Five Potential Consequences of Climate Change for Invasive Species

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Abstract: *Scientific and societal unknowns make it difficult to predict how global environmental changes such as climate change and biological invasions will affect ecological systems. In the long term, these changes may have interacting effects and compound the uncertainty associated with each individual driver. Nonetheless, invasive species are likely to respond in ways that should be qualitatively predictable, and some of these responses will be distinct from those of native counterparts. We used the stages of invasion known as the "invasion pathway" to identify 5 nonexclusive consequences of climate change for invasive species: (1) altered transport and introduction mechanisms, (2) establishment of new invasive species, (3) altered impact of existing invasive species, (4) altered distribution of existing invasive species, and (5) altered effectiveness of control strategies. We then used these consequences to identify testable hypotheses about the responses of invasive species to climate change and provide suggestions for invasive-species management plans. The 5 consequences also emphasize the need for enhanced environmental monitoring and expanded coordination among entities involved in invasive-species management.*

Keywords: climate change, invasion pathway, invasive species, invasive-species management

Cinco Consecuencias Potenciales del Cambio Climático para Especies Invasoras

Resumen: *Los enigmas científicos y sociales dificultan la predicción de los efectos de los cambios ambientales globales, como el cambio climático y las invasiones biológicas, sobre los sistemas ecológicos. En el largo plazo, estos cambios pueden tener efectos que interactúen y componer la incertidumbre asociada con cada factor individual. Sin embargo, es probable que las especies invasoras respondan de maneras que serían pronosticables cualitativamente, y algunas de esas respuestas serán distintas a las de sus contrapartes nativas. Utilizamos las etapas de invasión conocidas como la "vía de invasión" para identificar 5 consecuencias no exclusivas del cambio climático sobre especies invasoras: (1) mecanismos de transporte e introducción alterados; (2) establecimiento de especies invasoras nuevas; (3) alteración en el impacto de las especies invasoras existentes; (4) alteración en la distribución de especies invasoras existentes; y (5) alteración en la efectividad de las estrategias de control. Posteriormente utilizamos estas consecuencias para identificar hipótesis comprobables sobre las respuestas de especies invasoras al cambio climático y aportar sugerencias para planes de manejo de especies invasoras. Las 5 consecuencias también enfatizan la necesidad de un monitoreo ambiental mejorado y la expansión de la coordinación entre entidades involucradas en el manejo de especies invasoras.*

Palabras Clave: cambio climático, especies invasoras, manejo de especies invasoras, vía de invasión

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Introduction

Climate change is expected to substantially alter biodiversity, causing changes in phenology, genetic composition, and species ranges, and affecting species interactions and ecosystem processes (Walther et al. 2002; Root et al. 2003). Most treatments of species responses focus on native species for which preservation is the primary concern (e.g., Thomas et al. 2004; Botkin et al. 2007). Other authors consider how climate change might affect pests of economically important crops or species causing human disease, some of which are non-native (e.g., Rosenzweig et al. 2001). Invasive species will also respond to climate change, and their responses will have ecological and economic implications.

For several reasons it is useful to examine climate-change responses of invasive species separately from those of native species. Invasive species typically are successful and abundant, whereas many native species are rare. Many invasive species also have characteristics that differ from non-invasive species. For example, many invasive plants have broad climatic tolerances and large geographic ranges (Rejmanek 1995; Goodwin et al. 1999; Qian & Ricklefs 2006), and these characteristics may affect their responses to climate change. Invasive plant species also often have characteristics that facilitate rapid range shifts, such as low seed mass and short time to maturity (Rejmanek & Richardson 1996). Lastly, invasive species are managed in a fundamentally different way than most native species, and this leads to virtually opposite sets of concerns under climate change (i.e., control vs. conservation).

Although some previous publications suggest that climate change is likely to favor some invasive species (e.g., Dukes & Mooney 1999; Thuiller et al. 2007; Vilà et al. 2007), few authors have identified specific consequences of climate change for invasive species. These potential consequences are important to (1) stimulate discussion about the distinctive (and nondistinctive) consequences of climate change for invasive species, (2) identify key hypotheses that must be tested to develop general theories about invasive species and climate change, and (3) inform adaptive management. We used the stages of invasion known as the "invasion pathway" (Theoharides & Dukes 2007; for variations on the invasion pathway, see, e.g., Williamson & Fitter 1996; Richardson et al. 2000) to identify 5 possible consequences of climate change. Several of the consequences are unique to invasive species because of traits and qualities associated with invasion (consequences 1, 4, and 5). In other cases the qualitative response of native and invasive species may be similar (consequences 2 and 3), but the mechanisms or the outcomes are distinct. Rather than offering a comprehensive review of the invasion literature, we used the existing literature to characterize the potential issues for invasive species and identified key hypotheses that are testable in research and adaptive-management frameworks.

The Interaction of Climate Change and Invasion

Because of its pervasiveness and potential effect on fundamental biological processes, climate change will interact with other existing stressors to affect the distribution, spread, abundance, and impact of invasive species (Gritti et al. 2006). Climate change also will challenge the definition of invasive species because some taxa that were previously invasive may diminish in impact; other, previously noninvasive species, may become invasive; and many native species will shift their geographic distributions, moving into areas where they were previously absent. These are all reasons to specify carefully what is meant by an invasive species. We define invasive species as those taxa that have been introduced recently and exert substantial negative impact on native biota, economic values, or human health (Lodge et al. 2006). Therefore, we do not consider a native species that has expanded its range under climate change to be invasive unless it causes discernable damage.

A key research question is whether or not climate change will be a zero-sum game for invasive species, causing the emergence of new invasive species but also reducing the impact of extant invasive species such that they may no longer be invasive. Anecdotal evidence suggests that climate change is not likely to substantially decrease the impact of current invasive species because many of them already span a range of environmental conditions (e.g., Qian & Ricklefs 2006). Meanwhile, for example, new species with the potential to invade will likely arrive as climate change alters which species are successfully transported. Even if climate change leads to the demise of some invasive species and the rise of others, leaving the richness of invasive species the same, it would be valuable to identify *which* species are likely to change. The framework of consequences and hypotheses delineated here can facilitate such distinctions.

The Invasion Pathway

To identify how invasive species may respond to climate change, we started by examining the crucial stages in the invasion process. A species must pass through a variety of environmental filters to become invasive (e.g., Vermeij 1996; Williamson 2006; Williamson & Fitter 1996; Theoharides & Dukes 2007; Fig. 1, dashed lines), and success at each of these phases depends on a distinct set of mechanisms, some of which are likely to be affected by climate change (Rahel & Olden 2008 [this issue]).

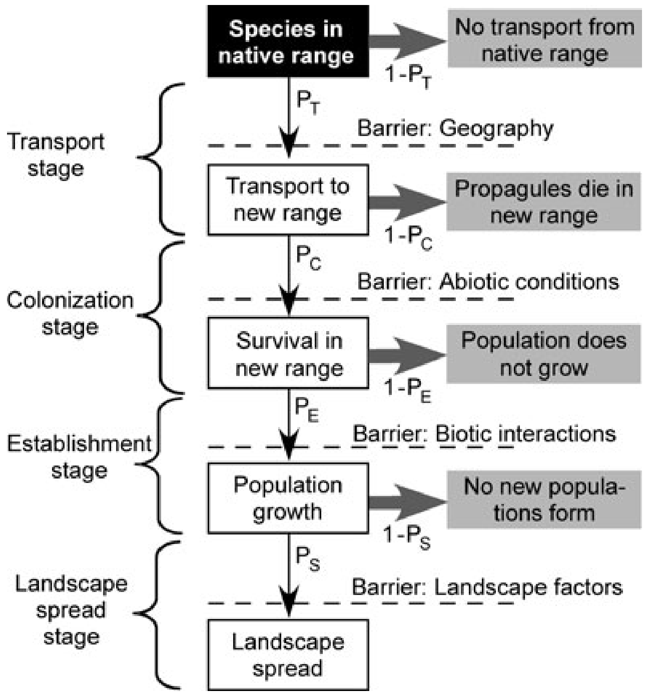

Figure 1. Conceptual model of the process of species invasion. Transition probabilities between 4 distinct stages of invasion are marked P_i. Arrows indicate key transitions that could be affected by climate change.

First, a species must travel across major geographic barriers to its new location. The ability of a species to pass through the transport stage depends on the rate at which propagules are moved from one site to another and their viability upon arrival. Second, a species must survive and tolerate environmental conditions at the arrival site. Third, a species must acquire critical resources, survive interactions with natural enemies, and possibly form mutualistic relationships at the new site. Invasive species that are more successful in establishing and that consequently become more abundant are likely to have larger effects on the local community. Finally, the species must spread, establishing populations in new sites across the landscape. The emergence of populations in new locations depends on establishment success, the connectivity of viable habitat patches, and the mode and pattern of dispersal. The rate at which a species spreads depends on many system- and species-specific factors, and these factors make it difficult to form broad generalizations. Nevertheless, the presence of disturbance corridors across the landscape can be important in terrestrial systems (D'Antonio et al. 2000), and land-use changes, flow-driven disturbance, and water quality may be important in aquatic ecosystems (Kim et al. 2001; Schreiber et al. 2003). Because the overall impact of an invasive species is partly determined by the area it occupies, factors that affect the spread of an invasive species across a landscape can influence its effect (Parker et al. 1999).

Consequences for Invasive Species under Climate Change

On the basis of the invasion pathway (Fig. 1), we specified 5 possible consequences of climate change for invasive species (Fig. 2): (1) altered mechanisms of transport and introduction, (2) altered climatic constraints on invasive, species, (3) altered distribution of existing invasive species, (4) altered impact of existing invasive species,

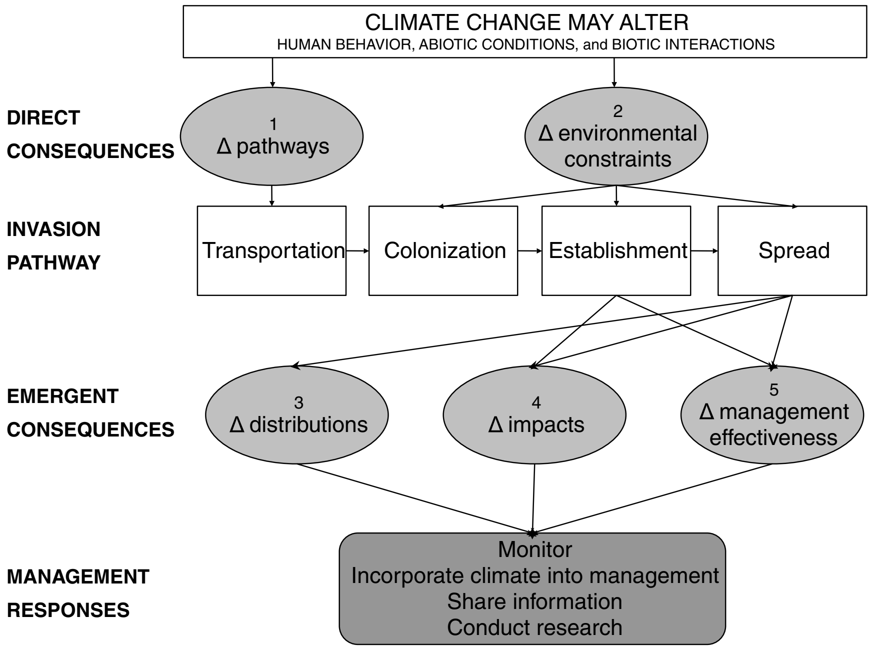

Figure 2. Relationship between the invasion pathway (Fig. 1) and the 5 consequences described for invasive species under climate change. Numbers refer to consequences described in text (∆, change in).

and (5) altered effectiveness of management strategies for invasive species. These consequences are not mutually exclusive because more than one outcome is likely, but they are comprehensive. The consequences focus on climatic change (i.e., temperature and precipitation), but the effects of elevated CO_2 itself also can be incorporated into the 5 groupings. Specific examples for each scenario appear in Table 1, and key hypotheses arising from the consequences that require empirical testing are listed in Table 2.

Altered Mechanisms of Transport and Introduction

Invasive species typically reach new regions via human-aided transport. Species are purposefully introduced for a variety of reasons (e.g., biocontrol, sport fishing, horticulture, agriculture, aquaculture), and accidental introductions occur during the course of other economic activities. Climate change could alter patterns of human transport, changing the propagule pressure of species with the potential to become invasive (Fig. 1; Tables 1 & 2). Propagule pressure could grow because of new or increased transport between a source and target region or because of enhanced survivorship of propagules during transport. In the former, climate change could link geographic areas previously separated; in the latter, climate change could affect biological processes associated with transport events.

Three examples illustrate the potential for new geographic regions to be linked by climate change. First, climate change could alter tourism or commerce. The use of particular geographic regions for recreation may be altered by climate change or climate could alter demand for nursery species on the basis of changing hardiness zones or precipitation levels (Van der Veken et al. 2008). Further research is needed, but the results of several studies suggest that economic choices are sensitive to climate (e.g., Fukushima et al. 2002). Second, pathways of international transport could change. If warming leads to loss of Arctic sea ice, a viable Northwest Passage will substantially cut travel time for some ships. This could affect survival rates of organisms in ballast water and on ships' hulls (Pyke et al. 2008 [this issue]). Third, extreme weather or altered circulation patterns could enhance dispersal of some invasive species to regions that received few propagules previously (e.g., Schneider et al. 2005). Hurricanes sometimes carry birds, marine larvae, and insects considerable distances from their native range (Richardson & Nemeth 1991; Michener et al. 1997; Green & Figuerola 2005), for example, and hurricanes may become more frequent or intense under climate change (IPCC 2007).

For many species the process of transport itself is fatal or reduces the efficacy of arriving propagules. Wonham et al. (2001) show that over 98% of organisms collected in ballast water at the start of vessel voyages are not detected at the end of voyages, and starvation, predation, low light availability, and altered temperature are likely sources of mortality during transport. Climate change may alter these odds.

In other cases humans intentionally help many nonnative species through the transport and colonization phases of invasion. A classic case of purposeful introduction is the sport-fishing industry (Rahel 2000; Ruesink 2005). As new areas become suitable for such fish under climate change, future introductions can be anticipated (Rahel & Olden 2008). Several ecologists and resource managers also suggest intentionally moving species to climatologically favorable areas outside their historical geographic range for conservation purposes (Hulme 2005;

Table 1. Examples of the 5 consequences of climate change for invasive species.

Potential consequences	*Example species**
1. Altered transport of invasive species	monkey goby (*Neogobius fluviatilis*): longer shipping season in Great Lakes could create greater propagule pressure of this potential invader (Kolar & Lodge 2002); Florida torreya (*Torreya taxifolia*): endangered endemic that might be moved northward for conservation (McLachlan et al. 2007); switchgrass (*Panicum virgatum*): prairie species that may be planted for biofuel outside its native range (Tilman et al. 2006)
2. Altered climatic constraints on invasive species	white-cloud mountain minnow (*Tanichthys albonubes*): aquarium-trade fish could invade the Great Lakes region if water temperatures increase (Rixon et al. 2005)
3. Altered distributions of existing invasive species	brook (*Salvelinus fontinalis*) and brown (*Salmo trutta*) trout: impacts are highly temperature dependent (Rahel & Olden 2008)
4. Altered impact of existing invasive species	exotic ascidians (*Styela clava* and *Molgula manhattensis*) (Carlton 2000); red imported fire ant (*Solenopsis invicta*) (Morrison et al. 2005)
5. Altered effectiveness of management strategies	water hyacinth (*Eichhornia* spp.): may overwinter in New England rendering mechanical control ineffective (U.S. EPA 2008); salt cedar leaf beetle (*Diorhabda elongata*): biocontrol agent may tolerate increased temperatures (U.S. EPA 2008)

**These examples focus on temperature change, but changes in precipitation and other climatic factors also will affect invasion.*

Table 2. Key hypotheses associated with the 5 consequences of climate change for invasive species.*

Consequences	*Key hypotheses*
1. Altered mechanisms of transport & introduction	Human transport due to altered commercial and recreational activities will increase the propagule pressure of some non-native species from zero (e.g., connecting new regions) or increase propagule pressure beyond a threshold that allows for establishment. Survivorship of propagules during transport will be enhanced. Longer shipping seasons will increase the number of voyages with non-native propagules. There will be more purposeful introductions for recreation or conservation purposes.
2. Altered climatic constraints on invasive species	Some, currently unsuccessful, non-native species will be able to colonize if conditions become more like the species' native range. Some non-native species will be able to overcome historic biotic constraints and establish persistent populations. Some mutualistic relationships among native species will be weakened, reducing their fitness and competitive ability; as fewer non-native species depend on mutualistic relationships, they will be less affected by this mechanism. Invasive species are more likely than noninvasive species to have traits that favor them in a changing environment; these traits include broad environmental tolerances, short juvenile periods, and long-distance dispersal.
3. Altered distribution of existing invasive species	Cold-temperature constraints on invasive species will be reduced at their higher-latitude or upper-elevation range limits. Warm-temperature constraints on invasive species will increase at their lower-latitude or lower-elevation range limits. Hydrologic constraints on invasive species will be altered by changing precipitation patterns and the frequency (timing & volume) of stream flow. Hydrologic constraints on invasive species will be altered through changes in salinity. Many invasive species are fast-growing and responsive to resources and will be favored by environmental changes that increase resource availability, which will facilitate their spread. Many invasive species have been selected for traits that facilitate long-distance dispersal, but this is less true for native species; shifts in suitable climatic zones will thus tend to favor invasive species. Other environmental changes will interact with climate change to affect range expansion of invasive species; these interactions will be nonlinear.
4. Altered impact of existing invasive species	The population densities of some invasive species and thus their impact on native species will be altered. Per capita or per biomass impacts of some invasive species will be altered through effects on their competitive interactions with native species. Relative impact of some invasive species will increase when the abundance of valued native species or resources decrease in response to the invader.
5. Altered effectiveness of management strategies for invasive species	Mechanical control will become less effective for invasive species that are currently limited by cold, hard freezes, or ice cover. Fate and behavior of pesticides and their effectiveness in controlling invasive species will change. The tolerance of some invasive species to some herbicides will increase (e.g., due to increases in CO_2). Relationships between some biocontrol agents and their targets will decouple. Effectiveness of other biocontrol agents will increase as greater portions of species ranges overlap. Utility of natural disturbance regimes to control invasive species will be altered (e.g., simulated flooding will be more effective in areas with increased precipitation).

**Several of these hypotheses have been posed elsewhere, but few have been tested.*

McLachlan et al. 2007). This "assisted migration" is a drastic measure aimed to address a catastrophic problem, but assisted species could become invasive and negatively affect taxa native to the introduced region. An analysis of historical invasions in North America suggests that the risk of causing new invasions by assisted migration may be relatively small, however (Mueller & Hellmann 2008 [this issue]).

Altered Climatic Constraints on Invasive Species

Climate change can lead to the establishment of new invasive species via 3 mechanisms. First, species currently unable to persist in a location because of climatic constraints may be increasingly able to survive and colonize that area (Fig. 1; Tables 1 & 2). For example, Lee and Chown (2007) show that *Mytilus galloprovincialis*, an invasive mussel species in South Africa, has traveled to Antarctica inside storage chests of a support ship for a scientific expedition. Presumably, this species has not yet taken hold in Antarctica because temperatures are too severe for successful establishment, but warming could increase the probability of establishment. A similar situation exists for plants and animals kept by humans. Some of these species inevitably escape (Mack 2000) but do not establish because of an unsuitable climate.

Second, arriving species that can tolerate the climate may have a greater chance of overcoming biotic constraints on their growth and establish persistent populations under climate change. Because climate change is expected to shift native species out of the conditions to which they are adapted, competitive resistance from native species may lessen (Byers 2002).

Third, established non-native species could become invasive if climate change increases their competitive ability or rate of spread. The "lag phase" in invasions, in which species that establish small seemingly non-invasive populations shortly after arrival and later become aggressively invasive, is well recognized (Crooks & Soulé 1999). Explanations for the phenomenon are diverse and difficult to distinguish (Pyšek & Hulme 2005), but it is likely that strong selection for tolerance of local environmental conditions takes place in these initial populations. Climate change could move small populations closer to, or farther from, environmental conditions to which they are optimally adapted, thus influencing lag times. (For discussion of existing invasive species changing their impact under climate change, see "Altered Impact of Existing Invasive Species.")

Altered Distribution of Existing Invasive Species

For invasive species with established populations, range change results from successful spread into new areas (Fig. 1; Tables 1 & 2). Spread is likely to follow changes in temperature constraints that occur with warming or changes in hydrologic constraints as a result of altered precipitation patterns. For example, Byers and Pringle (2006) show that warmer ocean temperatures increase development times of marine larvae, altering their spread by currents. Other environmental constraints such as soil moisture, wildfire frequency, and salinity of coastal estuaries also may shift under climate change (Burkett & Kusler 2000; Vörösmarty et al. 2000; IPCC 2007).

Warmer conditions are of particular concern in temperate regions because many invasive species have range limits set by extreme cold temperatures or ice cover (Grodowitz et al. 1991; Owens & Madsen 1995; Ayres & Lombardero 2000; Owens et al. 2004). Managers in the northeastern United States are concerned that aquatic invasive species such as hydrilla (*Hydrilla verticillata*) and water hyacinth (*Eichhornia crassipes*) will be able to overwinter if temperatures increase, snowfall is reduced, the frequency of freeze–thaw cycles increase or seasonal ice cover melts earlier in the year (Hayhoe et al. 2007; U.S. EPA 2008). Milder winters would not only increase survival but also create longer growing seasons, potentially increasing reproductive output.

We also expect that, on average, dispersal traits and other mechanisms enabling invasion will allow existing invasives to expand their ranges into newly suitable habitat more quickly than native species. Species that shift ranges quickly could have a competitive advantage if native populations become progressively poorer competitors for resources in a changing climate.

Range changes of several invasive species related to climate already have been described. For example, on the U.S. Pacific coast, 2 species of exotic ascidians (*Styela clava*, *Molgula manhattensis*) have moved substantially northward in the last 20–50 years (Carlton 2000). This trend is similar for other exotic taxa, including Cnidarians, bryozoans, crustaceans, and mollusks (Carlton 2000). The distributions of invasive species are particularly difficult to relate to climate, however, because they may not have had time to spread to their climatic limits.

Altered Impact of Existing Invasive Species

Invasive species are a problem because they affect ecosystem properties, ecosystem processes, and community structure (Perrings et al. 2000; Levine et al. 2003; Lodge et al. 2006). The total impact of an invasive species on a community, ecosystem, or resource can be defined as the product of 3 terms: the size of the range occupied by the invasive species (its spatial extent), its average abundance within that range, and its per capita (or per-unit biomass) impact (Parker et al. 1999). The significance of this impact on a target native species or resource depends on the size of the native population or scarcity of native resources, factors that may be affected by climate change (Fig. 3).

A limited body of literature examines how climate change could alter invasive species impacts via changes in range, abundance, and per capita effect (Tables 1 & 2). We discussed possible effects of climate change on range sizes in sections above on climatic constraints and distribution of existing invasive species. Few researchers have examined whether invasive species will become more abundant with climate change, although there are several reasons to think this may occur (Theoharides & Dukes 2007; Vila et al. 2007). Results of one study show that warmer winter conditions lead to earlier and increased recruitment of non-native tunicates, facilitating their expansion and dominance in New England coastal waters (Stachowicz et al. 2002). In general, climate change may

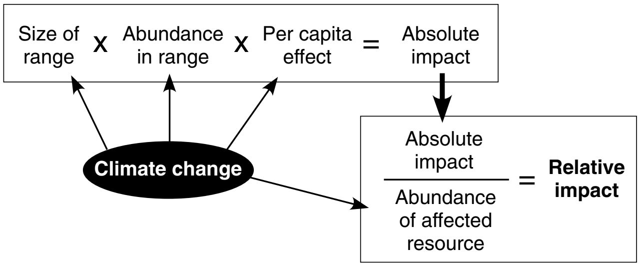

Figure 3. Conceptual diagram of mechanisms through which climate change can affect the ecological and economic impacts of invasive species. The absolute impact describes the actual change in populations, processes, or ecosystem services caused by the invasive species. The relative impact scales the importance of any absolute impact and can be expressed as a unitless proportion. More complex economic models should be used to accurately estimate the value of impacts (e.g., Zavaleta 2000).

put native species at a disadvantage because they will no longer experience the ranges of environmental variables to which they are best adapted (Byers 2002).

Under some conditions, climate change could alter the relative impact of an invasive species. For example, water shortages in the southwestern United States will affect the perceived impact of the invasive species *Tamarix* spp. (Seager et al. 2007). *Tamarix* are thought to use more water than native riparian taxa (Zavaleta 2000), and increasing scarcity of water under climate change could enhance the relative impact of water uptake by this species. Despite evidence that impacts from invasive species will change, however, there are few good predictions of which invasive species will have greater effects under climate change.

Altered Effectiveness of Management Strategies for Invasive Species

A key difference between invasive species and their native counterparts is management—the former require control and some of the latter require preservation. Management strategies therefore differ for invasive versus native species, with invasive species being managed to prevent their establishment and spread (Fig. 1; Tables 1 & 2). Management includes mechanical, chemical, and biological tools and restoration of natural disturbance regimes.

Mechanical control is useful for some species in particular portions of their range (Hulme 2003), but the effectiveness of this technique may change in some locations. For example, the geographic distribution of water hyacinth (*E. crassipes*) and water lettuce (*Pistia stratiotes*) is currently limited by cold, hard freezes, or ice cover (Grodowitz et al. 1991; Owens & Madsen 1995; Owens et al. 2004); in these areas hand pulling is sufficient control. If warmer winter temperatures allow these plants to overwinter, management will need to be more aggressive, sustained, and expensive. Further monitoring is needed at the margin of invasive species' ranges, where thresholds in generation number are likely to occur. Increased survival rates and numbers of generation times will likely necessitate the use of other control methods.

Chemical control is effective for several invasive species, including hydrilla. If climatic change enhances some invasive plants, increased use of herbicides may be required, which may amplify negative effects on nontarget organisms (e.g., sublethal effects of glyphosate on amphibians; Howe et al. 2004; Cauble & Wagner 2005). In general, however, the effect of climate change on the fate and behavior of pesticides is not well understood (Bloomfield et al. 2006). There is also some evidence in terrestrial invasive species that increasing carbon dioxide concentrations may enhance their tolerance to certain herbicides, undermining the effectiveness of chemical treatments (Ziska et al. 1999, 2004).

Climate change also may alter the effectiveness of biocontrol. Successful biocontrol agents are highly specific to the invasive species they are targeted to control, and changes in climatic factors may alter these interspecific interactions (Bryant et al. 2002; Stireman et al. 2005; van Asch & Visser 2007). Taxa currently controlled by a predator or herbivore, therefore, may reemerge as problem species. For example, managers in Colorado are concerned that the saltcedar leaf beetle (*Diorhabda elongata*) will stop being effective at controlling Tamarisk (*Tamarix ramosissima*) if air temperatures increase (U.S. EPA 2008). Conversely, climate change may increase the effectiveness of biocontrol agents in some locations. For example, one of the most effective biological control agents for alligator weed (*Alternanthera philoxeroides*) in the southeastern United States is the alligator weed flea beetle (*Agasicles hygrophila*). Climatic tolerances for the beetle and plant do not match exactly, and the beetle is only effective in the warmer part of the invasive plant's distribution (Julien et al. 1995; Stewart et al. 1999). Warmer temperatures could allow this biocontrol agent to become effective in a larger part of the invasive species' range (Hruska et al. 1985). Unfortunately, these warming trends are likely to also allow alligator weed to spread northward. Future biocontrol attempts must consider climate variables in evaluating long-term effectiveness (Zalucki & van Klinken 2006).

Finally, climate change may alter the utility of restoring natural disturbance regimes as a way to control invasive species. For example, natural resource managers have simulated natural flood regimes through dam releases to increase native biodiversity and control invasive species, but if these areas see a significant decrease in water availability, conflicts between human and environmental uses may reduce the acceptability of this tool (Seager et al. 2007). In contrast, sea-level rise may be an example of how managers can use climate change for their benefit, at least in the short term. Restoration of tidal flows in coastal wetlands is one strategy that may effectively control *Phragmites australis* and purple loosestrife (*Lythrum salicaria*), particularly for wetlands along the U.S. Atlantic coast that were previously dominated by smooth cordgrass (*Spartina alterniflora*) (Chambers et al. 2002; Konisky & Burdick 2004; Vasquez et al. 2006). Managers of invasive species in Connecticut use this restoration technique to control these invasive plants in areas where native vegetation is more salt tolerant (U.S. EPA 2008). Detailed maps of estimated sea-level rise and distributions of *Spartina*-dominated salt marshes would inform where tidal management could be used effectively.

The potential for changes in temperature, precipitation, and sea level to affect invasive-species management will necessitate coordinated responses at large spatial scales, new research, and more extensive monitoring. Regional panels, such as the Northeast Aquatic Nuisance

Species Panel, are attempting to share data on regionally problematic species, success stories, management plans, and eradication efforts (U.S. EPA 2008), activities that can help determine changing management effectiveness and disseminate novel techniques.

Conclusions

The future of management of invasive species will involve new tools developed from research that integrates invasion and climate-change biology (Table 2). Increased monitoring and more interagency and interstate coordination will also be necessary (Bierwagen et al. 2008 [this issue]). Monitoring and coordination similar to the Early Detection and Rapid Response System envisioned by the National Invasive Species Management Plan may be a useful vehicle for new vigilance under climate change (NISC 2001; Westbrooks 2004). Some states, such as Kansas, already communicate with their southern and northern neighbors to determine species distributions and share successful management activities (U.S. EPA 2008). Delaware also is performing surveys to detect changes over time in aquatic invasive species (U.S. EPA 2008), and these activities will need to be more widespread. Finally, risk assessments over a broader geographic area than have traditionally been performed will be essential. It will be considerably easier to prevent the introduction of harmful non-native species than to project their impact in novel and changing environments.

Many problems with invasive species are immediate and severe. Climate change, in contrast, is more subtle and long term, and resource managers have a difficult time knowing when to start addressing it. It will take more research to understand how specific invasive species may behave under an altered climate and which new species will emerge as invasive (Table 2). The 5 consequences described earlier provide a starting point for that research. Unfortunately, the timescale for pursuing that research and using it to inform novel management techniques is short.

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Literature Cited

Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. The Science of the Total Environment **262:**263–286.

Bierwagen, B. G., R. Thomas, and A. Kane. 2008. Capacity of management plans for aquatic invasive species to integrate climate change. Conservation Biology **22:** in press.

Bloomfield, J. P., R. J. Williams, D. C. Gooddy, J. N. Cape, and P. Guha. 2006. Impacts of climate change on the fate and behaviour of pesticides in surface and groundwater—a U.K. perspective. Science of the Total Environment **369:**163–177.

Botkin, D. B., et al. 2007. Forecasting the effects of global warming on biodiversity. BioScience **57:**227–236.

Bryant, S. R., C. D. Thomas, and J. S. Bale. 2002. The influence of thermal ecology on the distribution of three nymphalid butterflies. Journal of Applied Ecology **39:**43–55.

Burkett, V., and J. Kusler. 2000. Climate change: potential impacts and interactions in wetlands of the United States. Journal of the American Water Resources Association **36:**313–320.

Byers, J. E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos **97:**449–458.

Byers, J. E., and J. M. Pringle. 2006. Going against the flow: retention, range limits and invasions in advective environments. Marine Ecology Progress Series **313:**27–41.

Carlton, J. T. 2000. Global change and biological invasions in the oceans. Pages 31–53 in H. A. Mooney and R. J. Hobbs, editors. Invasive species in a changing world. Island Press, Covelo, California.

Cauble, K., and R. S. Wagner. 2005. Sublethal effects of the herbicide glyphosate on amphibian metamorphosis and development. Bulletin of Environmental Contamination and Toxicology **75:**429–435.

Chambers, R. M., D. T. Osgood, and N. Kalapasev. 2002. Hydrologic and chemical control of Phragmites growth in tidal marshes of SW Connecticut, USA. Marine Ecology-Progress Series **239:**83–91.

Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of invasive species: causes and implications. Pages 103–126 in O. T. Sandlund et al., editors. Invasive species and biodiversity management. Kluwer, New York.

D'Antonio, C. M., T. Dudley, and M. Mack. 2000. Disturbance and biological invasions: direct effects and feedbacks. Pages 429–468 in L. R. Walker, editor. Ecosystems of disturbed ground. Elsevier, New York.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology & Evolution **14:**135–139.

Fukushima, T., M. Kureha, N. Ozaki, Y. Fujimori, and H. Harasawa. 2002. Influences of air temperature change on leisure activities—case study on ski activities. Mitigation and Adaptation Strategies for Global Change **7:**173–189.

Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. Conservation Biology **13:**422–426.

Green, A. J., and J. Figuerola. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. Diversity and Distributions **11:**149–156.

Gritti, E. S., B. Smith, and M. T. Sykes. 2006. Vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. Journal of Biogeography **33:**145–157.

Grodowitz, M. J., R. M. Stewart, and A. F. Cofrancesco. 1991. Population-dynamics of water-hyacinth and the biological-control agent neochetina-eichhorniae (*Coleoptera*, *Curculionidae*) at a southeast Texas location. Environmental Entomology **20:**652–660.

Hayhoe, K., et al. 2007. Past and future changes in climate and hydrological indicators in the U.S. Northeast. Climate Dynamics **28:**381–407.

Howe, C. M., M. Berrill, B. D. Pauli, C. C. Helbing, K. Werry, and N. Veldhoen. 2004. Toxicity of glyphosate-based pesticides to four North American frog species. Environmental Toxicology and Chemistry **23:**1928–1938.

Hruska, A. J., S. M. Gladstone, and K. G. Wilson. 1985. Expanded range of the alligatorweed flea beetle (*Agasicles-Hygrophila* Selman and Vogt) in South Carolina. Journal of Aquatic Plant Management **23:**92–93.

Hulme, P. E. 2003. Biological invasions: winning the science battles but losing the conservation war? Oryx **37:**178–193.

Hulme, P. E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology **42:**784–794.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth assessment report of the IPCC. Cambridge University Press, Cambridge, United Kingdom.

Julien, M. H., B. Skarratt, and G. F. Maywald. 1995. Potential geographical-distribution of alligator weed and its biological-control by *Agasicles Hygrophila*. Journal of Aquatic Plant Management **33:**55–60.

Kim, J. G., E. Rejmánková, and H. J. Spanglet. 2001. Implications of a sediment-chemistry study on subalpine marsh conservation in the Lake Tahoe basin, USA. Wetlands **21:**379–394.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science **298:**1233–1236.

Konisky, R. A., and D. M. Burdick. 2004. Effects of stressors on invasive and halophytic plants of New England salt marshes: a framework for predicting response to tidal restoration. Wetlands **24:**434–447.

Lee, J. E., and S. L. Chown. 2007. *Mytilus* on the move: transport of an invasive bivalve to the Antarctic. Marine Ecology Progress Series **339:**307–310.

Levine, J.M., M. Vila, C.M. D'Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London Series B-Biological Sciences **270:**775–781.

Lodge, D. M., et al. 2006. Biological invasions: recommendations for U. S. policy and management. Ecological Applications **16:**2035–2054.

Mack, R. N. 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. Biological Invasions **2:**111–122.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. Assisted migration in an era of climate change. Conservation Biology **21:**297–302.

Michener, W. K., E. R. Blood, K. L. Bildstein, M. M. Brinson, and L. Gardner. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. Ecological Applications **7:**770–801.

Morrison, L. W., M. D. Korzukhin, and S. D. Porter. 2005. Predicted range expansion of the invasive fire ant, *Solenopsis invicta*, in the eastern United States based on the VEMAP global warming scenario. Diversity and Distributions **11:**199–204.

Mueller, J. M., and J. J. Hellmann. 2008. An assessment of invasion risk from assisted migration. Conservation Biology **22:** in press.

National Invasive Species Council (NISC). 2001. Meeting the invasive species challenge: National Invasive Species Management Plan. Pages 1–80. NISC, Washington, D.C..

Owens, C. S., and Madsen J. D. 1995. Low-temperature limits of waterhyacinth. Journal of Aquatic Plant Management **33:**63–68.

Owens, C. S., R. M. Smart, and R. M. Stewart. 2004. Low temperature limits of giant salvinia. Journal of Aquatic Plant Management **42:**91–94.

Parker, I. M., et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1:**3–19.

Perrings, C., M.H. Williamson, and S. Dalmazzone. 2000. The Economics of Biological Invasions. Edward Elgar, Cheltenham, United Kingdom.

Pyke, C. R., R. Thomas, R. D. Porter, J. J. Hellmann, J. S. Dukes, D. M. Lodge, and G. Chavarria. 2008. Current practices and future opportunities for policy on climate change and invasive species. Conservation Biology **22:** in press.

Pyšek, P., and P. E. Hulme. 2005. Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience **12:**302–315.

Qian, H., and R. E. Ricklefs. 2006. The role of exotic species in homogenizing the North American flora. Ecology Letters **9:**1293–1298.

Rahel, F.J. 2000. Homogenization of fish faunas across the United States. Science **288:**854–856.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology **22:** in press.

Rejmánek, M. 1995. What makes a species invasive? Pages 3–13 in P. Pysek, K. Prach, M. Rejmánek, and M. Wade, editors. Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77:**1655–1661.

Richardson, D. M., P. Pysek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6:**93–107.

Richardson, H., and D. J. Nemeth. 1991. Hurricane-borne African locusts (*Schistocerca gregaria*) on the windward islands. GeoJournal **23:**349–357.

Rixon, C. A. M., I. C. Duggan, N. M. N. Bergeron, A. Ricciardi, and H. J. Macisaac. 2005. Invasion risk posed by the aquarium trade and live fish markets in the Laurentian Great Lakes. Biodiversity and Conservation **14:**1365–1381.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on animals and plants. Nature **421:**57–60.

Rosenzweig, C., A. Iglesias, X. B. Yang, P. R. Epstein, and E. Chivian. 2001. Climate change and extreme weather events: implications for food production, plant diseases, and pests. Global Change and Human Health **2:**90–104.

Ruesink, J. L. 2005. Global analysis of factors affecting the outcome of freshwater fish introductions. Conservation Biology **19:**1883–1893.

Schneider, R. W., C. A. Hollier, H. K. Whitam, M. E. Palm, J. M. McKemy, J. R. Hernandez, L. Levy, and R. DeVries-Paterson. 2005. First report of soybean rust caused by *Phakopsora pachyrhizi* in the continental United States. Plant Disease **89:**774.

Schreiber, E.S.G., G.P. Quinn, P.S. Lake. 2003. Distribution of an alien aquatic snail in relation to flow variability, human activities, and water quality. Freshwater Biology **48:**951–961.

Seager, R. M., et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science **316:**1181–1184.

Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the United States of America **99:**15497–15500.

Stewart, C. A., R. B. Chapman, R. M. Emberson, P. Syrett, and C. M. A. Frampton. 1999. The effect of temperature on the development and survival of *Agasicles hygrophila* Selman & Vogt (*Coleoptera: Chrysomelidae*), a biological control agent for alligator weed (*Alternanthera philoxeroides*). New Zealand Journal of Zoology **26:**11–20.

Stireman, J. O., et al. 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proceedings of the National Academy of Sciences of the United States of America **102:**17384–17387.

Theoharides, K. A., and J. S. Dukes. 2007. Plant invasion pattern and process: factors affecting plant invasion at four spatio-temporal stages. New Phytologist **176:**256–273.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature **427:**143–148.

Thuiller, W., D. M. Richardson, and G. F. Midgley. 2007. Will climate change promote alien invasions? Pages 197–211 in W. Nentwig, editor. Biological invasions. Springer-Verlag, Berlin.

Tilman, D., J. Hill, and C. Lehman. 2006. Carbon-negative biofuels from low-input high-diversity grassland biomass. Science **314:**1598–1600.

U.S. EPA (Environmental Protection Agency). 2008. Effects of climate change on aquatic invasive species and implications for management and research. EPA, Office of Research and Development, Washington, D.C.

van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. Annual Review of Entomology **52:**37–55.

Van Der Veken, S., M. Hermy, M. Velland, A. Knapen, and K. Verheyen. 2008. Garden plants get a head start on climate change. Frontiers in Ecology and the Environment **6:**212–216.

Vasquez, E. A., E. P. Glenn, G. R. Guntenspergen, J. J. Brown, and S. G. Nelson. 2006. Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. American Journal of Botany **93:**1784–1790.

Vermeij, G. J. 1996. An agenda for invasion biology. Biological Conservation **78:**3–9.

Vilà, M., J. D. Corbin, J. S. Dukes, J. Pino, and S. D. Smith. 2007. Linking plant invasions to global environmental change. Pages 93–102 in J. Canadell, D. Pataki, and L. Pitelka, editors. Terrestrial ecosystems in a changing world. Springer-Verlag, New York.

Vörösmarty, C. J., P. Green, J. Salisbury, and R. Lammers. 2000. Global water resources: vulnerability from climate change and population growth. Science **289:**284–288.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416:**389–395.

Westbrooks, R. G. 2004. New approaches for early detection and rapid response to invasive plants in the United States. Weed Technology **18:**1468–1471.

Williamson, M. 2006. Explaining and predicting the success of invading species at different stages of invasion. Biological Invasions **8:**1561–1568.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology **77:**1661–1666.

Wonham, M. J., W. C. Walton, G. M. Ruiz, A. M. Frese, and B. S. Galil. 2001. Going to the source: role of the invasion pathway in determining potential invaders. Marine Ecology Progress Series **215:**1–12.

Zalucki, M. P., and R. D. van Klinken. 2006. Predicting population dynamics of weed biological control agents: science or gazing into crystal balls? Australian Journal of Entomology **45:**331–344.

Zavaleta, E. 2000. The economic value of controlling an invasive shrub. Ambio **29:**462–467.

Ziska, L. H., J. R. Teasdale, and J. A. Bunce. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. Weed Science **47:**608–615.

Ziska, L. H., S. Faulkner, and J. Lydon. 2004. Changes in biomass and root:shoot ration of field-grown Canada thistle (*Cirsium arvense*), a noxious, invasive weed, with elevated CO_2: implications for control with glyphosate. Weed Science **52:**584–588.