driver (changes in interactions between plant species and enemies or mutualists) is also likely to affect species' distributions and community composition. However, our knowledge of the impact of climate change on these interactions, and particularly on differential impacts on native and alien invasive species, is quite limited. It seems likely that climate change will impact interactions between plant species and enemies or mutualists in many complex and unpredictable ways.

In summary, the combination of climate change drivers 1, 2, and 3 is likely to result in a shift to alien-dominated vegetation assemblages, with a reduction in vegetation resilience (driver 3 - reduced biomass or mortality of individuals, resulting in the creation of colonization opportunities) in combination with typical invader traits of good dispersal ability and capacity for fast growth, being the most important. This has clear implications for management options, including increasing vegetation resilience and monitoring, and early eradication efforts in response to disturbance events such as fire, storms, and floods (as outlined below in section 16.4).

16.4 Issues of Management of Invasive Plants under Climate Change

Climate change poses a distinct set of challenges for the management of invasive plants. In many instances, the application of established techniques for controlling populations may become increasingly ineffective, requiring the development of new approaches. A failure to incorporate the potential effects of climate change into prevention measures that target key stages of the invasion continuum may lead to poor management outcomes.

16.4.1 Weed Risk Assessment

Pre-border Weed Risk Assessment (WRA) protocols aim to identify potentially problematic species prior to their introduction from foreign locations. Screening typically involves the use of a standardised set of questions on the biology and invasive behaviour of the species for which permission to import is being sought, as well as an assessment of the match between the climate in the native range of the species and of the recipient region (Pheloung, 2001; Groves *et al.*, 2001). Whilst current WRA protocols have been shown to be highly effective in preventing new weed establishment (Gordon *et al.*, 2008), they do not address the potential for changes in climate over coming decades to alter patterns of weed establishment (Beaumont *et al.*, 2014). Given increasing evidence that climate change may affect the growth (Smith *et al.*, 2000), spread (Crossman *et al.*, 2011), and extent of suitable habitat of weeds (Murray *et al.*, 2012; Gallagher *et al.*, 2013; Duursma *et al.*, 2013), the omission of clear questions about climate change in the WRA process requires attention. To do this, models which integrate spatial information about weed spread in the landscape and biological traits have been developed (e.g. Crossman *et al.*, 2011), but are yet to be widely adopted into formal WRA decision tools.

16.4.2 Controlling Weeds

Methods for controlling established weeds may also suffer from a lack of an integration of knowledge about the drivers of climate change, such as elevated atmospheric CO_2. For instance, the tolerance of some C_4 grasses to glyphosate-based herbicides has been shown to increase under elevated CO_2 levels (Manea *et al.*, 2011). This increased tolerance was attributed to a dilution effect from increased biomass production, also reported for a C_3 species — Canada Thistle (*Cirsium arvense* (L.) Scop.) (Ziska *et al.*, 2004). Whilst chemical control will still be feasible for weed species under elevated CO_2, dosage and frequency of application may need to increase in order to maintain a regulatory effect on population growth. Chemical-free methods, such as biological control, are also predicted to become less effective in some regions under climate change due to changes in host-plant and control-agent interactions (Hellmann *et al.*, 2008). Biocontrol agents, in particular insects, may use environmental cues like air temperature to precisely time life-cycle events, such as overwintering or emergence. Where climate change alters these signals, peak periods of host-plant growth or seed set and insect abundance may become decoupled, reducing the potential for control (Lu *et al.*, 2013). However, this effect will be site-specific and may lead to increased efficacy in regions where changing temperatures bring the phenology of host-plant and agent into better synchrony (Hellmann *et al.*, 2008; Gerard *et al.*, 2013).

16.4.3 Management Following Extreme Climatic Events

As discussed above (section 16.2.1), climate change is projected to lead to an increase in the frequency and magnitude of extreme climatic events (Field *et al.*, 2012). In addition to facilitating new arrivals, extreme climatic events may facilitate already-established alien plants by the creation of colonisation opportunities associated with disturbances such as cyclones, floods, and wildfires. For example, non-native vines may form thick infestations in canopy gaps and forest edges following cyclones (Elmqvist *et al.*, 1994; Murphy *et al.*, 2008). Strategies for targeted weed eradication and management following disturbance would be a valuable way of limiting the impact of invaders on ecosystems as climate changes. Pre-emptive monitoring in areas projected to provide suitable habitat for multiple species under future climate scenarios may also be a useful tool for detecting new weed incursions and fast-tracking local eradication (O'Donnell *et al.*, 2012).

16.4.4 Weed Management in the Wider Context of Biodiversity Planning

Whilst planning to limit the effects of climate change on ecosystems is an essential part of biodiversity conservation, some adaptation measures may inadvertently promote the dispersal and establishment of invasive plants. For instance, actions which increase the connectivity of the landscape through the introduction or reinstatement of dispersal corridors may facilitate the spread of invasive plants (Simberloff & Cox, 1987; Minor & Gardner, 2011; however see Noss, 1991 for counter-arguments). Similarly, deliberate translocation of native species deemed at-risk from climate change beyond their current range limits (assisted colonisation) may lead to an increased risk of native plants showing invasive behaviour (Gallagher *et al.*, 2015). That is, native plants that become decoupled from co-evolved pests or pathogens following translocation may become highly abundant, potentially displacing other native species in recipient communities. Whilst translocation for climate change is still in its infancy, there is substantial evidence of native plants becoming invasive when introduced outside historical range boundaries (e.g. acacias in Australia; Richardson *et al.*, 2011) that should be taken into account when designing translocation programs. In addition, defining which populations are native and which are invasive will become an increasingly difficult task for those species that shift their range without human assistance (Walther *et al.*, 2009). Balancing the need to allow species to colonise new areas that feature optimal conditions for their growth and survival against the potential for invasive behaviour will be a challenging management issue in coming decades.

16.5 What Research Is Needed to Inform Successful Management of Invasive Plants under Climate Change?

Whilst substantial progress has been made towards understanding potential synergies between plant invasions and climate change over the last two decades, research is still lacking in key areas. These areas range across a need for pure ecological research into factors such as accurately predicting dispersal dynamics and demography, to more practical questions of how to better engage the agricultural and horticultural sectors to reduce new species introductions, and novel ways to control weeds once they are established in a high CO_2 world. Below, we outline major topics where research is needed in order to effectively plan for the prevention and control of invasive plants in coming decades. Whilst we do not advocate for one research area over another, we have attempted to prioritise these topics in terms of their influence on reducing the impact of invasions under climate change.

Preventing invasions: The development of proactive weed management strategies that capitalise on the short window of opportunity following extreme events such as cyclones and floods, and large-scale disturbances such as fires, are needed to limit the damage associated with weed encroachment in affected areas, before weeds colonise and spread. A proactive approach to weed management will help to achieve better eradication outcomes at local scales and help to direct the typically finite funds available for weed management towards actions with the highest likelihood of long-term success.

Multiple drivers of invasion: The combined effects and interactions between multiple drivers and consequences of climate change on invasive plants (e.g. elevated CO_2, rising temperatures, increased drought conditions, increased extreme climatic events) are relatively poorly understood. Despite a rise in the amount of research on this topic, we still lack a clear theoretical framework based on a mechanistic understanding for predicting how interactions between climate change factors may affect alien plant populations and vegetation more generally. Similarly, more research is needed into the interactive effects of propagule pressure, resource availability, and competition between natives and invaders in order to increase our predictive capacity.

Mutualists and enemies: Little is known about how the interactions between invasive plants and mutualists, or equally, enemies such as herbivores and pathogens, may be altered by changing climate regimes. Filling this knowledge gap, particularly in relation to epidemiology of plant diseases and pests, will have important consequences for the continued efficacy of biocontrol as a means to suppress weed populations. However, beneficial relationships between plants and mutualists (e.g. N-fixing bacteria, soil-borne microorganisms) may also be affected by climate change in ways that may favour alien invasive species over co-occurring native species or, conversely, increase native plant community resistance to invasion.

Reproductive biology: The impact of climate change on the reproductive biology of invasive plants and the native species they co-occur with requires research attention. Establishment is a key demographic phase governed by multiple factors such as seed availability (linked to seed output and adult population dynamics, and dispersal — including biotic, abiotic, and human-mediated) and seed quality (linked to maternal provisioning and rates of seed-set). Without an understanding of how changes in temperature, rainfall, and CO2 concentration may affect seed production and storage within seed banks, the ability to predict how invaders may be advantaged by changing climate will be limited. This type of information on key demographic stages could also be coupled to spatial models to better predict how key invasive plants may respond to climate change.

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In a nutshell

- The last two decades have seen an upsurge in research into the potential synergies between invasive species and climate change, with evidence emerging of increased invader success under climate change. All stages along the naturalization-invasion continuum are likely to be affected, from the introduction and establishment of alien species to their spread and transition to serious invaders. A key question is whether alien plants will have a relative advantage under climate change conditions.
- So far, evidence for differential responses of alien invasive and native species to climate change drivers (elevated CO_2) and outcomes (increasing temperature, changing rainfall patterns, changes in disturbance regimes) is mixed. Although alien invasive plants appear to be more responsive to elevated CO_2 than many native species, plant response to elevated CO_2 and other climate change components is dependent on environmental conditions and resource availability. Similarly, correlative modelling of species-climate relationships has not revealed clear evidence that invasive plants are likely to be able to increase the extent of suitable habitat under future climates any more than their native counterparts.
- We suggest that the most important driver of a shift to alien-dominated vegetation under climate change will be the superior capacity of alien invasive plants to take advantage of colonisation opportunities arising from climate change, such as extreme climatic events, changes in disturbance regimes, and widespread reduction in vegetation resilience as range margin populations decline.
- There are substantial challenges ahead for managing invasive plants under future climates. Weed risk assessment and management approaches must incorporate consideration of future climatic conditions. Most importantly, we will need a shift in management approaches away from a focus on the control of undesirable alien plant species to building resilience of resident vegetation assemblages, in association with targeted monitoring and early eradication of alien plant species.

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