12 Will Climate Change Promote Alien Plant Invasions?

Wilfried Thuiller, David M. Richardson, and Guy F. Midgley

12.1 Introduction

Invasive alien plant species pose significant challenges to managing and maintaining indigenous biodiversity in natural ecosystems. Invasive plants can transform ecosystems by establishing viable populations with growth rates high enough to displace elements of the native biota (Rejmánek 1999) or to modify disturbance regimes (Brooks et al. 2004), thereby potentially transforming ecosystem structure and functioning (Dukes and Mooney 2004). Because the numbers of invasive plant species and the extent of invasions are increasing rapidly in many regions, concern has grown about the stability of these novel, emerging ecosystems (Hobbs et al. 2006). The question of how climate change will interact in this global process of ecosystem modification is becoming highly relevant for natural resource management.

Although many studies have addressed the potential threats to ecosystems from invasive alien plants and climate change separately, few studies have considered the interactive and potentially synergistic impacts of these two factors on ecosystems (but see Ziska 2003). Climatic and landscape features set the ultimate limits to the geographic distribution of species and determine the seasonal conditions for establishment, recruitment, growth and survival (Rejmánek and Richardson 1996; Thuiller et al. 2006b). Human-induced climate change is therefore a pervasive element of the multiple forcing functions which maintain, generate and threaten natural biodiversity.

A widely stated view is that climate change is likely to enhance the capacity of alien species to invade new areas, while simultaneously decreasing the resistance to invasion of natural communities by disturbing the dynamic equilibrium maintaining them. Links between invasion dynamics and climate change are, nevertheless, particularly difficult to conceptualize (Fig. 12.1). The determinants of plant invasiveness per se are extremely complex (Rejmánek et al. 2005). Consequently, efforts to combat plant invasions

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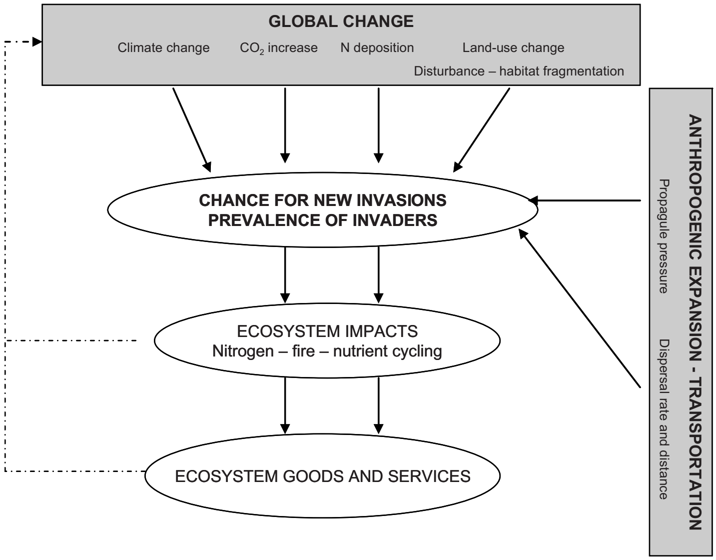

Fig. 12.1 Impacts of global change on invasions and the associated processes

have been largely reactive in nature: another species becomes invasive, and a plan must then be developed to combat it. Similarly, the question of whether invasibility is positively or negatively related to community diversity (defined in various ways) is still under debate (Lonsdale 1999). Given the level of uncertainty around determinants of invasiveness and invasibility, even without the additional complexity introduced by changed climatic conditions, it is clear that precise forecasts of the dynamics of invasions with climate change is a very tall order. Therefore, while climate change is a relatively slow ongoing process, human-induced fragmentation and disruption of disturbance regimes have probably a much greater impact on the dynamic of both native and alien species than does climate change in the short to medium term (Bond and Richardson 1990). Still, does this pragmatic view conceal underlying pressures which could eventually thwart current management approaches to alien species?

Changing climate affects natural communities, ecosystems and habitats in many ways (Parmesan and Yohe 2003) but most immediately through shifts in geographic range. Not all ecosystems seem equally vulnerable to global environmental change (Walther et al. 2002). For instance, arctic-alpine communities might see their distributions substantially reduced to the benefit of more temperate ones (Grabherr et al. 1994), and early work on climate impacts on ecosystems focused on potential geographic range shifts of species assemblages or even of biomes. However, given the idiosyncratic responses of species to past climate change (e.g. Prentice 1986), we can be sure that ongoing and future climate change will not harm or benefit all component species in any assemblage to the same extent. Shifts in the range of individual indigenous species under climate change involve processes closely akin to those driving the spread of alien species; the two can thus be addressed using a similar theoretical approach. This theory relates both to the demographic impacts of climate change as a consequence of individual physiological constraints, and also to changes in the outcomes of interactions between species – and not simply between species at the same trophic level (e.g. plants, but also plant–animal interactions; Davis et al. 1998). Finally, regional changes in community and ecosystem structure have the potential to influence both micro- and regional climate, providing a complex feedback effect which might exacerbate or retard the rate of ecosystem change.

Is it possible to simplify this plethora of impacts and interactions? As a starting point, it seems likely that the response of a few species (positive or negative) or functional groups will determine ecosystem resistance to biological invaders and changes in ecosystem functioning (Zavaleta and Hulvey 2004). Also, recent empirical evidence has provided support for the biomass ratio hypothesis (Grime 1998), showing that biogeochemical pools and fluxes are controlled by the expression of individual traits of the dominant plant species. This is especially the case in stressful environments such as alpine and artic ecosystems, where fewer than 10 species of higher plants make up more than 90 % of the vascular-plant biomass (Chapin III and Körner 1996). If such keystone species suffer population declines under climate change, then this is highly likely to increase the susceptibility of these communities to invasion by aliens, and to the disruption of key processes (Zavaleta and Hulvey 2004). Understanding how changes in species distributions resulting from global change may cascade to changes in ecosystem processes therefore requires advancing simultaneously our understanding of the processes determining community assembly and of the mechanisms through which species influence ecosystem functioning.

Climate change may, however, favour a subset of species with certain sets of traits (particularly those related to dispersal abilities and tolerance of disturbance) or species well adapted to, or tolerant of, warmer and/or drier environments and responsive to elevated atmospheric CO_2 levels. There are a number of pathways by which invasive species and climate change can interact (Fig. 12.1, Dukes and Mooney 1999). The system of complex interactions can be considered transient because the main players – anthropogenic environment, invasive species, and the components of the "host" ecosystem – are all dynamic (Sutherst et al. 2000). Climate change will likely increase this dynamism and transience, leading to a substantial impact on an already complex and almost certainly non-equilibrium relationship between invasive species and the host ecosystem. For example, climate change has been predicted to lead to greatly increased rates of species turnover (exceeding 40 %) in local communities in Europe (Thuiller et al. 2005a). Such species turnover will undoubtedly lead to severe ecological perturbation (disruption/disturbance) of these communities. Disturbance is a crucial mechanism in mediating the establishment, persistence and dramatic expansion (explosion in numbers) of invasive alien species (hence, ecosystem invasion; Brooks et al. 2004). Additionally, these new communities and ecosystems will have unknown properties, including the likely presence of species which exhibit all the traits of invasive alien species. This is the concern of an emerging concept, that of "novel ecosystems" (Hobbs et al. 2006), which we discuss below within a climate change context.

We first review the current knowledge of the potential synergies between climate change and invasive alien species, and then provide some perspectives and areas of research needed to manage biological invasions in the face of climate change.

12.2 Current and Emerging Knowledge

It is widely considered that climate change will enhance the success of invasive alien species (Dukes and Mooney 1999; Mooney and Hobbs 2000). For instance, the Union of Concerned Scientists (2001), synthesizing the views of many scientists in the USA, issued a press release stating that "Climate change could potentially favor invasive non-native species by either creating more favourable environmental conditions for them, e.g., increasing fire frequency, or by stressing native species to the point of being unable to compete against new invasives." Climate change could alter almost very facet of invasion dynamics and every interaction between different factors. In this section, we discuss some important aspects. Invasions generally have two distinct phases, separated by a time lag ranging from decades to a century: a quiescent phase, during which ranges shift only slightly, followed by a phase of active population growth and expansion. Numerous factors potentially act as trigger to start the rapid growth phase, notably natural or human-induced disturbances (Mooney and Hobbs 2000). Changing climate could provide new triggers, or fine-tune existing triggers, for instance, by creating disturbance events which open opportunities for previously quiescent alien species, e.g. by facilitating reproduction, survival, or enhancing competitive power.

Sutherst et al. (2000) suggest that climate change may impact on the overall invasion process by affecting three significant constraints: sources of invasive species, pathways of dispersal, and the invasion process in host ecosystems. Of these, we suggest that the last is by far the most important and relevant constraint, since climate change is not likely to generate additional sources of invasive species, and pathways of dispersal are overwhelmingly defined by human economic and trade activity. How, then, might climate change affect the process of invasion? This topic has been explored most succinctly by Dukes and Mooney (1999), and we build on elements of their argument. Essentially, we argue that climate change is likely to affect patterns of alien plant invasions through its effect on three overarching aspects: the invasibility of the host ecosystem, the invasive potential of the alien species, and climate impacts on indigenous species. Synergistic combinations between two or, in a worst-case scenario, all three elements is likely to lead to significantly increased vulnerability to climate change. What are the probabilities that positive synergies (i.e. increased invasiveness) will result? In the next section, we review these possibilities by assessing the potential impacts of important elements of climate change.

12.2.1 Elevated Carbon Dioxide

12.2.1.1 Observations and Experimental Findings

The significance of the direct CO_2 effect on vegetation and on invasive alien species is important – ambient CO_2 levels are currently 30 % higher than the pre-industrial level, and are higher than at any time in at least the last 750,000 years. There is general consensus on the direct physiological impact of increasing CO_2 on plant photosynthesis and metabolism (Ainsworth and Long 2005). Increasing CO_2 stimulates growth and development significantly in hundreds of plant species (Drake et al. 1997). Increasing atmospheric CO_2 generally increases the resource-use efficiency of plants (Drake et al. 1997), due to direct stimulation of photosynthetic CO_2 uptake rate or a reduction in stomatal conductance. Thus, more carbon is fixed per unit of water or nitrogen used in the process of fixation. This effect is evident in plants with both C_3 and C_4 photosynthetic pathways; species with these pathways dominate the world's flora. Preliminary work suggests that CAM plants also respond to higher CO_2 levels by increasing carbon uptake and metabolism (Dukes 2000).

The benefits of CO_2 stimulation predicted purely by photosynthetic theory and single-species experiments are difficult to extrapolate to multi-species communities. Nonetheless, the few experiments which have been done on invasive alien species suggest a strong positive response to elevated CO_2 (Dukes and Mooney 1999). However, it is difficult to tease species-specific effects from effects on native species vs. invasive species. For example, Hattenschwiler and Körner (2003) show that two indigenous European temperate forest species had a muted response to elevated CO_2 whereas an indigenous ivy, an indigenous deciduous species, and the invasive alien *Prunus laurocerasus* showed significant responses. By contrast, Nagel et al. (2004) show a clear CO_2 stimulation of an invasive grass species, and lack of response in a co-occurring native species. This is corroborated by Smith et al. (2000) who found that aboveground production and seed rain of an invasive annual grass increase more at elevated CO_2 than in several species of native annuals in the deserts of western North America. They also suggest that this increase in production would have the potential to accelerate the fire cycle, reduce biodiversity, and alter ecosystem function in these arid ecosystems. In some cases, species-specific effects are maintained in multi-species communities (Polley et al. 2002) but, to date, the number of case studies is too small to be able to make general conclusions.

Should we expect invasive alien species to have different responses than native species? It is possible that faster-growing species may benefit more than slower growers in more productive environments. Since rapid growth rate is a typical characteristic of invasive plant species, this may underpin the stronger response of the aliens. Combined with a higher reproductive output (Nagel et al. 2004) and possibly greater seedling survivorship (Polley et al. 2002), elevated CO_2 may well provide significant advantages to fast-growing alien species within the context of the host ecosystem, especially for invasive woody plants. Recently, Ziska (2003) suggested that increases in atmospheric CO_2 during the 20th century may have been a factor in the selection of six plant species widely recognised as among the most invasive weeds in the continental United States.

Ecosystem feedbacks through changes in the fire, water and nutrient cycles also complicate the issue. Recently, Kriticos et al. (2003) concluded that the invasive potential of the woody species *Acacia nilotica* in Australia may be enhanced by elevated CO_2, through improvements in plant water-use efficiency. Woody species invasions, which have the potential to subdue fire regimes in currently grass-dominated ecosystems, could drive rapid switches in ecosystem structure and function, with significant implications for the biodiversity of both flora and fauna. For example, invasion of grasslands by *Quercus macrocarpa* seedlings in the American Midwest may necessitate focused fire management strategies (Danner and Knapp 2003). Alternatively, it is conceivable that CO_2-driven increases in flammable woody or herbaceous plants will accelerate fire regimes in fire-prone systems (Grigulis et al. 2005).

12.2.1.2 Future Expectations

Looking at effects on host ecosystems, some simulations suggest that ecosystem structure might be significantly altered by elevated CO_2 (Bond et al. 2003), leading to switches in plant-functional type dominance and the opportunity for increased success of woody invaders, for example. In his experiments, Ziska (2003) argued that the average stimulation of plant biomass among invasive species from current (380 $\mu mol\ mol^{-1}$) to future (719 $\mu mol\ mol^{-1}$) CO_2 levels averaged 46 %, with the largest response (+72 %)

observed for Canada thistle *Cirsium arvense*. This study suggests that the CO_2 increase during the 20th century has selected for invasive alien species based on their positive response, and that further CO_2 increase into the future, as predicted by IPCC, will enhance the invasive potential of these recognised weeds.

In a more theoretical perspective, Gritti et al. (2006) using LPJ-GUESS, a generalized ecosystem model based on dynamic processes describing establishment, competition, mortality and ecosystem biogeochemistry, simulated the vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. They simulated the vegetation dynamics using a set of native plant-functional types based on bioclimatic and physiological attributes (tree and shrub) and two invasive plant-functional types, an invasive tree type and invasive herb type, according to two climate change and CO_2 increase scenarios projected for 2050. The major point of relevance here is that these simulations suggested that the effect of climate change alone is likely to be negligible in several of the simulated ecosystems. The authors pointed out that the simulated progression of an invasion was highly dependent on the initial ecosystem composition and local environmental conditions, with a particular contrast between drier and wetter parts of the Mediterranean, and between mountain and coastal areas. They finally concluded that, in the longer term, almost all Mediterranean ecosystems will be dominated by exotic plants, irrespective of disturbance rates. Although there is no way of validating such projections, they do shed light on the extreme complexity of attempts to predict invasion success, especially when invoking synergies between climate change, CO_2 increase, disturbance regimes, and initial conditions.

12.2.2 Changing Climate with Respect to Temperature and Rainfall

There is overwhelming evidence of individual species responses to changing temperature regimes over the past century, the vast majority of range shift responses having been recorded in insect, bird and marine species (Parmesan and Yohe 2003). By contrast, plant responses to temperature increases over the past century have been mainly phenological (i.e. a change in timing of growing season). Changes in moisture regime are far more difficult to attribute to anthropogenic climate change, and therefore studies of these have been mainly experimentally based, rather than focused on historical trends and their impacts. With a few exceptions (e.g. tundra invasion by indigenous woody species, alpine range shifts, tree invasion in boreal regions, "laurophyllization" of European forests (Walther et al. 2002), plant range shifts appear unsurprisingly much slower that those of animals. The implications of this lag between animals and plants are most obvious in North American forests, where an indigenous insect species (pine bark beetle) appears to have extended its poleward range limit, with devastating consequences for indigenous forest tree species. Therefore, in addition to alien species invading new habitats/countries as a result of climate change, concern has also been raised over the potential of those species currently causing problems in managed ecosystems to becoming more widespread and damaging (Cannon 1998). These impacts are best observed on sub-Antarctic islands, where invasive plant species currently benefit from increasing temperature and decreasing rainfall trends, in synergy with enhanced success of invasive small mammals (Frenot et al. 2005).

12.2.3 Future Expectations

The impacts of temperature and rainfall change on plant species and ecosystems have been extensively investigated using modelling approaches, which fall into two main groups: mechanistically based models which simulate simplified, abstract versions of ecosystems, and statistically based (i.e. niche-based) models which match individual species to their ecological niches and simulate potential changes in range. Such models seem poorly capable of projecting the complex interactions observed in the natural world (cf. above). Nevertheless, they may provide guidelines on which ecosystems are vulnerable to the development of such interactive effects.

In general, dynamic global vegetation models predict quite significant changes in vegetation structure and function at a global scale (Cramer et al. 2001). This type of approach yields some insights into the potential structural and functional changes accompanying climate change. For instance, Gritti et al. (2006) projected that, although climate change alone could enhance exotic invasion in Mediterranean landscapes, the interaction with the direct effect of CO_2 was the most important driver controlling the invasion by shrubs. This interaction between climate change and CO_2 to drive vegetation distribution and structure was corroborated by Harrison and Prentice (2003), who showed that both climate change and CO_2 controlled the global vegetation distribution during the last glacial maximum.

Alternatively to dynamic global vegetation models, niche-based models (Guisan and Thuiller 2005) have been the tools of choice when addressing the biodiversity implications of climate change (Thuiller et al. 2005a) and invasion potentials (Welk et al. 2002; Thuiller et al. 2005b). Niche-based models simulate quite strong negative effects of climate change on species range sizes in specific ecosystems such as Alpine environments (Guisan and Theurillat 2000), dry and hot areas (Thuiller et al. 2006a) or Mediterranean ecoregions (Midgley et al. 2003).

Such negative impacts on native ecosystems are likely to trigger and promote invasion. However, very few studies have investigated potential climate change impacts on exotic species ranges. Interestingly, potential range contractions are projected for a number of invasive alien species in South Africa (Richardson et al. 2000), in a pattern matching projections for indigenous species.

Given the strong interactions between plants and insect "pests", it is relevant to briefly highlight applications of the CLIMEX model to several species (Sutherst et al. 2000). These generally focus on areas which may become bioclimatically suitable, as opposed to areas from which the exotic species may be lost (although exceptions do occur, such as the models for the New Zealand flatworm, *Arthurdendyus triangulatus*; Evans and Boag 1996), and therefore provide a skewed impression of future range change of invasive and pest species. In addition, some models may not be based on the total suitable current climate space (e.g. Thuiller et al. 2004). In the UK, nevertheless, increases amounting to 102 % of suitable climate space by 2060–2070 are predicted for the Colorado potato beetle (*Leptinotarsa decemlineata*; Baker et al. 2000), and a substantial increase in the risk of the Southern pine beetle (*Dendroctonus frontalis*) has also been predicted (Evans and Boag 1996). Similarly, simulations at global scales are likely to shed light on the potential new areas susceptible to be invaded by specific species (Roura-Pascual et al. 2004) or even species from specific biomes (Thuiller et al. 2005b). For instance, the Argentine ant (*Linepithema humile*), native to central South America, is now found in many Mediterranean and subtropical regions around the world. Projections using niche-based models onto four general circulation model scenarios of future (2050s) climates predicted the species to retract its range in tropical regions but to expand in higher-latitude areas, tropical coastal Africa and southeast Asia. Although niche-based models lack the predictive rigour of more mechanistic models – the inherent correlative approach relies indeed on many assumptions – they nevertheless offer rapid and useful tools for screening purposes (Panetta and Lawes 2005).

Alternatively, more process-based models, principally based on the description of plant-functional types, have shown that worldwide ecosystems are likely to experience change which can be likened to a sustained and intensifying disturbance, in that ongoing plant-functional type distribution and dynamic changes will occur in combination with (and possibly accelerated by) changes in structure and function (Cramer et al. 2001). This will alter the availability of resources, and create the physical and niche space to favour species or plant-functional types with opportunistic responses to increasing resource availability.

Examples can be found across the spectrum of plant-functional types: aggressive shrub species such as sagebrush, for example, require only minor disturbance and space creation through the removal of herbaceous species to establish in the Sierra Nevada of California (Berlow et al. 2002). Increasing minimum temperatures reduce productivity in indigenous short grass prairie dominants, favouring invasive herbaceous species (Alward et al. 1999). In the forests of Panama, a slight lengthening of the dry season is projected to cause extinction of 25 % of indigenous species, and favour drought-tolerant invasive species (Condit et al. 1996).

Greater niche availability may also occur for insect herbivores. This may be due to a combination of increased levels of disturbance, and a potential increase in resources. This may be affected through an increase in plant height and changes in plant architecture, which may provide additional feeding and sheltering sites, as well as through an increase in the growing season and, thus, a lengthening in the temporal availability of resources. Additionally, departures (extinctions) of native species as their climatic tolerances are exceeded may also provide vacant niches.

12.2.4 Other Factors

Besides elevated CO_2 levels, warming, and changes in rainfall patterns, climate change is also expected to increase the frequency of droughts, floods, storms, and extreme events such as hurricanes and wildfires (Chaps. 13–17). Not only are these likely to cause large-scale ecosystem disturbances but can also affect the composition and structure of ecosystems, and these factors may provide opportunities for invasion (due to niche availability) and increase in abundance of alien species. Variability in climate is predicted to change, with models indicating that there may be greater extremes in dry and wet seasons, and also in temperature, and this may allow non-native species to become problematical, even in areas where the average climate is unsuitable. Reservoirs of such species may occur in urban areas or in protected environments such as greenhouses. In other cases, propagule pressure will be high, and establishment and spread may take place during these windows of opportunity. For example, the CLIMEX model run for the Colorado potato beetle (*L. decemlineata*) in Norway suggests that both in the last decade and in the future, there will be periods during which it is possible for establishment to take place over a substantial area, although average climate is unsuitable in most locations (Rafoss and Sæthre 2003). Climatic variability may also lead to disruptions in the synchrony between natural enemies and their hosts, and may alter the effectiveness of biocontrol agents which have been released against non-native species. Under intensifying climate change conditions, it is conceivable that novel niches will become available, mainly to species with high rates of fecundity and dispersal – typical of exotic species and attributes of an invasive.

12.2.5 Increased Fire Frequency

Overall predictions of climate change on fire frequency are strongly limited by the lack of a globally applicable model of fire in ecosystems. A substantial fraction of the world's natural ecosystems are strongly influenced by fire, especially but not exclusively in the southern Hemisphere (Bond et al. 2005). Changing fire regimes have the strong potential to radically alter ecosystems, leading to switches in vegetation dominance and structure with substantial implications for management strategies and biodiversity (Briggs et al. 2002).

Invasive C_4 grasses are causing accelerated fire cycles (Brooks et al. 2004), reduced nutrient availability, and leading to forest loss in Asia, Africa and the Americas (Sage and Kubien 2003), and on oceanic islands (Cabin et al. 2002). Fecundity and dispersal potential may be key attributes in such invasions – the invasion of *Hyparrhenia* grass species in South America is due to seed availability at post-fire sites, fire-stimulated seed germination, and rapid seedling growth (Baruch and Bilbao 1999). C_4 grass invasions may be further promoted by even warmer and drier conditions (Sage and Kubien 2003), which may have ever stronger negative impacts on indigenous species and fire regimes.

Overall, it seems feasible that increasing temperatures and dry spells, combined with the positive effects of rising atmospheric CO_2 on plant productivity, may facilitate an increased fire frequency in fire-prone ecosystems. However, an even more powerful interaction may arise where invasive species themselves generate sufficient biomass to fuel accelerated fire regimes, such as in the Cape Floristic Region, or even introduce fire as a novel disturbance (Brooks et al. 2004). Even in the Cape Floristic Region, where extensive work on invasive alien species has been done, little is known about how fire and invasive alien species will interact in the future (van Wilgen and Richardson 1985). However, it is clear that the interaction has the potential to significantly increase extinction risk for many species (Mooney and Hobbs 2000).

In summary, the possible synergy between warmer conditions and productive exotic species has the potential to transform host ecosystems, with major negative implications for biodiversity.

12.3 Perspectives

The above sections have outlined and explored key facets of the complexity challenging our developing understanding of how climate change and CO_2 increase could potentially affect the dynamics of alien plant invasions around the globe. We show that it is difficult to identify clear determinants of future invasibility of ecosystems and invasion potential of introduced species, due to the complexity of both main drivers of change, to interactions with disturbance, and to species interactions. Some already-established alien plant species are likely to be strongly favoured whereas others will probably show little response or even a negative response, where their bioclimatic requirements closely match those of the invaded ecosystem. Given the multiple linkages and complex feedback and feed-forward loops implicated, we need to draw heavily on natural experiments and ongoing observations to inform us of the nature and magnitude of effects which are likely or possible. Manipulative experiments are currently underway – these will shed light on crucial aspects which will fine-tune our understanding and our ability to model the spread of alien plant invasions within the context of global environmental change. Finally, dynamic modelling tools must continue to guide new research questions and identify key unknowns to accelerate our understanding of this critical issue.

New paradigms for conservation are needed to accommodate potential changes in the status of biological invasions worldwide. For example, alien species, even those known to be highly invasive, may well be better than *no* species in some ecosystems, e.g. where such species provide essential cover/binding or other key ecosystem services, or act as nurse plants for native species. There is a clear need to give urgent attention to building such scenarios into frameworks for conservation planning.

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