CAMBRIDGE

Cambridge University Press
978-1-107-19526-4 — Grasslands and Climate Change
Edited by David J. Gibson , Jonathan A. Newman
More Information

CHAPTER NINE

Grassland invasion in a changing climate

JANE A. CATFORD
King's College London
LIZZIE P. JONES
Royal Holloway, University of London

9.1 Introduction

Climate shapes the distribution and abundance of all organisms, so changes in climate will necessarily prompt biotic change. The impact of climate change on community composition will depend on the major forces of change, their geographic location, and the species of concern (1). It is well-established that there will be both winners and losers with climate change, where some species experience increases in range and population sizes, while others experience reductions (2). However, considerable uncertainty remains, especially for effects of precipitation change, the projections of which are highly uncertain themselves (3). Nevertheless, a key prediction remains that exotic species invasion will increase with climate change, especially with rises in temperature and increases in extreme climatic events (4,5). Given that – like native species – individual exotic species can be helped or hindered by climate change (1,6,7), why does this remain a general prediction? It makes sense that some species will benefit from changes in climate regimes and others will not, but why should some species experience an advantage simply because they are non-native?

In this chapter, we address these questions by concentrating on the effects of climate change on exotic plant invasion in global grasslands. We specifically ask whether climate change will favour exotic species, why that might be the case, and what sort of species (including their functional traits) will be favoured. To consider these questions, we divide the effects of climate change into three components: (i) changes in background climatic conditions, namely temperature and precipitation regimes; (ii) increases in disturbance from extreme climatic events; and (iii) changes in human behaviour – both through attempts to lessen the extent of climate change (mitigation), and through climate change adaptation where human activities are altered to suit the new conditions, which may affect invasion. Changes in human behaviour that may affect invasion include greater use of biofuels, the intensification of agriculture, the use of new plant species (or plant varieties) in gardens and agriculture, and altered approaches and effectiveness of vegetation management (Figure 9.1).

Although other global changes are linked or co-occur with climate change, including elevated CO_2, nitrogen deposition, changes in land use, wildfires and increased trade, in this chapter we focus on changes in temperature, precipitation, extreme climatic events, and human responses to climate change. We do not consider invasions of grasslands by woody vegetation, or expansions of native species' ranges; these are covered elsewhere in this book. Here, the term 'exotic species' refers to species that are transported and introduced beyond their historical biogeographic boundaries by humans (also called alien, non-native, non-indigenous, introduced), and then go on to establish self-sustaining populations (i.e. become naturalised) in their new range. We have not scrutinised the definitions of exotic, naturalised or invasive species used in publications that we cite; we adopt the terms used by the primary authors, although we recognise that different people use these terms in different ways (8).

We approached the literature through means of a systematic review, searching SCOPUS for keyword synonyms of 'invasion', 'grassland', 'climate change', and 'traits' to investigate publication trends. We used 'revtools' to visualise trends in the titles, abstracts and keywords of 176 publications (https://github.com/mjwestgate/revtools), and read over 70 of these publications in full. We also examined the bibliographies of these papers, reading additional papers that looked relevant. We note that more research is published every day on the topic of the chapter, making it impossible to comprehensively cover this vast body of knowledge in this short chapter. Here, we aim to give a succinct overview of the primary themes in this literature.

9.2 Current levels of grassland invasion

Biological invasions affect all ecosystems worldwide. Covering at least 35 percent of the ice-free land surface, grasslands are certainly no exception. Globally, grasslands experience some of the highest levels of invasion, in terms of both relative cover and relative species richness (Table 9.1) (9). Research from the global 'Nutrient Network' in 2013 revealed that worldwide, mesic grasslands and pasture had over 20 percent exotic cover, and old fields and annual grasslands had over 40 percent and 75 percent exotic cover, respectively (Figure 9.1). This trend seems to relate to levels of human activity: grasslands in alpine, montane, salt marsh, and steppe sites experience low levels of invasion (i.e. less than 1 percent of vegetation cover is exotic in these systems), whereas grasslands with stronger ties to human activities experience high levels of invasion (Figure 9.1) (9). Importantly, there was a high degree of variation in exotic cover across and within regions – Europe, Asia,

Table 9.1 *Summary details of 78 prominent exotic plant species that currently invade grasslands worldwide. Data from the Global Invasive Species Database (GISD; (12)), which was filtered to include non-woody vascular plants that are recorded as invading 'grasslands and rangelands'. Species marked with an asterisk appear in the GISD list of '100 of the World's Worst Invasive Alien Species' (12).*

Species	Common names	Growth form	Native range	Introduced range
Abelmoschus moschatus	Abelmosk, annual hibiscus	Forb	Asia	Pacific Islands
Aegilops triuncialis	Barbed goatgrass	Grass	Europe, Africa, Asia	Asia, North America
Agave americana	Sentry plant, century plant, maguey, American aloe	Succulent	North America	Australia, Europe, Africa, Asia, Central America, South America, Pacific Islands
Agave sisalana	Sisal	Succulent	North America	Australia, Europe, Africa, North America, Central America, Pacific Islands
Ageratum conyzoides	Gobu	Forb	North America, Central America	Australia, Europe, Africa, Asia, North America, Pacific Islands
Agrostis capillaris	Common bent	Grass	Europe, Middle East, Asia	Australia, North America, South America, Pacific Islands
Agrostis gigantean	Black bent, redtop	Grass	Europe, Asia	North America
Andropogon virginicus	Whiskey grass, broomsedge bluestem	Grass	North America, Central America	Australia, Pacific Islands
*Arundo donax**	Giant cane, giant Spanish cane, giant reed	Grass	Middle East, Asia	Australia, Europe, Africa, North America, Central America, South America, Pacific Islands
Austroeupatorium inulifolium	Austroeupatorium	Forb	South America	Asia
Bidens pilosa	Blackjack	Forb	Australia, North America, Central America, South America	Europe, Middle East, Africa, Asia, North America, Pacific Islands
Bothriochloa pertusa	Pitted beardgrass	Grass	Asia	Australia, North America, Central America, Pacific Islands
Brassica tournefortii	Asian or African mustard, pale cabbage	Forb	Europe, Africa, Asia	Australia, North America

Table 9.1 (*cont.*)

Species	Common names	Growth form	Native range	Introduced range
Bromus inermis	Smooth brome	Grass	Europe, Asia	North America
Bromus rubens	Foxtail brome	Grass	Europe, Africa, Asia	North America
Bromus tectorum	Cheat grass, drooping brome, downy brome	Grass	Europe, Asia	Australia, Europe, Asia, North America, Pacific Islands
Calluna vulgaris	Common heather	Forb	Europe, Africa, Asia	Australia, North America, Pacific Islands
Camelina sativa	False flax, camelina	Forb	Europe, Asia	North America
Campuloclinium macrocephalum	Pom pom weed	Forb	North America, Central America, South America	Africa
Carduus nutans	Nodding thistle, musk thistle	Forb	Europe, Asia	Australia, North America, South America, Pacific Islands
Cenchrus ciliaris	Buffel grass	Grass	Europe, Africa, Asia	Australia, North America
Cenchrus clandestinus	Kikuyu grass	Grass	Africa	Australia, Africa, Asia, Pacific Islands
Cenchrus echinatus	Common or Southern sandbur	Grass	Central America	Australia, Africa, Pacific Islands
Cenchrus macrourus	African feather grass	Grass	Africa	Australia, Pacific Islands
Cenchrus polystachios	Mission grass	Grass	Africa, Asia	Australia, Asia, Pacific Islands
Cenchrus setaceus	Fountain grass	Grass	Africa	Australia, Africa, North America, Pacific Islands
Centaurea diffusa	Diffuse knapweed	Forb	Europe, Asia	North America
Centaurea melitensis	Maltese knapweed	Forb	Europe, Africa	North America
Centaurea solstitialis	Yellow starthistle	Forb	Europe, Africa, Asia	North America
Chromolaena odorata	Siam weed	Forb	Central America	Africa, Asia, Pacific Islands

Coronilla varia	Crown vetch	Forb	Europe, Africa, Asia	Australia, Asia, North America, Pacific Islands
Cortaderia jubata	Purple pampas grass, Jubatagrass	Grass	South America	Australia, Africa, North America, Pacific Islands
Cynara cardunculus	Artichoke thistle, cardoon	Forb	Europe, Africa	Australia, North America, South America
Cynodon dactylon	Bermuda grass, wiregrass	Grass	Europe	Australia, Asia, North America, Central America, South America, Pacific Islands
Cynoglossum officinale	Hound's tongue, gypsy flower	Forb	Europe, Middle East, Asia	North America
Erodium cicutarium	Redstem filaree, redstem stork's-bill, pinweed	Forb	Europe, Africa, Asia	Australia, Asia, North America, South America, Pacific Islands
*Euphorbia esula**	Green spurge, leafy spurge	Forb	Europe, Middle East	North America, South America
Gunnera manicata	Chilean rhubarb	Forb	South America	Australia, Europe, Pacific Islands
*Hedychium gardnerianum**	Kahili ginger	Forb	Asia	Europe, Africa, North America, Central America, Pacific Islands
Heliotropium curassavicum	Seaside heliotrope	Forb	North America, Central America, South America	Central America
Heracleum mantegazzianum	Giant hogweed, hogsbane, giant cow parsley	Forb	Asia	Australia, Europe, North America
Heteropogon contortus	Spear grass, tanglehead	Grass	Australia, Africa, Asia	Australia, Africa, Asia, North America, Central America, South America, Pacific Islands
Hieracium aurantiacum	Devil's paintbrush, orange hawkweed	Forb	Europe	Australia, North America, Pacific Islands
Hieracium pilosella	Mouse-ear hawkweed	Forb	Europe, Asia	Australia, North America, Pacific Islands
Hypericum perforatum	St John's wort	Forb	Europe, Africa, Asia	Australia, Asia, North America, Central America, South America, Pacific Islands
Impatiens glandulifera	Himalayan balsam	Forb	Asia	Europe, North America, Pacific Islands
*Imperata cylindrica**	Cogon grass, rubra, red baron, blood grass	Grass	Australia, Asia	Australia, Europe, Middle East, Africa, Asia, North America, Central America, South America, Pacific Islands

Table 9.1 *(cont.)*

Species	Common names	Growth form	Native range	Introduced range
Ischaemum polystachyum	Paddle grass	Grass	Pacific Islands	Australia, Pacific Islands
Lepidium latifolium	Broadleaved pepperweed, pepperwort, peppergrass	Forb	Europe, Africa, Asia	Australia, Asia, North America, Pacific Islands
Lespedeza cuneata	Chinese bushclover	Forb	Australia, Asia	Africa, North America, South America
Linaria vulgaris	Yellow toadflax, common toadflax	Forb	Europe, Asia	Australia, North America, Central America, South America, Pacific Islands
Melilotus alba	Honey clover, white sweet clover	Forb	Europe, Asia	Australia, North America
Nassella neesiana	Chilean needlegrass	Grass	South America	Australia, Europe, Pacific Islands
Nassella tenuissima	Mexican feathergrass	Grass	North America, Central America, South America	Australia, Africa, North America, Pacific Islands
Neyraudia reynaudiana	Burma reed, silk reed, cane grass, false reed	Grass	Asia	Central America
Onopordum acanthium	Scotch thistle, cotton thistle	Forb	Australia, Asia	Australia, North America
Oxalis latifolia	Garden pink-sorrel, broadleaf woodsorrel	Forb	North America, Central America, South America	Australia, Europe, Africa, Asia, South America, Pacific Islands
Oxalis pes-caprae	Bermuda buttercup	Forb	Africa	Australia, Europe, Africa, Asia, North America, Pacific Islands
Parthenium hysterophorus	Parthenium weed, Santa-Maria	Forb	North America, Central America, South America	Australia, Africa, Asia, North America, Central America, Pacific Islands
Paspalum scrobiculatum	Kodo millet, ricegrass paspalum	Grass	Australia, Africa, Asia	North America, Pacific Islands
Poa pratensis	Smooth meadowgrass, Kentucky bluegrass	Grass	Australia, Europe, Africa, Asia, North America, South America	Africa, North America, Pacific Islands

Rottboellia cochinchinensis	Itchgrass	Grass	Australia, Africa, Asia	North America, Central America, South America
Rumex crispus	Curly dock, curled dock, yellow dock	Forb	Europe, Africa, Asia	Australia, Asia, North America, South America, Pacific Islands
Sacciolepis indica	Glen woodgrass	Grass	Australia, Asia, Pacific Islands	Pacific Islands
Sagina procumbens	Procumbent pearlwort, birdeye pearlwort, matted pearlwort	Forb	Europe, Africa, Asia	Australia, Europe, Africa, South America, Pacific Islands
Senecio angulatus	Creeping groundsel, cape ivy	Forb	Africa	Australia, Pacific Islands
Senecio viscosus	Sticky ragwort, sticky groundsel	Forb	Europe, Asia	North America, South America
Senecio vulgaris	Common groundsel, old-man-in-the-spring	Forb	Europe, Asia	North America, South America
*Sphagneticola trilobata**	Wedelia, Bay Biscayne creeping-oxeye, Singapore daisy	Forb	Central America	Australia, Pacific Islands
Sporobolus indicus var. *capensis*	Rat-tail grass	Grass	Africa	Australia, Pacific Islands
Stellaria alsine	Bog stitchwort, bog chickweed	Forb	Europe	Pacific Islands
Striga asiatica	Asiatic witchweed	Forb	Africa, Asia	Australia, Asia, North America, Pacific Islands
Taraxacum officinale	Common dandelion	Forb	Europe, Asia	Central America, Pacific Islands
Trifolium dubium	Lesser trefoil, suckling clover, little hop clover	Forb	Europe, Africa	Australia, Asia, North America, South America, Pacific Islands
Trifolium repens	White clover, Dutch clover	Forb	Europe, Middle East, Africa	Australia, Europe, North America, Central America, South America, Pacific Islands
Verbena brasiliensis	Brazilian verbena, Brazilian vervain	Forb	South America	Australia, Europe, Africa, North America, Pacific Islands
Verbena rigida	Slender vervain, tuberous vervain	Forb	South America	Australia, Europe, Africa, Asia, Central America, Pacific Islands
Vulpia bromoides	Squirreltail fescue, barren fescue	Grass	Europe, Africa, Asia	Australia, Asia, North America, Central America, Pacific Islands

Cambridge University Press
978-1-107-19526-4 — Grasslands and Climate Change
Edited by David J. Gibson , Jonathan A. Newman
More Information

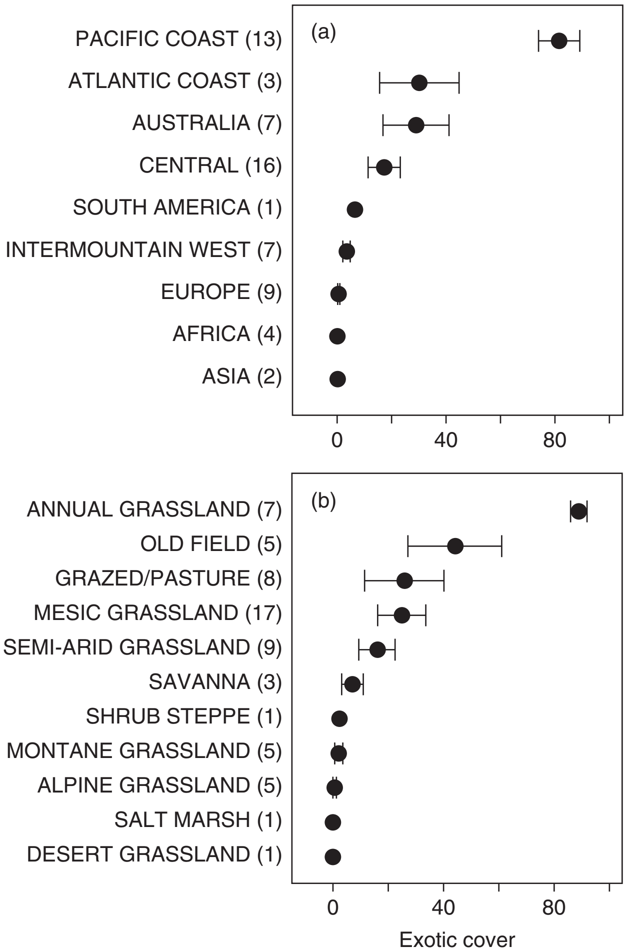

Figure 9.1 Exotic plant cover (percent of total) by (a) region and (b) ecosystem at 62 sites in 13 countries. Pacific Coast, Central, Intermountain West, and Atlantic coast are regions within North America. Error bars are 1 standard error of the mean and numbers in parentheses are the number of sites in each category. Reprinted with permission from (9): Seabloom et al. (2013) Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness? *Global Change Biology*, 19, 3677–3687, figure 4. Wiley.

and Africa had lower levels of invasion than North America and Australia (Figure 9.1), illustrating that factors other than ecosystem characteristics influence invasion levels (e.g. propagule pressure, introduction history (10), genetic potential, and strength of competition in the home range of exotic species (11)).

Using information about 458 higher plant species in the Global Invasive Species Database (GISD; (12)) and plant community composition data from Victoria, Australia (10), we compare the extent of invasion in grasslands versus other types of ecosystems. Incorporating over 20 major habitat types that vary from coastal scrubs to semi-alpine grasslands, rainforests to drylands, and with a rainfall gradient of 200 to 2000 mm per annum, the state of Victoria in south-eastern Australia provides a good example of the higher levels of invasion often experienced by grasslands (10). Based on the proportion of the species invading any given ecosystem type, grassland ecosystems were ranked the sixth most frequently invaded ecosystem globally and in Victoria (Figure 9.2). For the GISD, 31 percent of the invasive plants are known to invade grasslands (Figure 9.2a). In the Victorian data set, 45 percent of the exotic species pool was observed in Plains Grasslands and Chenopod Shrublands (Figure 9.2b), where they

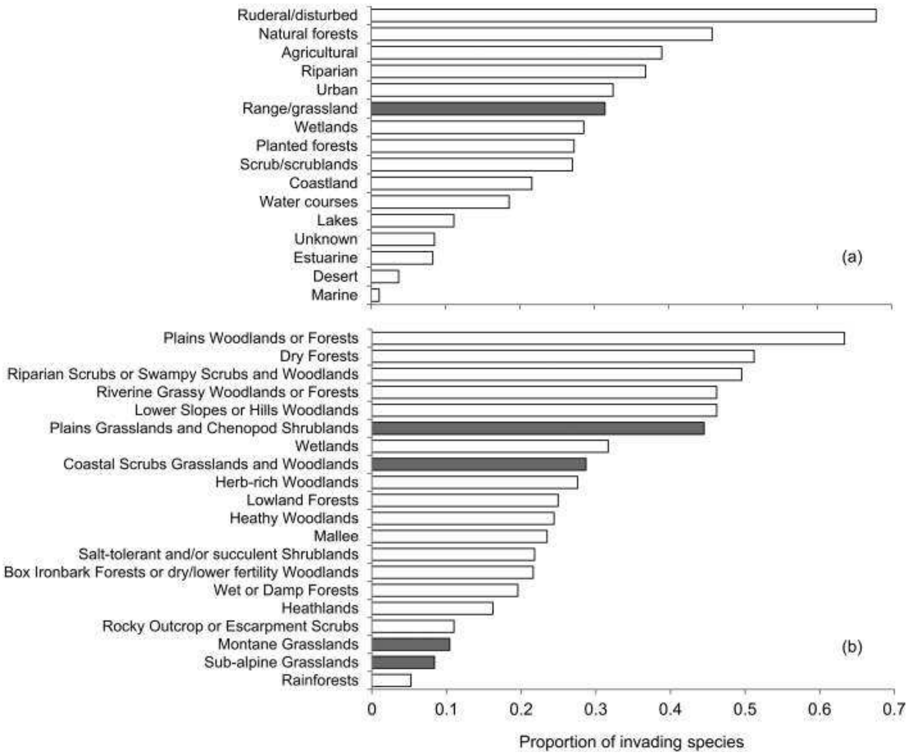

Figure 9.2 Proportion of (a) 458 invasive vascular plant species in the Global Invasive Species Database that invades each of 16 habitat types, and (b) 1036 exotic plant species in Victoria, Australia that invades each of 20 habitat types. Grassland ecosystems are shaded in grey. The Victorian data set includes all exotic species (invasive and non-invasive), whereas the GISD is restricted to invasive exotic species only. Modified from Catford and Jansson (14).

contributed over 40 percent of the total species richness in this ecosystem (Figure 9.3). In Victoria, the two most heavily invaded habitat types in 2011 were lowland grasslands; approximately 25 percent of vegetation cover in these grassland habitats was made up of exotic species (Figure 9.3). Montane and sub-alpine grasslands were distinct though, with only 5 percent exotic species cover, making them one of the least invaded of the 20 habitat types (Figure 9.3). Although exotic species are not currently dominant in Victorian grasslands (indicated by relative cover being less than relative richness in Figure 9.3), findings from the Nutrient Network show that exotics are more likely than native species to dominate grasslands globally; they were six times more likely to have 80 percent cover or more, and four times more likely to have at least 50 percent cover (13).

9.3 Why would climate change alter or exacerbate invasion?

For a species to invade a site, it must have a sufficient number of propagules (often captured by the term 'propagule pressure'), and be able to tolerate local environmental conditions and interactions with other biota (including predators, pathogens, competitors, mutualists) at that site (15,16). Propagule pressure, abiotic conditions, and biotic interactions must all be accommodating, if not favourable, for invasion to occur. Dozens of hypotheses have been proposed to explain invasion, all of which warrant scrutiny when considering how climate change may facilitate invasion (see (15) for a review of invasion hypotheses). However, hypotheses of invasion that relate to episodic disturbance and altered environmental conditions seem particularly worthy of attention when considering climate change (17–19).

There are three major ways in which climate change could facilitate invasion: (a) altering background abiotic conditions such that they give a comparative advantage to exotic species; (b) increasing disturbance through extreme climatic events, resulting in greater and more frequent fluctuations in resource availability and (c) through human responses to climate change (Figure 9.4). We address each of these in turn below, but note that they are interconnected and usually synergistic. Although we focus on grassland ecosystems and the species that inhabit them, these three factors are equally applicable to other ecosystem types. However, the close connection between human activities and grasslands (9) means that the third, at least, is particularly pertinent in grassland ecosystems.

The overriding theme underpinning these three components is – unsurprisingly – change. Change is important in and of itself when considering invasions, because invaders are generally well-suited to change, by definition (1,20): to invade, species necessarily have to expand their historical distributions, and with that expansion comes an alteration in the ecological conditions they experience.

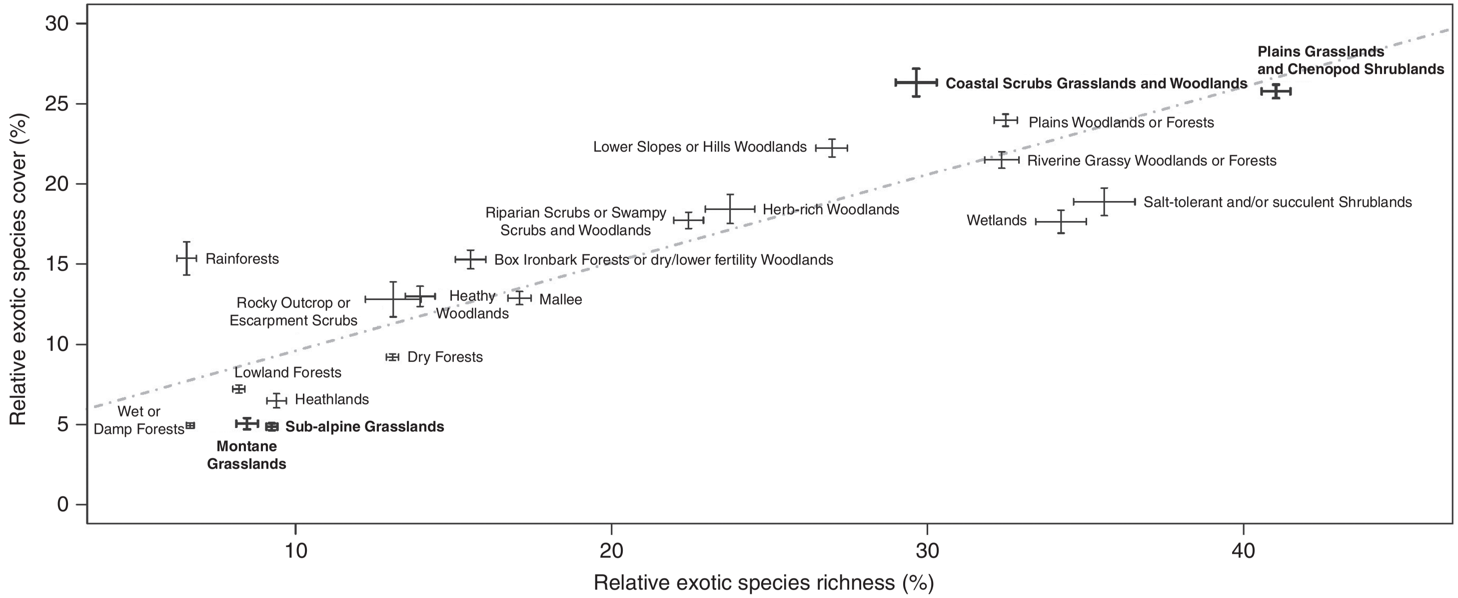

Figure 9.3 Relationships between relative exotic species richness and relative exotic species cover in 20 habitat types in Victoria, Australia. Means (points of intersecting lines) and standard errors (whiskers) are shown; grey dashed line indicates the line of best fit ($y = 4.021 + 0.548x$); the four types of grassland ecosystem are in bold. Data collected from 29,991 30 m × 30 m quadrats between 1970 and 2011 by the Victorian Department of Environment, Land, Water and Planning. Modified from Catford and Jansson (14).

Jane A. Catford, King's College London

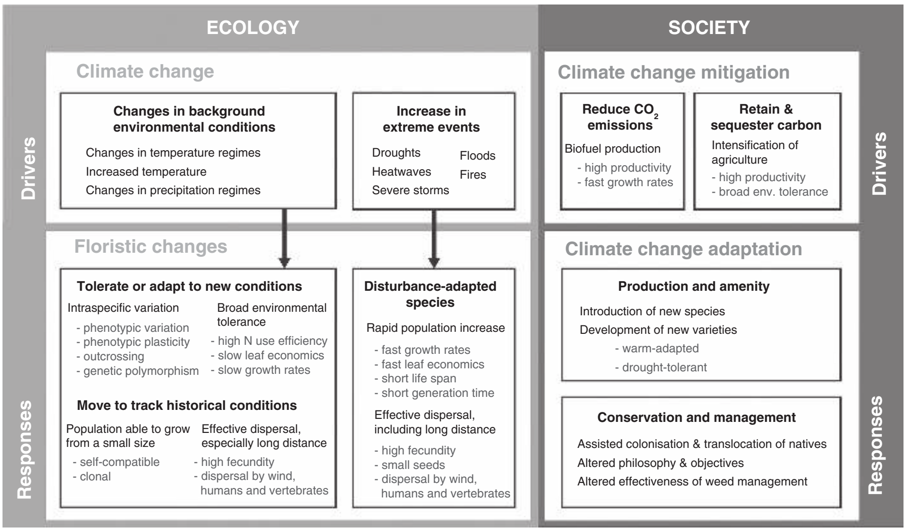

Figure 9.4 Ways in which climate change, and societal changes related to climate change, affect plant communities and species invasion. Green font shows examples of plant traits likely to be favoured by these changes; many, though not all, of these traits are associated with invasion and invasive species. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

9.3.1 Changing background environmental conditions

To colonise, grow, and reproduce in a given location, species must be able to tolerate the environmental conditions of that site, including its climate. Reflecting evolution and community assembly processes, native species are typically adapted to historical environmental conditions such that environmental modification might lead to declines in their occupancy and abundance (17,21,22). The concept of environmental filters, or environmental sorting, provides an elegant way to conceive of this. In a given location, only species with the requisite characteristics will be able to tolerate the environmental conditions of a site; species without suitable traits will be filtered out, such that they are unable to become members of the local community (21,23).

Not every species will be sensitive to every environmental condition or every environmental filter, but most species will be affected by temperature and precipitation regimes. We use the word regime to encapsulate all aspects of temperature and precipitation: whether that is means, minimums or maximums, the timing and predictability of certain conditions, the form of precipitation that occurs (snow, rain, mist), and the sequences and history of climatic conditions. In essence, there are two key ways that species can persist following changes in background environmental conditions: they can tolerate and adapt to the new conditions, or they can move to track their preferred climate. There are several reasons why exotic species may be more tolerant or better adapted to new environmental conditions, or be able to move their ranges more readily than native species.

9.3.1.1 *Exotic species may be better adapted than native species to new environmental conditions*

Unlike native species, exotic species are less likely to have adapted ecophysiological traits that suit the specific historical environmental conditions of a site (20,22) (but see (11)). Invasive species are characteristically known for being generalists, and have been shown to tolerate a wider range of environmental conditions than their native counterparts (5,24,25). As such, exotic species may be better adapted, or more tolerant, of altered environmental conditions than natives (22). In this way, invasions are very much a symptom, or passenger, of environmental change, rather than the cause of it (19); they may only be able to invade a site if environmental change has first prompted a decline in native species abundance (thereby reducing competition for limited resources), or if environmental conditions have been altered such that the exotic species are now better adapted than the natives.

Species can inhabit a wide range of environmental conditions through broad environmental tolerance, high intraspecific variation, or through rapid adaptation. The ability to maintain population growth rates over diverse environmental conditions, referred to as population fitness homeostasis, has been linked with invasiveness (26,27). Population fitness homeostasis may be best achieved through intraspecific variability that includes genetic polymorphism, phenotypic variation, and phenotypic plasticity (27). There are multiple examples of alien species that flower earlier or later than native species (28,29), or have changed their phenology more rapidly than native species in response to climate change (30). For example, invasive yellow starthistle (*Centaurea solstitialis*) in Californian grasslands and spotted knapweed (*Centaurea stoebe*) in the intermountain grasslands of Montana and Idaho are active later in the season than most co-occurring native species, whereas European grasses (e.g. *Bromus* spp., *Vulpia* spp.) invasive in grasslands of California and Nebraska are active earlier in the season than their native counterparts ((29) and references therein). Earlier flowering has been shown to be favourable under warming climates, and appears to be associated with a 'faster return on investment' strategy, which invasive species often possess (Figures 9.4 and 9.5) (30,31). As well as earlier and longer flowering periods, other traits that are favoured in grasslands under warmer climates and disproportionately possessed by exotic (cf. native) species include an annual life cycle, greater maximum heights, larger leaves, and higher specific leaf area (32).

Although plasticity is clearly very important, some climatic changes will favour species that already possess certain characteristics. An increase in

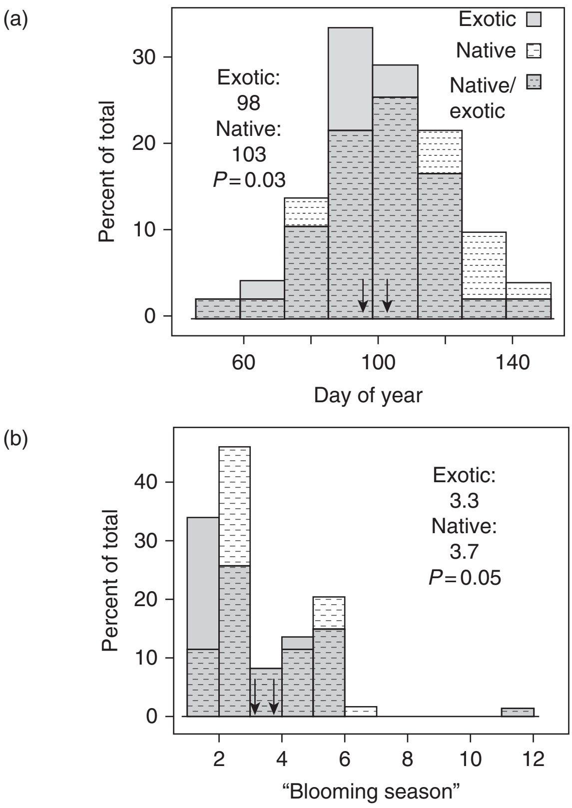

Figure 9.5 Plant phenologies from (a) Project BudBurst data from North Carolina, and (b) graminoids (grasses) from the USDA PLANTS database show a consistent trend for exotic species to bloom earlier than native species. 'Blooming season' is a numerical representation of USDA PLANTS seasonal periods, from early spring (1) to late fall (12). Arrows and values within the graph represent mean values for exotic versus native species. Reprinted with permission from (29), Wolkovich, E.M. and Cleland, E.E. (2011) The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment*, 9, 287–294.

temperatures will likely facilitate the spread of invasive species that are currently limited by cold temperatures, frost, or ice cover, as these species may be able to expand their ranges as the climate becomes more suitable (33). Milder winters may increase survival, but also extend the growing season, enabling larger populations and greater reproductive output (33), further strengthening the advantages that these sorts of species might experience. This could be particularly important in montane grasslands, where the extent of invasion is currently low (Figures 9.1–9.3), presumably an outcome of low propagule and introduction pressure, and poor climate suitability (34).

In areas that become warmer, C_4 grasses are predicted to become more invasive (35,36), as their optimal temperature range is 20–45°C, in contrast to C_3 grasses, which have an optima of 10–30°C (37). However, the effects of warming on the relative abundance of C_3 and C_4 species are conditional on precipitation and the water balance (32,37), with wetter conditions enabling species to cope with warming through changes in resource allocation and growth through their life cycle (3), reducing the importance of drought tolerance in some areas. (For a detailed appraisal of C_3 and C_4 grass distributions under climate change, we refer readers to Chapter 14 of this book). A recent meta-analysis that examined responses of 74 invasive exotic plant species and 117 native plant species to components of global environmental change revealed that higher temperatures and elevated CO_2 favoured invasive exotic plants over native plants (5).

Although certainly not a uniform prediction, it seems likely that naturalised and invasive exotic species will be more tolerant of a changing climate than native species, which would enable exotics to retain (or expand) their current distributions while native species' ranges contract or are forced to shift.

9.3.1.2 *Exotic species may be more able than native species to move to suitable environmental conditions*

A key prediction and observation of warming is a shift in species' ranges into higher latitudes and high altitudes than those they occupied historically (1,3,38). Populations unable to tolerate or adapt to the new climatic conditions must be able to shift their ranges fast enough to track environmental change. The ability to move fast has other advantages; species that shift ranges most rapidly will potentially experience less competition and thus reach higher abundances, and could exert priority effects in the newly colonised range.

Fast population spread rates are related to effective dispersal, capacity to grow from small population size, and rapid population growth. Effective dispersal of viable propagules is facilitated by high fecundity and low seed mortality. Few, if any, traits are strongly and consistently linked with long-distance dispersal (39), but dispersal distance is typically greater for species that use multiple dispersal modes, especially if dispersal vectors include humans, vertebrates, water, and wind (40). The establishment of satellite populations, even if only temporary, facilitates spatial spread and requires the ability of species to grow from a small population. Species that reach reproductive maturity quickly may achieve high rates of population growth, providing an additional source of propagules that will accelerate rates of spread, especially when the population is at the frontier of the species' current range. Many of these traits are possessed by invasive grassland species (8,31).

Range shifts basically involve the same steps as the process of invasion (15,41): a species must arrive at a new site, and then it must colonise and persist by forming self-sustaining populations. Exotic species that become widely naturalised in their invaded range can evidently establish in a new location and spread beyond a site of initial introduction, and thus seem well placed to do it again. Many naturalised exotic species possess long-distance dispersal traits (33) and can shift and expand their ranges rapidly (35). Together with high propagule pressure, these characteristics can enable them to respond more positively to environmental change than native species (35).

9.3.2 Disturbance from extreme climatic events facilitates invasion and exotic species

A key element of climate change is an increase in the occurrence of extreme climatic events (Chapter 4), which can have bigger effects on invasion than changes in background climatic conditions (42). Strong winds or storm surges can promote the transport of propagules into new regions (43), but it is the role of extreme events in causing disturbance that is most pertinent for invasion. Extreme events like heatwaves, fires, severe storms, droughts, and floods will invariably destroy and damage extant vegetation, reducing the uptake of resources, and disturbances like floods may also increase resource supply. Disturbance and fluctuations in resource availability are known to facilitate invasion (18), and many invasive and exotic species are adapted to high rates of disturbance, and thus invade disturbed ecosystems (Figure 9.2) (44).

There has been considerable research in invasion ecology and plant ecology more generally into the species traits associated with disturbed environments (Figure 9.4). Not only will these species have the capacity to move and track suitable climatic conditions because of their fast generation times and widespread dispersal, but they will also be able to increase in abundance because of the elevated rates and intensity of disturbance (44). Even if the climate is only suitable for a short period of time, their rapid population growth rates and life cycles will mean that they can profit from these opportunities.

Ruderal species (*sensu* (45)), or colonists (*sensu* (46)) that complete their life cycle rapidly can dominate a site through fast population growth when resources are available (47). Ruderal characteristics include high relative growth rates, rapid maturation, short generation times and lifespans, high fecundity, small seeds, fast leaf economics, high leaf area ratio, and low root biomass – characteristics that are well represented among naturalised and invasive species (31).

Adaptation to disturbance, including good dispersal ability, is one of the explanations for the current dominance of exotic annual herbs in grasslands in western North America (48,49). Invasive *Bromus* grasses may be temporarily suppressed by drought (49) – consistent with findings from Liu et al.'s meta-analysis (50). However, these European grasses can recover more rapidly than native vegetation when drought eases, which has allowed them to invade areas in North America formerly dominated by woody species (49). As disturbance is set to intensify, and the need for high propagule pressure and long-distance dispersal increases (44), exotic ruderal species could experience an even greater advantage in systems like these. Despite these advantages, it is important to note that ruderals are vulnerable to competition, herbivory, and pathogens, which they may not always be able to avoid (51).

As well as being adapted to high rates of disturbance, some invasive exotic species can facilitate disturbance themselves by acting as 'transformers' (or ecosystem engineers) of the environment (52). Many grasses introduced worldwide for pasture production can increase the frequency and intensity of wildfires because they have higher fuel loads than their native counterparts (53). Because they are better adapted to the types of fires that they promote (e.g. bigger, hotter fires), they trigger a grass–fire cycle, where the exotic grasses facilitate fire and fire facilitates the exotic grasses. These species include: *Bromus tectorum* in western North America; *Schizacharium condensatum, Pennisetum cetaceum*, and *Melinis minutiflora* in Hawaii; *Hyparrhenia rufa*, *Melinis minutiflora, Panicum maximum*, and *Brachiaria* species in tropical America; *Cenchrus ciliaris, Pennisetum polystachyon*, and *Andropogon gayanus* in Australia (54,55). As climate change increases the frequency of wildfires, the widely observed grass–fire cycle may strengthen, and these exotic grasses may expand their ranges further.

9.3.3 Human responses to climate change may promote current and new invaders

As well as through changes in environmental conditions, climate change may facilitate invasion by altering human behaviour, the impacts of which should not be underestimated (56). First, humans may alter their behaviour to try to ameliorate and limit the extent of climate change. The increasing use and adoption of biofuels is one example. Although biofuels are mostly sourced from waste biomass and monoculture crops grown in agricultural areas (57), rangelands and old fields may increasingly be used for biofuel production, with new species being introduced or highly productive species being planted in more areas of the landscape and at higher densities. Originally introduced from Asia to North America for ornamental use, *Miscanthus sacchariflorus* and *Miscanthus sinensis*, and their hybrid offspring, are being developed for large-scale biofuel production in North America, as well as other parts of the world, despite a demonstrated history of escape from production and subsequent invasion (58). Although climate change may limit the potential range of *Miscanthus* species in the southern hemisphere, their potential range will likely expand in North America and Scandinavia under future climate scenarios (58). *Panicum virgatum* (switch grass) is also used for biofuel production and can pose an invasion risk (33,59), but it is usually planted in its native range and its invasion risk is tempered by its need for access to water year round (60).

Efforts to sustainably intensify agriculture by increasing pasture productivity may also inadvertently increase invasion risk (61). Based on a survey of leading agribusinesses in eight countries and six continents, Driscoll et al. (62) found that over 90 percent of plants developed for pasture are invasive somewhere in the world, and 30 percent are invasive and exotic in the country in which they are sold and produced. Globally, agribusinesses are developing new varieties of pasture species with traits, such as fast growth rates and wide environmental tolerance including drought tolerance, which will enhance the invasiveness of these species, especially in grasslands (62).

The second main way that humans respond to climate change is through adaptation. Climate change adaptation may include changes in production and amenity through the introduction and use of species better suited to the new environmental conditions. The increasing introduction and use of drought-tolerant and warm-adapted species in pasture, agriculture, and gardens, e.g. through 'xeriscaping', presents an invasion risk to nearby grasslands and other natural ecosystems (63,64).

Approaches to grassland conservation and management will also likely change under a modified climate (38). As the effects of climate change intensify, it is likely that: there will be greater use of assisted colonisation and translocation of species; philosophies around invasive species management, including its desirability and feasibility, will change; and there may be a reduction in the effectiveness of historical weed management approaches including biocontrol, such that reasonably well-controlled invasive species will be less well-controlled in future, allowing populations of these species to grow and expand (33,63). This scenario is complicated by the evolution of herbicide resistance in exotic species that invade grasslands, which can have the perverse outcome of herbicide use facilitating invasion through unintended damage to native plants (65).

9.4 The importance of other factors and their interactions

As well as direct effects of climate change and climate change adaptation on the distribution and abundance of species, species will be affected by interactions between climate and other environmental factors, like elevated CO_2 and N deposition (5,66,67), and through interactions with other biota that are themselves affected by global change (68). In Californian grasslands, Bansal and Sheley (69) found evidence suggesting that a decline in perennial native grass cover and native diversity with increasing temperatures facilitated exotic annual grasses such that exotic grasses abundance was positively related to temperature, especially during the winter establishment phase. Working across a climate gradient in the Swiss alps, Alexander and colleagues (70) used a transplant experiment to reveal that competition with new species could have larger effects on plant fitness than warming. Grassland species that were exposed to warmer temperatures (equivalent to their ranges not shifting to track climate change) were more negatively affected by new competitors (vs. their historical competitors), which had shifted upwards with climate warming. Intriguingly, species that migrated upwards themselves, tracking their historical climatic conditions, also benefitted from their competitive novelty; they were able to compete more strongly with species from the higher altitudes, with which they did not occur historically (70). Given that climate change occurs alongside other forms of global environmental change and necessarily alters biotic interactions, effects of such interactions on invasion are crucial to understand.

9.5 Conclusion

Based on our review of the literature and research to date, evidence strongly suggests that – overall – climate change will favour and facilitate exotic species invasion in grasslands around the world. Other than warm-adapted species, species that are likely to do well in a period of massive environmental change are those that are phenotypically plastic, highly adaptable, have broad environmental tolerance, are good dispersers with high fecundity, have rapid growth rates and short generation times, and are associated with human activities. In comparison with native grassland species, these characteristics are disproportionately represented in the current pool of naturalised and invasive species. It therefore seems likely that – regardless of their specific adaptations to temperature or precipitation regimes – grassland species that are currently invasive will expand their ranges and increase their populations as the effects of climate change set in. It seems probable that exotic species invasion will be exacerbated by a desire of humans to both mitigate and adapt to climate change, with increased introductions of warm-adapted and drought-tolerant ornamental species, and greater use of exotic species in agriculture and the burgeoning biofuel industry.

This is a somewhat gloomy picture to read and to write, but perhaps it has some value in that it emphasises the need to earnestly develop and enact conservation and management plans that put native and exotic species on a more level playing field. It also highlights the need to consider the full impact of strategies used to ameliorate and adapt to climate change. Is it better for the environment to have drought-tolerant exotic species in gardens that provide food and habitat for other organisms, or to water native garden plants to keep them alive, or to replace gardens with some other sort of impervious surface? That these questions aren't straightforward to answer makes for a very interesting future.

9.6 Acknowledgements

We thank Martin Westgate for help with his software package 'revtools' (https://martinwestgate.com/software/revtools/), which we used to sort and visualise trends in the literature; the editors for inviting us to write this chapter; and two anonymous reviewers for helpful feedback.

9.7 References

1. Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH. Predicting plant invasions in an era of global change. Trends in Ecology & Evolution. 2010;25(5):310–8.
2. Bowler DE, Hof C, Haase P, Kröncke I, Schweiger O, Adrian R, et al. Cross-realm assessment of climate change impacts on species' abundance trends. Nature Ecology & Evolution. 2017;1:0067.
3. Blumenthal DM, Resco V, Morgan JA, Williams DG, Lecain DR, Hardy EM, et al. Invasive forb benefits from water savings by native plants and carbon fertilization under elevated CO_2 and warming. New Phytologist. 2013;200(4):1156–65.
4. Hulme PE. Climate change and biological invasions: evidence, expectations, and response options. Biological Reviews. 2017;92(3):1297–313.
5. Liu Y, Oduor AMO, Zhang Z, Manea A, Tooth IM, Leishman MR, et al. Do invasive alien plants benefit more from global environmental change than native plants? Global Change Biology. 2017;23(8):3363–70.
6. Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F. Will climate change promote future invasions? Global Change Biology. 2013;19:3740–8.
7. Bradley BA. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology. 2009;15(1):196–208.
8. Catford JA, Baumgartner JB, Vesk PA, White M, Buckley YM, McCarthy MA. Disentangling the four demographic dimensions of species invasiveness. Journal of Ecology. 2016;104(6):1745–58.
9. Seabloom EW, Borer ET, Buckley Y, Cleland EE, Davies K, Firn J, et al. Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness? Global Change Biology. 2013;19 (12):3677–87.
10. Catford JA, Vesk PA, Richardson DM, Pyšek P. Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Global Change Biology. 2012;18(1):44–62.
11. Fridley JD, Sax DF. The imbalance of nature: revisiting a Darwinian framework for invasion biology. Global Ecology and Biogeography. 2014;23(11):1157–66.
12. Invasive Species Specialist Group (ISSG). The Global Invasive Species Database (IUCN) 2015 [available from: www.iucngisd .org/gisd/].
13. Seabloom EW, Borer ET, Buckley YM, Cleland EE, Davies KF, Firn J, et al. Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. Nature Communications. 2015;6.
14. Catford JA, Jansson R. Drowned, buried and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytologist. 2014;204(1):19–36.
15. Catford JA, Jansson R, Nilsson C. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity & Distributions. 2009;15(1):22–40.
16. Mitchell RM, Bakker JD, Vincent JB, Davies GM. Relative importance of abiotic, biotic, and disturbance drivers of plant community structure in the sagebrush steppe. Ecological Applications. 2017;27(3): 756–68.

17. Moles AT, Flores-Moreno H, Bonser SP, Warton DI, Helm A, Warman L, et al. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. Journal of Ecology. 2012;100(1):116–27.
18. Davis MA, Grime JP, Thompson K. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology. 2000;88: 528–34.
19. MacDougall AS, Turkington R. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology. 2005; 86(1):42–55.
20. Blumenthal DM, Kray JA. Climate change, plant traits, and invasion in natural and agricultural ecosystems. In: Ziska L, Dukes JS, editors. Invasive species and global climate change. Wallingford: CABI Press; 2014. pp. 62–80.
21. Catford JA, Downes BJ, Gippel CJ, Vesk PA. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. Journal of Applied Ecology. 2011;48(2):432–42.
22. Catford JA, Morris WK, Vesk PA, Gippel CJ, Downes BJ. Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. Diversity and Distributions. 2014;20(9):1084–96.
23. Dawson SK, Warton DI, Kingsford RT, Berney P, Keith DA, Catford JA. Plant traits of propagule banks and standing vegetation reveal flooding alleviates impacts of agriculture on wetland restoration. Journal of Applied Ecology. 2017;54(6):1907–18.
24. Tecco PA, Díaz S, Cabido M, Urcelay C. Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? Journal of Ecology. 2010;98 (1):17–27.
25. Bradley BA, Early R, Sorte CJB. Space to invade? Comparative range infilling and potential range of invasive and native plants. Global Ecology and Biogeography. 2015;24(3):348–59.
26. Higgins SI, Richardson DM. Invasive plants have broader physiological niches. Proceedings of the National Academy of Sciences of the USA. 2014;111(29):10,610–4.
27. Rejmánek M. Invasiveness. In: Simberloff D, Rejmánek M, editors. Encyclopedia of biological invasions. Berkeley, CA: University of California Press; 2011. pp. 379–85.
28. Wainwright CE, Wolkovich EM, Cleland EE. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology. 2012;49(1):234–41.
29. Wolkovich EM, Cleland EE. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment. 2011;9(5):287–94.
30. Wolkovich EM, Cleland EE. Phenological niches and the future of invaded ecosystems with climate change. AoB Plants. 2014;6:plu013.
31. van Kleunen M, Weber E, Fischer M. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters. 2010;13(2):235–45.
32. Sandel B, Dangremond EM. Climate change and the invasion of California by grasses. Global Change Biology. 2012;18(1): 277–89.
33. Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS. Five potential consequences of climate change for invasive species. Conservation Biology. 2008;22(3):534–43.
34. Petitpierre B, McDougall K, Seipel T, Broennimann O, Guisan A, Kueffer C. Will climate change increase the risk of plant invasions into mountains? Ecological Applications. 2016;26(2):530–44.
35. Dukes JS, Mooney HA. Does global change increase the success of biological invaders? Trends in Ecology & Evolution. 1999;14(4): 135–9.
36. White TA, Campbell BD, Kemp PD, Hunt CL. Impacts of extreme climatic

events on competition during grassland invasions. Global Change Biology. 2001;7(1):1–13.

37. Bremond L, Boom A, Favier C. Neotropical C_3/C_4 grass distributions – present, past and future. Global Change Biology. 2012;18(7):2324–34.
38. Walther G-R, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, et al. Alien species in a warmer world: risks and opportunities. Trends in Ecology & Evolution. 2009; 24(12):686–93.
39. Berg RY. Plant distribution as seen from plant dispersal: general principles and basic modes of plant dispersal. In: Kubitzki K, editor. Dispersal and distribution: an international symposium. Hamburg: Paul Parey; 1983. pp. 13–36.
40. Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A. Mechanisms of long-distance seed dispersal. Trends in Ecology & Evolution. 2008;23(11):638–47.
41. Bates AE, Pecl GT, Frusher S, Hobday AJ, Wernberg T, Smale DA, et al. Defining and observing stages of climate-mediated range shifts in marine systems. Global Environmental Change – Human Policy Dimensions. 2014;26:27–38.
42. Sheppard CS, Alexander JM, Billeter R. The invasion of plant communities following extreme weather events under ambient and elevated temperature. Plant Ecology. 2012;213:1289–301.
43. Diez JM, D'Antonio CM, Dukes JS, Grosholz ED, Olden JD, Sorte CJB, et al. Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment. 2012;10(5):249–57.
44. Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA, et al. The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. Perspectives in Plant Ecology, Evolution and Systematics. 2012;14:231–41.
45. Grime JP. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist. 1977;111(982):1169–94.
46. Tilman D. Resource competition and community structure. Princeton, NJ: Princeton University Press; 1982.
47. Mata TM, Haddad NM, Holyoak M. How invader traits interact with resident communities and resource availability to determine invasion success. Oikos. 2013;122(1):149–60.
48. Seabloom EW, Harpole WS, Reichman OJ, Tilman D. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the USA. 2003;100(23):13,384–9.
49. Kane JM, Meinhardt KA, Chang T, Cardall BL, Michalet R, Whitham TG. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. Plant Ecology. 2011;212(5): 733–41.
50. Liu Y, Oduor AMO, Zhang Z, Manea A, Tooth IM, Leishman MR, et al. Do invasive alien plants benefit more from global environmental change than native plants? Global Change Biology. 2017;23(8):3363–70.
51. Blumenthal D, Mitchell CE, Pyšek P, Jarošík V. Synergy between pathogen release and resource availability in plant invasion. Proceedings of the National Academy of Sciences of the USA. 2009;106(19):7899–904.
52. Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions. 2000;6:93–107.
53. D'Antonio CM, Vitousek PM. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics. 1992;23(1):63–87.

54. Rossiter NA, Setterfield SA, Douglas MM, Hutley LB. Testing the grass–fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity & Distributions. 2003;9(3):169–76.
55. D'Antonio CM. Fire, plant invasions, and global changes. In: Mooney H, Hobbs RJ, editors. Invasive species in a changing world. Washington, DC: Island Press; 2000. pp. 65–94.
56. Kueffer C. Transdisciplinary research is needed to predict plant invasions in an era of global change. Trends in Ecology & Evolution. 2010;25(11):619–20.
57. Tilman D, Hill J, Lehman C. Carbon-negative biofuels from low-input high-diversity grassland biomass. Science. 2006;314(5805):1598–600.
58. Hager HA, Sinasac SE, Gedalof Ze, Newman JA. Predicting potential global distributions of two *Miscanthus* grasses: implications for horticulture, biofuel production, and biological invasions. PLoS ONE. 2014;9(6):e100032.
59. Parrish DJ, Fike JH. The biology and agronomy of switchgrass for biofuels. Critical Reviews in Plant Sciences. 2005;24 (5–6):423–59.
60. Barney JN, DiTomaso JM. Bioclimatic predictions of habitat suitability for the biofuel switchgrass in North America under current and future climate scenarios. Biomass and Bioenergy. 2010; 34(1):124–33.
61. Driscoll D, Catford J. Invasive plants: new pasture plants pose weed risk. Nature. 2014;516(7529):37.
62. Driscoll DA, Catford JA, Barney JN, Hulme PE, Inderjit, Martin TG, et al. New pasture plants intensify invasive species risk. Proceedings of the National Academy of Sciences of the USA. 2014; 111(46): 16,622–7.
63. Bradley BA, Blumenthal DM, Early R, Grosholz ED, Lawler JJ, Miller LP, et al. Global change, global trade, and the next wave of plant invasions. Frontiers in Ecology and the Environment. 2012;10(1):20–8.
64. Haeuser E, Dawson W, van Kleunen M. The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. Journal of Ecology. 2017;105(6): 1698–708.
65. Rinella MJ, Maxwell BD, Fay PK, Weaver T, Sheley RL. Control effort exacerbates invasive-species problem. Ecological Applications. 2009;19(1):155–62.
66. Mueller KE, Blumenthal DM, Pendall E, Carrillo Y, Dijkstra FA, Williams DG, et al. Impacts of warming and elevated CO_2 on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. Ecology Letters. 2016;19(8):956–66.
67. Blumenthal DM, Kray JA, Ortmans W, Ziska LH, Pendall E. Cheatgrass is favored by warming but not CO_2 enrichment in a semi-arid grassland. Global Change Biology. 2016;22(9):3026–38.
68. Adler PB, Leiker J, Levine JM. Direct and indirect effects of climate change on a prairie plant community. PLoS ONE. 2009;4(9):e6887.
69. Bansal S, Sheley RL. Annual grass invasion in sagebrush steppe: the relative importance of climate, soil properties and biotic interactions. Oecologia. 2016;181(2): 543–57.
70. Alexander JM, Diez JM, Levine JM. Novel competitors shape species' responses to climate change. Nature. 2015;525(7570): 515–8.