Predicting plant invasions in an era of global change

Bethany A. Bradley^{1,2}, Dana M. Blumenthal³, David S. Wilcove^{4,5} and Lewis H. Ziska⁶

¹ Department of Biology, Amherst College, Amherst, MA 01002, USA

² Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA 01003, USA

³ USDA-ARS Rangeland Resources Research Unit, Fort Collins, CO 80526, USA

⁴Woodrow Wilson School, Princeton University, Princeton, NJ 08544, USA

⁵ Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

⁶ USDA Crop Systems and Global Change Lab, Beltsville, MD 20705, USA

The relationship between plant invasions and global change is complex. Whereas some components of global change, such as rising CO₂, usually promote invasion, other components, such as changing temperature and precipitation, can help or hinder plant invasion. Additionally, experimental studies and models suggest that invasive plants often respond unpredictably to multiple components of global change acting in concert. Such variability adds uncertainty to existing risk assessments and other predictive tools. Here, we review current knowledge about relationships between plant invasion and global change, and highlight research needed to improve forecasts of invasion risk. Managers should be prepared for both expansion and contraction of invasive plants due to global change, leading to increased risk or unprecedented opportunities for restoration.

The complex relationship between global change and plant invasion

Intentionally and unintentionally, humans have moved thousands of plant species outside of their native ranges. Some of these non-native plants have become invasive, spreading away from their initial site of establishment [1], often with detrimental effects on native and managed ecosystems [2,3]. Previous research indicates that ongoing global change will alter the impacts of invasive plants on native and managed ecosystems [4–11]. Changes that influence plant invasion include rising temperature, altered precipitation, increased atmospheric carbon dioxide (CO₂), nitrogen (N) deposition, and novel disturbances associated with changes in land use or land cover. Most of these factors are expected to increase invasion risk [5,6,9,12], although recent research highlights the potential for reduced invasion risk [9,13]. A recent spate of studies on invasive plants and global change point to circumstances where global change is likely to favor or inhibit invasive plants. A better understanding of invasion risk under global change is essential for developing effective policies and programs to manage invasive plants in the $21^{\rm st}$ century.

There are two fundamental reasons why we might expect invasion risk to increase with global change. First, invasive species are by definition well suited to succeed in novel environments (Box 1), and global change creates novel environments. Second, many invasive species are most successful in environments with high resource availability [14–18], and several types of global change directly increase the availability of plant resources. For example, increased CO_2 , N deposition and changes in land use or land cover have been observed to facilitate invasion (Table 1).

However, the effects of climate change *per se* are more difficult to predict. For example, while changes in temperature and precipitation could benefit invasive species by creating novel environments, they do not consistently increase resource availability. Indeed, rising global temperature might decrease water availability even when precipitation remains the same. Modeling and experimental studies have shown both increased [19,20] and decreased invasion risk [13,21] associated with climate change. Hence, the relative impacts of global change on plant invasions will depend on the dominant forces of change, the geographical location of the area and the invasive species under consideration.

The research needed to develop risk assessments for individual species and locations is not simple; forecasting global change is fraught with considerable complexity and uncertainty [22]. Adding to this uncertainty is a lack of concordance among methods of ecological forecasting

Glossary

Global change: large-scale alteration of the natural environment. All of the components considered here are anthropogenic in origin

Invasive plant: non-native plants spreading away from original naturalization site with potential to spread across large areas [1].

Native plant: plant species that have evolved in a given geographic location and were not introduced by humans.

Process-based or Mechanistic model: a model of potential habitat based on species characteristics that could include demography, physiology, competition etc.

Transformative restoration: the translocation of novel species assemblages that can survive and reproduce under climate change conditions. This action could be necessary if invasive plants retreat from some areas.

Corresponding author: Bradley, B.A. (bbradley@nrc.umass.edu)

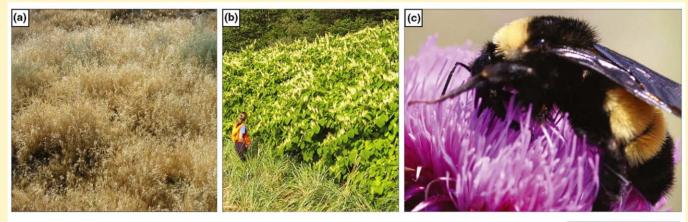
Climate change: long-term changes in global climate (e.g. rising temperatures, altered precipitation). Climate change is one component of global change. **Ecological forecasting**: projections of future risk to species and/or ecosystems as a result of global change.

Envelope or Niche model: a model of potential habitat based on empirical relationships between species distribution and abiotic factors (climate for the examples described here).

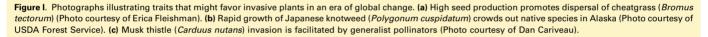
Box 1. Does global change favor invasive species over native species?

Invasive plants are a tremendously variable group. However, on average, native and invasive plants differ with regard to some traits [16], and some of these traits predispose invasive species to thrive in the face of global change [5,12]. Perhaps most importantly, invasive species are generally well suited to change. To become a successful invader, a plant species must disperse into, tolerate, and then thrive in new environments, which is essentially what species coping with global change will have to do. The following traits could enable invasive plants to thrive in the face of global change:

- Short generation times, high fecundity and strong dispersal ability could help invasive plants expand into newly suitable habitat as the environment changes. Short generation times might also help invasive species evolve more rapidly and adapt to changing environments (Figure Ia).
- Broad environmental tolerances for processes such as germination, seedling survival and flowering could allow invasive species to persist in marginal conditions, providing more opportunities for adaptation to change.
- Rapid growth and high fecundity might allow invasive species to rapidly colonize niches that are opened due to change [6,100] (Figure Ib). Furthermore, rapid growth, and associated traits such as low construction costs and strong enemy release, might make invasive species particularly well suited to changes that increase resource availability (elevated CO₂, N deposition, changes in land use or land cover and increased precipitation).
- Independence from mutualists might help invasive species thrive in novel environments where they can take advantage of generalist pollinators, seed dispersers or mycorrhizae (Figure Ic).



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(e.g. models, experiments, observations, theory). Moreover, realistic risk assessments demand input from many different disciplines such as ecology, geography, economics and climate science. In this review, we focus on three manifestations of global change: climate change, increased resource availability through rising CO_2 and N deposition, and changes in land use or land cover. We highlight both scientific advances and research needs for improving invasive plant forecasting with global change.

Climate change: temperature, precipitation, and extreme weather

Rising global temperatures, altered precipitation regimes, and changing magnitudes and durations of extreme weather events are likely to alter the distribution and prevalence of invasive plant species [5,6,9,11,12]. Climate change could directly affect the physiological ability of an invasive plant to persist in a given location, as well as alter competitive interactions with native species. In the following sections, we discuss recent results from modeling, experimental and observational studies of climate change and invasion.

Insights from modeling

Models predict how invasive plant distributions will shift with climate change and model results provide managers with spatially explicit risk assessments that can inform future prevention and control efforts. Two types of modeling approaches are typically used to project distribution shifts: envelope models and process-based models.

Envelope (also known as niche-based, species distribution or habitat) models define suitable climate habitat using species' geographic distributions [23,24] and, although simplistic [25], are commonly used for regional

Table 1. Likely impacts of global ch	hange on the prevalence of	f a typical invasive plan	nt species (updated from [12])
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Element of global change	Prevalence of plant invaders ^a	Refs
Increased atmospheric CO ₂	+	[59–65]
Rising temperature	±	[13,20,21,28,30–36,55]
Changing precipitation regime	±	[13,20,28,31,32,34–36,51–54]
Changing land use or land cover	+	[83–89]
Increased N deposition	+	[54,55,58,68–70,73,74]
Increased global commerce	+	[8,10]

^a+ Likely to increase invasion risk for many plant species; \pm Might increase or decrease invasion risk

Distribution used	Strengths and weaknesses	Refs
for modeling		
Invaded range	Strengths:	
	 Includes competition with relevant native species 	
	 Approximates 'realized niche', or the environment in which an invasive plant can survive 	
	given both abiotic conditions and biotic interactions	
	Weaknesses:	
	 Species might not be at equilibrium with environment[*] 	
	 Distribution data might be lacking or biased[†] 	
Native range	Strengths:	[29,37,38]
	Distribution close to equilibrium with environment	
	Weaknesses:	
	• Cannot account for niche changes between native and invaded range due to novel biotic interactions	
	 Distribution data might not be available, depending on the location of the native range 	
Total range	Strengths:	[29,99]
	• Approximation of the 'fundamental niche' or abiotic conditions in which the invasive plant can survive	
	Weaknesses:	
	• Fundamental niche over-estimates current invasion risk, but could be a useful guide under climate change	

Table 2. Strengths and weaknesses of using the invaded, native, and total ranges of invasive plants for niche-based model projections

*Niche-based models of *Lythrum salicaria* invasion in North America did not approach equilibrium until 100 years after invasion [96] [†]Point presence records can severely under-represent invasive plant distribution, and might be biased towards areas with low abundance [97], which in turn biases model results [98]

risk assessments of climate change impacts [26,27]. Envelope models have become increasingly popular for projecting regional invasion risk as both distribution data and climate change projections become more widely available [13,20,28–36]. In addition to species-specific risk assessments with climate change, the recent envelope modeling literature has yielded two important findings.

First, projections of invasion risk are most accurate when based on the invasive plants' distribution in the geographic range where it is invasive [29]. Envelope models based on the species' native distribution could misrepresent invasion risk [37], whereas models based on the total global distribution of the species could overestimate risk (Table 2). Thus, the combination of novel biotic interactions [38] and novel environments that occurs in invaded areas probably makes the invaded distribution the best predictor of invasion risk under current and future climate conditions. An added complication is that within the same nation or region a single species can be invasive in some areas but not invasive in others [1,30]. Hence, envelope-based risk models could be improved by selecting only species occurrence data from that portion of the invaded range where the species truly can be classified as 'invasive' [1] and therefore global information systems for invasive plants that catalogue this type of information should be supported [39,40]

The second important finding from the recent envelope modeling literature is that climate change could reduce the risk of some plant invasions. Models that predict that climate change will impede plant invasion, or even lead to invasive plant retreat, have been constructed for species in the U.S.A. [13,28], Australia [32], and South Africa [9,33]. The retreat of invasive plants could lead to opportunities for restoration of currently invaded landscapes [13] but further research is needed to identify these opportunities and to provide sound guidance for ecological restoration.

Process-based (also known as mechanistic) modeling, uses estimates of species physiology, population dynamics, dispersal ability and/or competitive interactions to project distribution under current and future climate conditions [41-43], and might ultimately be more robust than empirical envelope models [43]. Because process-based models are data hungry, they are rarely applied to native plants and very rarely applied to invasive plants [but see 44,45]. For native plants, the necessary physiological data are often simply lacking. However, invasive species present a unique opportunity for process-based model development since the physiological traits, competitive relationships and dispersal abilities of invasive plants are often well known from applied research (for example, information compiled on invasive Prosopis spp. in South Africa [9]). Invasive plants could be particularly well suited for species-specific, process-based models aimed at assessing the consequences of climate change.

Process-based models are needed for invasive plant risk assessments, both on their own and in conjunction with envelope models in an ensemble approach [46]. Combining these two modeling approaches, as has been done for native forests [47], could improve invasion risk assessments, which, in turn, could inform management decisions for a given invasive species (Figure 1).

Insights from experiments and observations

Several recent studies have tested how rising temperatures and changing precipitation (both magnitude and seasonality) can affect competition between native and invasive plants. Experimental designs have included testing: invasive plant viability along latitudinal or topographic gradients [48–51]; the effects of season specific irrigation [19,52–54]; and the effects of increasing temperatures [21,55]. Observational studies have examined the roles of higher temperatures and increased precipitation on plant growth and range expansion [9].

Experiments have shown that increasing temperatures and changing precipitation do not consistently aid plant invasion. For example, warming reduced the growth and productivity of invasive plants in Australian temperate

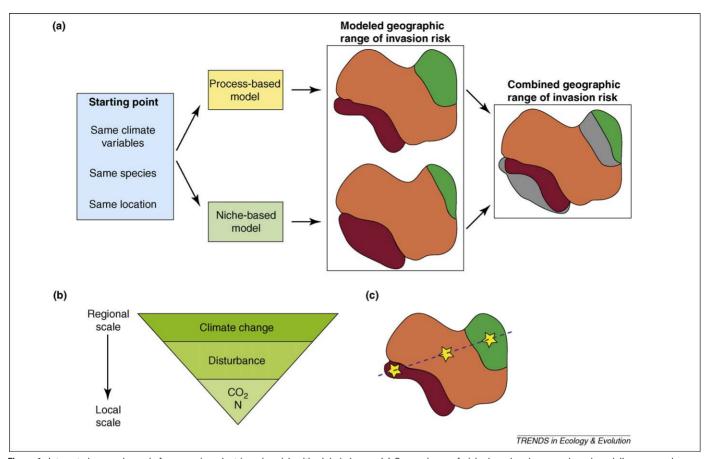


Figure 1. Integrated research needs for assessing plant invasion risk with global change. (a) Comparisons of niche-based and process-based modeling approaches are needed based on the same species, location and climate change conditions [47]. The figures represent the geographic range of invasion risk with global change forecast by the two types of models. Orange areas indicate maintained risk, red areas indicate expanded risk and green areas indicate reduced risk. When the two models are combined, areas where projections overlap (red increased risk, orange maintained risk, green reduced risk) have high confidence, whereas areas with inconsistent projections (grey areas) have lower confidence [46]. (b) Climate change projections provide a regional view of risk that must be refined for specific areas based on changes in land use or land cover at landscape scales and local effects of increasing CO_2 and N [23]. (c) Model results, whether individual or ensemble should be treated as hypotheses about how a given change in climate would affect invasion risk in a given location. Models can be used to plan observational transects (blue dashed line) and experiments (yellow stars) across a range of projected changes in invasion risk.

grasslands relative to natives [21], whereas increased winter precipitation enhanced invasive plant density and biomass in a North American mixed-grass prairie [54]. These findings indicate that changing temperature and precipitation could help or hinder invasive plants depending on the species, location, magnitude and seasonality of change.

Changes in precipitation during specific seasons appear to be a particularly important predictor of plant invasion. For example, in a North American mixed-grass prairie, higher winter precipitation greatly increased invasion, but higher summer precipitation had only minor effects [54]. In a California grassland, spring watering facilitated invasion, but winter watering did not [19]. In the Great Basin desert, fall and spring watering facilitated invasion, but winter watering did not [52]. Observations in South Africa indicate that increased rainfall enables tree invasion, but only during warm summer months [9]. The importance of seasonal changes in precipitation on invasion risk is also supported by model results [28].

Climate change is likely to shift the magnitude and duration of extreme events such as heat waves, droughts and hurricanes [22]. In New Zealand, heat waves promoted invasion of fast-growing C4 annuals [56]. In South Africa, large rainfall events increased germination and growth of invasive trees in arid savannah [9]. Research on the impacts of extreme climate events on invasive plants is rare, but, given that extreme events are likely to have large impacts on ecosystems [57], additional work on this topic is needed.

Although modeling and experimental approaches assessing the impacts of climate change on invasive plants have come to similar conclusions, only one study to date has attempted to integrate modeling and experimental approaches [50]. The authors experimentally tested the predictions of an envelope model with respect to the invasive plant *Triadica sebifera* and found that an index of climatic suitability derived from the model was indeed a good predictor of germination rates [50]. Extending this approach to other species, along with other integrated assessments, could vastly improve our confidence in ecological forecasting and provide more robust projections for management. In Figure 1, we outline a framework for such an integrated assessment.

Global increases in plant resources

Resource availability has been positively linked to ecosystem invasibility [14,15,58], suggesting that global changes

that increase resource availability will facilitate invasion. In the following sections, we discuss recent experimental results testing the impacts of rising atmospheric CO_2 and N deposition on plant invasion.

Rising CO₂

Rising atmospheric CO_2 has a direct 'fertilization' effect on plants, increasing resource availability in a relatively uniform manner across terrestrial ecosystems, and this is expected to favor invasive plants [14–18]. Although previous studies have reasoned that rising CO_2 levels could help or hinder invasive plants [12], recent studies have shown advantages for invasive plants for a range of species and growth habits, including annual grasses invading perennial shrublands [59,60], perennial shrubs invading forests [61,62], annual forbs invading annual grasslands [63], invasive perennial vines compared to native perennial vines [64] and invasive perennials outcompeting native annuals along an urban to rural CO_2 transect [65].

However, it is worth noting that only one study to date has measured the impact of rising CO_2 coupled with rising temperature [21]. In this study, which assessed growth and reproduction responses of invasive perennial herbs in Tasmania, experimental warming negated any positive impacts on invasive plants observed with rising CO_2 alone [21]. This finding suggests that the influence of CO_2 on invasion might depend on its interactions with other global changes.

N deposition

Human activities, particularly the use of hydrocarbonbased fuels and fertilizers, are dramatically increasing the supply of available N [66]. As with elevated CO_2 , N deposition directly increases plant resource availability. In many ecosystems, N is the primary limiting resource for plant growth [67]. Furthermore, N availability varies significantly in space and time, leading to a wide range of adaptations to N. Consequently, increasing N deposition can dramatically alter plant communities, for example by reducing plant diversity and causing extinctions of rare species [58].

It has been hypothesized that N deposition in N-limited areas will facilitate invasion because native species lose the competitive advantages they have in low-N environments, and because invasive plants are often more competitive with higher N. N deposition has been shown to increase invasive plant biomass and competitive ability relative to natives in ecosystems as varied as deserts [68], grasslands [54,69], and tidal marshes [70], although in other studies of invasive plant competition it has been shown to have no effect [e.g. 71,72]. To our knowledge, no studies have documented decreased competitiveness of invasive plants with N deposition. Given the large number of studies on N and invasion, meta-analyses could greatly improve our ability to predict when and where N could enhance plant invasion.

As with elevated CO_2 , the relative advantage that N provides to invasive plants could be strongly mediated by other forms of global change. For example N deposition increased biomass of the invasive forb *Linaria dalmatica* only in combination with increased winter precipitation [54]. Conversely, the relative growth rate of the invasive

forb *Hesperis matronalis* was increased by N deposition only in the absence of increased precipitation [73]. Another study found that N deposition combined with disturbance increased the area covered by invasive plants [74]. Although few studies have looked at interacting effects of global change on plant invasions, these examples for N deposition indicate that interactions could affect the impact of any single global change factor. This further complicates attempts to generalize invasive plant responses to global change.

Increasing plant introductions and disturbance

People facilitate the spread of invasive plants by altering ecosystems (landscape disturbance) and by transporting species to new locations [9,10,12]. In the following sections we discuss results pertaining to the influence of land cover change and increasing commerce on plant invasion.

Changes in land use or land cover

In the coming century, continued changes in land use or land cover are likely to affect ecosystems as profoundly as climate and resource changes [75,76]. For example, deforestation could cause an additional 30% reduction in the world's remaining forests by 2100 [77]. Roads, settlements and energy infrastructure at the wildland-urban interface doubled between 1970–2000 and are expected to continue to rise in coming decades [78]. These novel disturbances harm native species and provide opportunities for invaders to prosper [79]; they also form "corridor pathways" that act as invasion conduits into both fragmented [80] and undisturbed landscapes [81].

For many invasive plants, physical disturbance creates a rapid, large-scale increase in resource availability. For example, deforestation can increase light intensity by an order of magnitude, while simultaneously increasing below-ground resource availability, all within a short time period [74,82]. Recent studies have found strong positive relationships between invasive plant presence and disturbances such as roads [83–85], deforestation and forest canopy mortality [86,87], urban areas [65,88], energy development [85], grazing [9] and agriculture [85,89]. The novelty, magnitude and rate of these disturbances make it difficult for native plants to adjust and to resist invasion.

Given its dramatic effects on invasion, changes in land use or land cover could have a greater impact on invasion than other types of anthropogenic change. For example, recent shifts in invasive plant distribution in the UK have been linked to land-use rather than climate change, even though species invading the UK appear to be well suited to take advantage of recent warming [75].

However, in terms of the impacts of invasion on biological diversity, other global changes could be equally as important as disturbance. Although changes in land use or land cover increase invasion, they also directly decrease biological diversity, and therefore limit the potential for diversity loss associated with enhanced plant invasion *per se*. In contrast, altered CO₂, precipitation, temperature and N deposition affect invasion in both disturbed and undisturbed lands. Enhanced plant invasion caused by these global changes could diminish biodiversity in otherwise undisturbed areas.

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Locations where disturbance drives invasion might be the most successful candidates for restoration because, in the absence of substantial changes to the abiotic environment, reestablishment of native species might be sufficient to increase resistance to invasive plants [90]. In contrast, other global changes might facilitate invasion through changes in the abiotic environment that are difficult or impossible to reverse. Considering the costs associated with control and restoration once invasive plants are established, minimizing new disturbances, such as roads, might be the cheapest, most effective method of controlling invasion.

Global commerce

Global commerce increases invasion risk as plants or plant parts are brought in accidentally (e.g. seed contaminants) or intentionally (e.g. plant trade) [8]. Climate change could push the horticulture industry to import additional novel species as gardeners find that plants they have traditionally used no longer thrive in their gardens. Recent decades have seen a pronounced northward shift in the U.S. Department of Agriculture's Plant Hardiness Zones, which delineate the species capable of growing in different regions of the country (http://www.nwf.org/gardenersguide/ gardenzone.cfm). Thus, global commerce in conjunction with climate change seems likely to further alter invasion pathways by opening new trade routes [10] and by causing importers to seek out new species. More imports will almost certainly result in more invasions, given that a high proportion of today's invasive species originated as horticultural escapes [81]. A "polluter pays" policy, whereby plant importers bear the cost of controlling escaped species that become pests, could reduce future invasions by making importers more cautious about the species they sell; however, such a policy would require meticulous record-keeping and prompt detection of escapes, neither of which has proven easy.

Conclusions

Studies investigating the link between plant invasions and rising CO₂, increased global commerce and changes in land use or land cover show that global change might increase the risk of plant invasion (Table 1). Evidence also suggests that N deposition will generally favor invasive plants (Table 1). Locations where these global change forces dominate, such as urban areas [65], are likely to see substantial rises in invasive plant abundance. However, the situation is far less certain with respect to rising temperatures and changes in precipitation. Some studies point to advantages for plant invaders, whereas others show no effect or even disadvantages. In addition, there is clear evidence of interacting effects between different components of global change, such as warming and CO₂ rise [21], and precipitation and N deposition [54]. Uncertainty as to how changing climatic variables (precipitation and temperature) and interactions among global change factors will influence plant invasions appears to be due to the large range of responses and a lack of relevant studies. Future research has the potential to reveal both general patterns and rules specific to regions, ecosystems or types of invasive species (Box 2).

Even if future research uncovers additional commonalities, variation in both invasive plant species and the dominant forces of global change will make it difficult to apply general findings to specific species in specific locations. This level of variability necessitates speciesspecific assessments of invasion risk that factor in multiple components of global change and integrate across multiple forecasting methods. Modeling studies that present clear, testable hypotheses and experimental studies that directly test or build upon such hypotheses (Figure 1 and Box 2) would substantially increase confidence in projections, thereby making risk assessments and restoration targets more useful to management. Unfortunately, integrated assessments are challenging to organize and fund due to their broad scope and interdisciplinary nature. Thus, scientists are likely to be forced to continue to take a piecemeal approach to producing management-relevant results.

Opportunities created by the retreat of invasive plants due to climate change could greatly increase the scope and scale of restoration efforts. In many cases, native plants will be unable to reoccupy the sites once the invasive species have retreated, necessitating 'transformative' restoration, or the introduction of novel species where invasive populations decline [91]. This adds greater urgency to the ongoing debate over how and whether managers should engage in assisted migration [92,93]. The introduction of

Box 2. Critical research needs to improve forecasting of invasion risk

Several areas of research related to invasive plants and global change are currently under-represented in the literature. The most pressing research needs include:

Test invasive plant responses to new variables

Studies to date tend to focus on responses to single global change variables and neglect extreme events.

Researchers need to:

- Assess responses of invasive plants to multiple simultaneous changes (e.g. climate change coupled with disturbance)
- · Test the effects of extreme climate events on invasion risk

Integrate forecasting methodologies

The combination of multiple forecasting approaches would increase confidence in risk assessments.

Researchers in the modeling community need to:

- Use sensitivity analyses to generate hypotheses about global change impacts that can later be tested experimentally (Figure 1)
- Use model ensembles (multiple envelope models, multiple climate change models/scenarios, multiple process-based models) to increase confidence [46,47]

Researchers in the experimental and observational communities need to:

- Use models as hypotheses to plan experiments and observations, both in terms of locations and global change variables to be tested
- Perform meta-analyses of previously observed responses to seasonal climate conditions and factors of global change for particular invasive species and/or genera (e.g. [9,76])

Researchers in all communities need to:

 Compare existing projections for individual species based on different methodologies to improve projections [47,50]

Box 3. Critical management needs for combating plant invasions in an era of global change

Despite uncertainty about future invasion risk at the local level, there are many proactive steps that the management and science communities can take to diminish impending threats from invasive plants.

Prepare for change

Research shows that shifts in invasive plant distribution and abundance are very probable with global change. Managers need to:

- Use invasion risk assessments to identify areas where invasion is most likely to occur due to global change. Restrict land uses that facilitate the spread of invasive species, and increase surveillance for early invaders.
- Prepare for possible restoration opportunities in areas where climate change is likely to cause invasive plants to retreat [13].
 "Transformative" restoration, or the introduction of novel species assemblages, should be evaluated and tested if necessary [91,92].

Standardize information networks on invasive plants

Lack of access to information on distributions, successful treatment strategies, and factors that increase invasion risks for particular species can thwart appropriate management. Managers need to:

- Share information across global information networks (e.g. the recently launched Global Invasive Species Information Network www.gisinetwork.org) to facilitate control efforts [39,40].
- Record invasive plant distribution and management information in geographic information systems (GIS) to improve data sharing and assessment.

Expand outreach efforts

The public by and large does not appreciate the scope of the invasive plant problem, nor its impacts on ecosystems and the economy. As a community we need to:

- Increase efforts to translate the combined risks from climate change and plant invasion to the public through real-world examples
- Outreach targeting the horticulture and landscape industries in particular could reduce future introductions of species that become invasive

Increase resources to combat invasive plants

In many nations, laws and programs exist to prevent and control invasive plants, but low funding levels and insufficient staff make them unenforceable or ineffective. Institutions need to:

- Hire additional personnel to control existing invasions and to create management plans for future plant invasions
- Target pathways of invasive plant introduction through stricter enforcement of import laws

novel species assemblages might prove necessary to prevent re-invasion by new invasive plants [91].

Owing to the uncertainty associated with speciesspecific assessments, as well as chronically low levels of funding, management would be well served by targeting pathways of introduction and improved detection strategies (Box 3) in addition to studies of specific species [94]. Reducing mechanisms that promote invasion, such as poorly-regulated imports and changes in land use or land cover, might be as productive, and perhaps more cost effective, than focusing on particular species of invasive plants. Further, there are likely to be substantial ecological and economic gains associated with improved prevention and control [2,95].

In many cases, the problem is not one of putting the appropriate programs and policies into place, but rather of adequately funding programs and policies that already exist, along with improving coordination among agencies, institutions and stakeholders. Neglect of invasive plants in the face of global change will probably mean additional environmental damage, economic losses and missed opportunities for remediation.

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References

- 1 Richardson, D.M. et al. (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93-107
- 2 Mack, R.N. et al. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10, 689–710
- 3 Wilcove, D.S. $et\,al.$ (1998) Quantifying threats to imperiled species in the United States. Bioscience 48, 607–615
- 4 Dukes, J.S. (2000) Will the increasing atmospheric CO2 concentration affect the success of invasive species? In *Invasive Species in a Changing World* (Mooney, H.A. and Hobbs, R.J., eds), pp. 95–113, Island Press
- 5 Vila, M. et al. (2007) Linking plant invasions to global environmental change. In *Terrestrial Ecosystems in a Changing World* (Canadell, J. et al., eds), pp. 93–102, Springer-Verlag
- 6 Thuiller, W. et al. (2007) Will climate change promote alien plant invasions? In *Ecological Studies* (Vol. 193) (Nentwig, W., ed.), pp. 197–211, Springer-Verlag
- 7 Mooney, H.A. and Hobbs, R.J. (2000) Invasive Species in a Changing World, Island Press
- 8 Lodge, D.M. et al. (2006) Biological invasions: recommendations for US policy and management. Ecol. Appl. 16, 2035–2054
- 9 Richardson, D.M. et al. (2000) Invasive alien organisms and global change: a South African perspective. In *Invasive Species in a Changing World* (Mooney, H.A. and Hobbs, R.J., eds), pp. 303–349, Island Press
- 10 Hellmann, J.J. et al. (2008) Five potential consequences of climate change for invasive species. Conserv. Biol. 22, 534–543
- 11 Walther, G-R. et al. (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. 24, 686–693
- 12 Dukes, J.S. and Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends Ecol. Evol.* 14, 135–139
- 13 Bradley, B.A. et al. (2009) Climate change and plant invasion: restoration opportunities ahead? Glob. Change Biol. 15, 1511–1521
- 14 Davis, M.A. et al. (2000) Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88, 528–534
- 15 Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu. Rev. Ecol. Evol. Syst. 34, 183–211
- 16 Pysek, P. and Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? In *Biological Invasion, Ecological Studies* (Nentwig, W., ed.), pp. 97–126, Springer-Verlag
- 17 Blumenthal, D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecol. Lett.* 9, 887–895
- 18 Blumenthal, D. et al. (2009) Synergy between pathogen release and resource availability in plant invasion. Proc. Natl. Acad. Sci. U. S. A. 106, 7899–7904
- 19 Thomsen, M.A. et al. (2006) Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. Ecol. Lett. 9, 160–170
- 20 Kriticos, D.J. *et al.* (2003) Climate change and the potential distribution of an invasive alien plant: Acacia nilotica ssp indica in Australia. *J. Appl. Ecol.* 40, 111–124
- 21 Williams, A.L. et al. (2007) Warming and free-air CO2 enrichment alter demographics in four co-occurring grassland species. New Phytol. 176, 365–374
- 22 IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press

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- 23 Guisan, A. and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993-1009
- 24 Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186
- 25 Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. Basic Appl. Ecol. 8, 387-397
- 26 Thuiller, W. et al. (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspect. Plant Ecol. Evol. Syst. 9, 137–152
- 27 Jeschke, J.M. and Strayer, D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. In *Year* in Ecology and Conservation Biology (Ostfield, R.S. and Schlesinger, W.H., eds), pp. 1–24, Blackwell Publishing
- 28 Bradley, B.A. (2009) Regional analysis of impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Glob. Change Biol.* 15, 196–208
- 29 Broennimann, O. and Guisan, A. (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biol. Lett.* 4, 585–589
- 30 McDonald, A. et al. (2009) Climate change and the geography of weed damage: analysis of US maize systems suggests the potential for significant range transformations. Agric. Ecosyst. Environ. 130, 131–140
- 31 Ibanez, I. et al. (2009) Multivariate forecasts of potential distributions of invasive plant species. Ecol. Appl. 19, 359–375
- 32 Beaumont, L.J. et al. (2009) Modelling the impact of Hieracium spp. on protected areas in Australia under future climates. Ecography 32, 757-764
- 33 Parker-Allie, F. et al. (2009) Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective. Clim. Change 94, 87–103
- 34 Jarnevich, C.S. and Stohlgren, T.J. (2009) Near term climate projections for invasive species distributions. *Biol. Invasions* 11, 1373–1379
- 35 Watt, M.S. et al. (2009) The current and future potential distribution of Melaleuca quinquenervia. Weed Res. 49, 381–390
- 36 Bradley, B.A. et al. (In Press) Climate change increases risk of plant invasion in the Eastern United States. Biol. Invasions DOI:10.1007/ s10530-009-9597-y
- 37 Beaumont, L.J. *et al.* (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers. Distrib.* 15, 409–420
- 38 Mitchell, C.E. et al. (2006) Biotic interactions and plant invasions. Ecol. Lett. 9, 726–740
- 39 Ricciardi, A. et al. (2000) Toward a global information system for invasive species. Bioscience 50, 239-244
- 40 Simpson, A. *et al.* (2009) Invasive species information networks: collaboration at multiple scales for prevention, early detection, and rapid response to invasive alien species. *Biodiversity* 10, 5–13
- 41 Jeltsch, F. et al. (2008) The state of plant population modelling in light of environmental change. Perspect. Plant Ecol. Evol. Syst. 9, 171–189
- 42 Jongejans, E. et al. (2008) Dispersal, demography and spatial population models for conservation and control management. Perspect. Plant Ecol. Evol. Syst. 9, 153–170
- 43 Bond, W.J. and Richardson, D.M. (1990) What can we learn from extinctions and invasion about the effects of climate change? S. Afr. J. Sci. 86, 429–433
- 44 Bradford, J.B. and Lauenroth, W.K. (2006) Controls over invasion of Bromus tectorum: the importance of climate, soil, disturbance and seed availability. J. Veg. Sci. 17, 693–704
- 45 Higgins, S.I. and Richardson, D.M. (1998) Pine invasions in the southern hemisphere: modeling interactions between organism, environment and disturbance. *Plant Ecol.* 135, 79–93
- 46 Araujo, M.B. and New, M. (2007) Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47
- 47 Morin, X. and Thuiller, W. (2009) Comparing niche- and processbased models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90, 1301–1313
- 48 Thomsen, M.A. and D'Antonio, C.M. (2007) Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability, and environmental gradients. *Oikos* 116, 17–30
- 49 Ross, L.C. et al. (2008) Disentangling the roles of climate, propagule pressure and land use on the current and potential elevational

distribution of the invasive weed Oxalis pes-caprae L. on Crete. Perspect. Plant Ecol. Evol. Syst. 10, 251-258

- 50 Pattison, R.R. and Mack, R.N. (2008) Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. *Glob. Change Biol.* 14, 813–826
- 51 Har-Edom, O. and Sternberg, M. (In Press) Invasive species and climate change: *Conyza canadensis* (L.) Cronquist as a tool for assessing the invasibility of natural plant communities along an aridity gradient *Biol. Invasions* DOI:10.1007/s10530-009-9640-z
- 52 Miller, M.E. et al. (2006) Performance of Bromus tectorum L. in relation to soil properties, water additions, and chemical amendments in calcareous soils of southeastern Utah, USA. Plant Soil 288, 1–18
- 53 Maron, J.L. and Marler, M. (2008) Field-based competitive impacts between invaders and natives at varying resource supply. J. Ecol. 96, 1187–1197
- 54 Blumenthal, D. et al. (2008) Increased snow facilitates plant invasion in mixedgrass prairie. New Phytol. 179, 440–448
- 55 Bijoor, N.S. *et al.* (2008) Effects of temperature and fertilization on nitrogen cycling and community composition of an urban lawn. *Glob. Change Biol.* 14, 2119–2131
- 56 White, T.A. et al. (2001) Impacts of extreme climatic events on competition during grassland invasions. Glob. Change Biol. 7, 1-13
- 57 Jentsch, A. and Beierkuhnlein, C. (2008) Research frontiers in climate change: effects of extreme meteorological events on ecosystems. C. R. Geosci. 340, 621–628
- 58 Scherer-Lorenzen, M. et al. (2007) Nitrogen enrichment and plant invasions: the importance of nitrogen-fixing plants and anthropogenic eutrophication. In *Biological Invasions* (Nentwig, W., ed.), pp. 163– 180, Springer
- 59 Nagel, J.M. et al. (2004) Co-2 enrichment reduces the energetic cost of biomass construction in an invasive desert grass. Ecology 85, 100–106
- 60 Smith, S.D. et al. (2000) Elevated CO2 increases productivity and invasive species success in an arid ecosystem. Nature 408, 79-82
- 61 Belote, R.T. et al. (2004) Response of an understory plant community to elevated [CO2] depends on differential responses of dominant invasive species and is mediated by soil water availability. New Phytol. 161, 827–835
- 62 Hattenschwiler, S. and Korner, C. (2003) Does elevated CO2 facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? *Funct. Ecol.* 17, 778–785
- 63 Dukes, J.S. (2002) Comparison of the effect of elevated CO2 on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. *Plant Ecol.* 160, 225–234
- 64 Song, L.Y. et al. (2009) Different responses of invasive and native species to elevated CO2 concentration. Acta Oecol. 35, 128–135
- 65 George, K. et al. (2009) Macroclimate associated with urbanization increases the rate of secondary succession from fallow soil. Oecologia (Berl.) 159, 637–647
- 66 Vitousek, P.M. et al. (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol. Appl. 7, 737–750
- 67 LeBauer, D.S. and Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89, 371–379
- 68 Brooks, M.L. (2003) Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. J. Appl. Ecol. 40, 344–353
- 69 Wedin, D.A. and Tilman, D. (1996) Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274, 1720–1723
- 70 Tyler, A.C. et al. (2007) Nitrogen inputs promote the spread of an invasive marsh grass. Ecol. Appl. 17, 1886–1898
- 71 Thomsen, M.A. et al. (2006) The effect of soil nitrogen on competition between native and exotic perennial grasses from northern coastal California. Plant Ecol. 186, 23–35
- 72 Seastedt, T.R. and Suding, K.N. (2007) Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. *Oecologia* 151, 626–636
- 73 Hwang, B.C. and Lauenroth, W.K. (2008) Effect of nitrogen, water and neighbor density on the growth of *Hesperis matronalis* and two native perennials. *Biol. Invasions* 10, 771–779

- 74 Burke, M.J.W. and Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology* 77, 776–790
- 75 Hulme, P.E. (2009) Relative roles of life-form, land use and climate in recent dynamics of alien plant distributions in the British Isles. Weed Res. 49, 19–28
- 76 Richardson, D.M. (2006) Pinus: a model group for unlocking the secrets of alien plant invasions? *Preslia* 78, 375–388
- 77 Nakicenovic, N. and Swart, R. (2000) Special Report on Emissions Scenarios, Cambridge University Press
- 78 Theobald, D.M. and Romme, W.H. (2007) Expansion of the US wildland-urban interface. Landsc. Urban Plann. 83, 340-354
- 79 Hobbs, R.J. and Huenneke, L.F. (1992) Disturbance, diversity, and invasion - implications for conservation. *Conserv. Biol.* 6, 324–337
- 80 With, K.A. (2002) The landscape ecology of invasive spread. Conserv. Biol. 16, 1192–1203
- 81 Hulme, P.E. et al. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J. Appl. Ecol. 45, 403–414
- 82 Canham, C.D. et al. (1994) Causes and consequences of resource heterogeneity in forests - interspecific variation in light transmission by canopy trees. Can. J. For. Res. 24, 337–349
- 83 Gelbard, J.L. and Belnap, J. (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conserv. Biol.* 17, 420-432
- 84 Larson, D.L. (2003) Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie. *Plant Ecol.* 169, 317–333
- 85 Bradley, B.A. and Mustard, J.F. (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecol. Appl.* 16, 1132–1147
- 86 Eschtruth, A.K. and Battles, J.J. (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecol. Monogr.* 79, 265–280
- 87 Schneider, L.C. (2004) Bracken fern invasion in southern Yucatan: a case for land-change science. *Geogr. Rev.* 94, 229–241

- 88 Domenech, R. et al. (2005) Historical land-use legacy and Cortaderia selloana invasion in the Mediterranean region. Glob. Change Biol. 11, 1054–1064
- 89 Elmore, A.J. et al. (2003) Regional patterns of plant community response to changes in water: Owens Valley, California. Ecol. Appl. 13, 443–460
- 90 Prober, S.M. and Lunt, I.D. (2009) Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. *Biol. Invasions* 11, 171–181
- 91 Bradley, B.A. and Wilcove, D.S. (2009) When invasive plants disappear: transformative restoration possibilities in the western United States resulting from climate change. *Restor. Ecol.* 17, 715–721
- 92 Harris, J.A. et al. (2006) Ecological restoration and global climate change. Restor. Ecol. 14, 170–176
- 93 Ricciardi, A. and Simberloff, D. (2009) Assisted colonization is not a viable conservation strategy. *Trends Ecol. Evol.* 24, 248–253
- 94 Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46, 10-18
- 95 Leung, B. et al. (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc. R. Soc. Lond. B Biol. Sci. 269, 2407–2413
- 96 Welk, E. (2004) Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: purple loosestrife (Lythrum salicaria) in North America. Ecol. Model. 179, 551–567
- 97 Marvin, D.C. et al. (2009) A novel, web-based ecosystem mapping tool using expert opinion. Nat. Areas J. 29, 281–292
- 98 Thuiller, W. et al. (2004) Effects of restricting environmental range of data to project current and future species distributions. Ecography 27, 165–172
- 99 Kearney, M. (2006) Habitat, environment and niche: what are we modeling? Oikos 115, 186–191
- 100 Thuiller, W. et al. (2005) Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. U. S. A. 102, 8245–8250