Does global change increase the success of biological invaders?

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Biological invasions are gaining attention as a major threat to biodiversity and an important element of global change. Recent research indicates that other components of global change, such as increases in nitrogen deposition and atmospheric CO_2 concentration, favor groups of species that share certain physiological or life history traits. New evidence suggests that many invasive species share traits that will allow them to capitalize on the various elements of global change. Increases in the prevalence of some of these biological invaders would alter basic ecosystem properties in ways that feed back to affect many components of global change.

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As humans have broken down barriers to the long-distance dispersal of plants and animals, invasive alien species have increasingly altered the composition and functioning of the earth's ecosystems. Researchers now recognize biological invasions as an important element of global change[1]. Other commonly recognized elements of global change include change in atmospheric composition, greenhouse-gas driven climate change, increasing nitrogen (N) deposition and changing patterns of land use that fragment habitats and alter disturbance regimes. These latter global-change components can affect species distributions and resource dynamics in terrestrial and aquatic ecosystems, and consequently can interact with biological invasions.

Predicting the effects of the many other elements of global change on biological invasions is a daunting and complex task[2]. Ecologists are beginning to understand how species and ecosystems respond to many single aspects of global change, but our understanding of responses to the full complement of these factors is rudimentary. The task also has spatial complexity. Although the ongoing increase in carbon dioxide concentration, [CO_2], is imposing a relatively uniform direct perturbation across all regions of the world, changes in climate, nitrogen deposition and other processes differ in intensity between regions. To predict the effects of these elements of global change on invasions, ecologists must consider a complicated template of perturbations over a mosaic of independently responding invaders and ecosystems. Will some ecosystems become more (or less) susceptible to invasion? Will some alien species that are currently benign become invasive? Will impacts of existing invaders abate or become more severe? Currently, we must base our predictions on studies that have illustrated general principles of invasions and general principles of the various elements of global change. A pattern is beginning to emerge from these predictions: we expect most aspects of global change to favor invasive alien species and thus to exacerbate the impacts of invasions on ecosystems (Table 1, Box 1). These impacts include competitive effects, whereby an invading species reduces resources available to other species, and ecosystem effects, whereby an invader alters fundamental properties of the ecosystem. Either type of effect can threaten native biodiversity, and some ecosystem effects feed back to elements of global change[3] (Box 1).

In considering possible interactions between global change and biological invasions, we have chosen to focus more attention on interactions that have seldom been explored than on those that have been characterized extensively elsewhere (i.e. disturbance[4] and habitat fragmentation[5]). In discussing possible impacts of increasing [CO_2] and nitrogen deposition, we focus exclusively on plants, because we expect responses of most invasive animals to these factors to be indirect (i.e. mediated by plant responses).

Effects of rising atmospheric [CO_2] on biological invasions

Many invasive plants have been shown to respond positively to elevated [CO_2] when grown individually or in monoculture. Examples of these are species that have invaded North America, such as cheatgrass[6] (*Bromus tectorum*), kudzu[7] (*Pueraria lobata*) and Japanese honeysuckle[8] (*Lonicera japonica*, which has also invaded New Zealand and parts of Europe). Plant species respond less predictably to CO_2 enrichment when they are grown in diverse communities. For instance, although growth of individual lamb's quarters (*Chenopodium album*) plants can be stimulated by elevated [CO_2], this C_3 weed did not respond to CO_2 enrichment when grown in a Canadian pasture community, even in disturbed microsites[9]. CO_2 enrichment favors C_3 plants in North American salt marshes[10] and savannas[11] but can sometimes favor C_4 species in other communities[12]. It is thus risky to predict which species will 'win' and 'lose' in high-[CO_2] conditions on the basis of their photosynthetic pathway or their CO_2 response in the absence of other species.

In mixed-species competition, the CO_2 response of groups of species (such as N-fixers and C_4 species) might depend on local resource availability[13], which in turn could be affected by elevated [CO_2]. For example, most plants increase their water-use efficiency if grown in CO_2-enriched environments. If increased [CO_2] decreases the rate at which plants transpire in a given ecosystem, the soils beneath those plants will dry out more slowly. In ecosystems where plant growth is limited by water availability, species that can take advantage of the extra moisture might eventually become more abundant. An increase in late-season soil moisture in elevated-[CO_2]-exposed California grassland microcosms appeared to benefit one of the community's longest-lived annual species, *Hemizonia congesta* ssp. *luzulifolia*[14] (hayfield tarweed). Although *Hemizonia* is native to California (USA), such an increase in water availability might also benefit phenologically similar non-native

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Table 1. Possible general impacts of global change elements on the prevalence of invasive alien species[a]

Element of global change	Prevalence of invaders[b]
Increased atmospheric CO_2 concentration	+/−
Climate change	+
Increased nitrogen deposition	+
Altered disturbance regimes	+
Increased habitat fragmentation	+

[a]Although these predictions are speculative, they are based on observations that are mentioned or cited in the text.
[b]Key: +/−, might increase prevalence of some invaders and reduce prevalence of others; +, expected to increase prevalence of invaders in many affected regions.

species, such as the invasive yellow starthistle (*Centaurea solstitialis*) (J.S. Dukes, unpublished). CO_2-driven changes in ecosystem nutrient dynamics[15] could also affect a system's vulnerability to invasion.

Has the changing atmosphere already precipitated plant invasions? Rising CO_2 levels might have contributed to an increase in the abundance of mesquite (*Prosopis glandulosa*), a native C_3 shrub, in North American C_4 grasslands over the past century, although several studies have strongly implicated other mechanisms for this expansion[16]. The $[CO_2]$ increase might also have played a role in the invasion by cheatgrass of the intermountain West by contributing to an acceleration of fire regimes[6,17]. Elevated CO_2 levels stimulate plant growth and consequently increase fuel loading. Under the right conditions, more rapid fuel loading can increase both the frequency and severity of fires[18]. Although it seems likely that the rise in $[CO_2]$ has already favored some invasive alien plant species, no studies have addressed this question to date.

How will the $[CO_2]$ increase affect the course of future plant invasions? Experimental studies suggest that rising $[CO_2]$ might slow the process of succession in grasslands[19], which would increase the dominance of non-native species in many ecosystems. Few CO_2 studies have investigated the responses of invasive 'problem' species in the context of susceptible communities. From our knowledge of direct CO_2 effects, we might predict that the world's major crops, which are mostly C_3 species, will compete more successfully with the world's worst agricultural weeds, which are mostly C_4 species[20]. Although this prediction might be accurate for crop–weed associations[21], general speculations such as this fail to consider the interplay between direct and indirect $[CO_2]$ effects in more resource-limited natural systems. Complex interactions among these CO_2 effects and factors such as climate change will affect competition among natives and aliens in ways that we cannot yet predict with confidence.

Effects of global climate change on biological invasions

The increase in the proportion of greenhouse gases in the Earth's atmosphere is likely to cause an average global warming of 1−3.5°C over the next century. This warming will vary spatially and is predicted to be most intense in the winter at high northern latitudes[22]. Changes in global temperatures will also bring a change in precipitation regimes, but climate modelers are not yet confident that global circulation models (GCMs) can forecast the magnitude or direction of these changes for any given region of the world. On a local scale, the anticipated changes in climate will directly favor some species over others, and range shifts will consequently occur.

The following four approaches have been used to predict changes in the distribution and dominance of species under climate change:

- Small-scale experiments that study species dynamics under altered precipitation regimes or simulated warming.
- Identification of functional traits that are related to tolerance of different climates.
- Long-term observations of species composition changes and correlation of these changes with interannual or interdecadal climate variation.
- Modeling of species' future ranges based on aspects of their current ranges and predictions of climate change.

Each of these approaches can be instructive in predicting future biological invasions. However, biological invaders generally differ from non-invasive species in some traits that are not considered by these approaches, and that might favor aliens as climates shift.

Effects of changing climates on invasive plant species

Experimental studies have demonstrated that, under some circumstances, a short-term increase in water availability can facilitate the long-term establishment of alien plant species. Milchunas and Lauenroth[23] applied water, N, and water plus N treatments to Colorado shortgrass steppe communities over five years. Sixteen years after treatments were halted, communities that had been supplemented with water had large populations of non-native species, whereas the control communities remained alien-free. Non-native populations appeared to be cycling with time in all three resource-addition treatments, indicating that the initial perturbations had pushed the communities across some threshold to a new state.

Few experimental studies have investigated the responses of different plant species to global warming in an ecosystem context, and none of these has examined the response of biological invaders. However, the studies have shown that, in some (generally cold) ecosystems, shrubs will profit from a hotter climate. Simulated warming favored shrubs (primarily sagebrush, *Artemisia tridentata*) over forbs in Rocky Mountain meadows[24], and shrubs over nonvascular plants in arctic tundra[25].

Traits other than shrubbiness will also affect species dominance in a hotter climate. In areas where they co-occur, C_4 species might profit more from warmer temperatures than C_3 species, because they generally have a higher optimum temperature for photosynthesis. Some C_4 weeds with ranges that are currently restricted by cold temperatures (e.g. itchgrass, *Rottboellia cochinchinensis*, in southern USA sugar cane plantations) could expand and become problem species over larger areas if the limiting temperatures recede[20].

Long-term observational studies suggest that an increase in annual precipitation in arid and semiarid regions of western North America could increase the dominance of invasive alien grasses. In California, grassland communities that grow on patches of serpentine soil are primarily made up of native and endemic species. European annual grasses, such as soft chess (*Bromus hordeaceus*), are normally confined to surrounding, more fertile soil types. However, in years of high annual rainfall, these annual grasses invade the serpentine community[26]. If annual precipitation were to increase under climate change, these grasses might outcompete much of the native vegetation on serpentine soils. Wet years also favor non-native grasses in the transition zone between the Great Basin and Mojave deserts. After wet years in 1987 and 1988, alien grasses made up 97% of the ecosystem's aboveground biomass[27]. Burgess *et al.*[28] suggest that successive years of higher-than-normal warm-season rainfall in Arizona allowed Sonoran desert populations of buffel-grass (*Cenchrus ciliaris*), an introduced perennial, to expand. In these desert environments (and in many others), buildup of non-native grass litter can increase fire frequencies, leading to grass dominance[27,29].

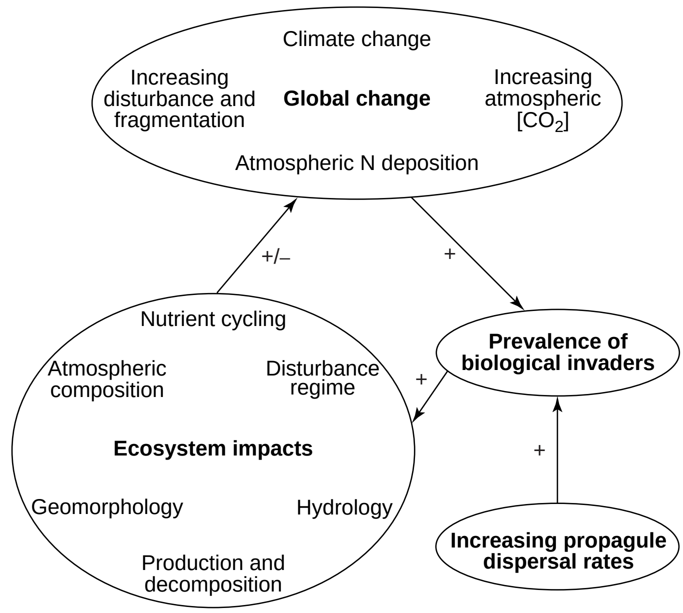
Models predict decreases in the potential ranges of some invasive plant species under future climate scenarios. Beerling *et al.*[30] used a model that correlates present climatic variables with present species distributions to forecast the future distribution of Japanese knotweed (*Fallopia japonica*) in Europe under two climate scenarios that have been predicted to occur after atmospheric [CO_2] doubles. For both climate scenarios, the model predicted that the invader's potential range would shift northward, and that most of central Europe would no longer support its growth. Given a doubled-[CO_2] climate scenario for South Africa, a similar model (that considered both climate and soil suitability) predicted range size decreases for five of that country's major plant invaders[31]. The model predicted that of the five invaders, silky hakea (*Hakea sericea*) will be least affected, and prickly pear (*Opuntia ficus-indica*) most affected, with future habitat areas 92% and 63% as large as the estimated current habitat, respectively. Although such models provide valuable insight into potential species ranges in new, stable climates, they do not take into account several variables that will influence the spread and distribution of a species, such as the dispersal mechanism of the modeled species, interactions with new assemblages of species, and the direct and indirect responses of the species to other aspects of global change.

Although a new climate might not directly favor alien plant species over natives, many invasive plant species share traits that could increase their dominance in a transitioning climate. A rapid anthropogenic climate change might disadvantage species that cannot quickly extend their ranges into newly suitable regions, such as plants with long generation times. A climate-driven decline of late-successional plant species could lead to increased dominance of early successional species, or could leave ill-adapted plant communities that are susceptible to invasion by species that can thrive in the area's new climate. In the latter scenario, species that are able to shift ranges quickly would be at an advantage. Rapid dispersal is a characteristic of many biological invaders. Within the genus *Pinus*, species that are invasive tend to have traits that facilitate rapid range shifting, such as a short juvenile period and low seed mass[32] (which is associated with long-distance wind dispersal). In many areas of the world, alien plant species thrive along roadsides. With the help of vehicles, seeds of these species can quickly disperse over great distances[33] and often arrive in disturbed habitats. Thus, roadside weeds should be some of the earliest species to shift their ranges as climates change.

Other common characteristics of plant invaders could also prove advantageous in a changing climate. For instance, within two families of herbaceous plants, those species whose native ranges cover the most latitudinal distance (and thus tolerate a wide range of climates) tend to be the most successful invaders[34]. These species could profit from their tolerance by increasing their dominance as climate change stresses their neighbors.

Many potentially invasive plant species might also benefit from having stable human-tended populations in areas far from their home ranges. Botanical and ornamental gardens have been the sources for many plant invasions worldwide, when alien species that were preadapted to the climate in the new region escaped[35]. Ornamental aliens that currently depend on the artificial climate of a garden might become invasive if climates shift in their favor. For instance, if arid regions become wetter, some plant species could spread from artificially watered gardens into natural areas. A similar phenomenon can be observed in California chaparral, where ornamental aliens have invaded patches that receive unnatural irrigation[36].

Box 1. Impact of global change on invasions, and feedbacks from invaders to global change



A variety of forces can affect the prevalence of alien species. In this conceptual model, various elements of global change favor alien species, and changes in global commerce increase the rate of arrival of alien propagules. Together, these forces lead to increased numbers and coverage of biological invaders. As alien species become more prevalent, they will alter ecosystem processes and properties, many of which interact with elements of global change. Feedbacks on global change will be positive or negative, depending on the invading species and on the element of global change. Examples of invaders that have important ecosystem-level impacts can be found in Refs 1,3 and 29. Key: N, nitrogen; [CO_2], carbon dioxide concentration.

(Online: Fig. I)

Effects of changing climates on invasive animal species

Observational studies suggest that climate change will affect interactions among native and alien animal species. For example, increased temperatures might benefit the Argentine ant (*Linepithema humile*), a combative invader of the world's mediterranean-climate regions, to the detriment of native ant species. In northern California, most native ant species reduce or cease their foraging during the hottest hours of summer days, but Argentine ants remain active[37]. If increased temperatures decrease the foraging time of native ants without affecting Argentine ant colonies, the ongoing displacement of native ant colonies by Argentine ants could accelerate.

Models have been used to predict future ranges of many animal species, including toads. Sutherst *et al.*[38] used their CLIMEX model to forecast an increase of the potential range of the introduced cane toad (*Bufo marinus*) in a warmer Australia.

Box 2. How will biological invasions be affected by other elements of global change?

- It is not yet clear whether rising concentrations of carbon dioxide, [CO_2], will generally favor non-native plant species over native plant species. Early research suggests that elevated [CO_2] might slow successional recovery of some plant communities, which would increase the dominance of invaders in some ecosystems.
- Although any given climate regime, if stable, is unlikely to affect the relative dominance of native plants and animals versus aliens, a changing climate might advantage the many alien species that can shift ranges quickly and/or tolerate a wide range of environments.
- Increases in nitrogen (N) deposition favor fast-growing plant species. In some regions of the world, such as Europe, plant communities have many native species that are responsive to N, and the impact of invaders might be minimal. However, in other regions (including parts of North America), many of the most responsive plant species are alien grasses. Thus, impacts of N deposition on invasions are likely to vary by region.
- Changes in land-use patterns that increase habitat fragmentation and alter disturbance regimes will increase the prevalence of non-native species.
- Interactions among the elements of global change might affect the prevalence of biological invaders, but remain largely unstudied.

By comparing the current ranges and estimated thermal requirements of 57 fish species with a GCM-derived future climate scenario, Eaton and Scheller[39] came to the conclusion that climate change will decrease habitat for cold, cool and even some warm-water fish species in North America. Some of the few warm-water species that might be able to expand their distributions are native to areas east of the North American Continental Divide, such as largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*) and bluegill (*Lepomis macrochirus*). These species have already attained dominance in many western North American watersheds, where they were introduced for sportfishing. A warmer climate might increase their dominance and, if stocking continues, extend it across more of the West's watersheds.

Models predict that warmer temperatures will decrease the generation time of insects, increase their winter survival, and cause species to shift their ranges poleward and up in elevation[40]. A warmer climate will also accelerate growth of the animal diseases that are carried by insects[41]. With a shortened generation time, livestock diseases and human maladies such as malaria and dengue could invade new territory.

Although models predict that animals will shift their ranges in response to climate change, anthropogenically driven changes in the distribution, phenology or abundance of key plant species could restrict their potential habitat[42]. 'Specialist' species that rely on a particular plant community for food or shelter are more likely to be disadvantaged by this phenomenon than 'generalist' species that can survive in a variety of different plant communities. By nature, invasive animal species are more likely to be generalists than specialists, and thus might (on average) be more successful than natives at adapting to new climates.

Effects of increasing nitrogen deposition on biological invasions

Fossil fuel combustion, the fertilization of agricultural fields and other human activities release nitrogenous compounds into the atmosphere that eventually return to the surface via precipitation and dry deposition. This N continuously fertilizes a large (and growing) portion of the terrestrial biosphere[43]. Increased N deposition onto natural systems disadvantages slow-growing native plants that are adapted to nutrient-poor soils by creating conditions favorable for faster-growing plants, such as grasses. High deposition rates have already transformed the species composition of Dutch heathlands and chalk grasslands[44]. Studies of many natural systems have shown that fertilization can increase the dominance of non-native species[23,45–48].

Although some of these fertilization studies used relatively large ($\geq$10 g m^{-2} year^{-1}) amounts of N in their fertilization treatments, other studies have shown that, where N is a limiting nutrient, even small N additions can advantage alien species. Over 12 years, Wedin and Tilman[46] added a gradient of N to macro- and micronutrient-supplemented plots of Minnesota grassland, and observed a shift in dominance from native C_4 grass species to introduced C_3 species. This shift appeared to occur between fertilization rates of 1 and 5 g N m^{-2} year^{-1}, rates comparable to the deposition currently experienced by many terrestrial ecosystems.

Nitrogen deposition might have already allowed introduced annual grasses to invade some of California's nutrient-poor serpentine grasslands. Although many of these grasslands are still dominated by native species, some in highly polluted areas now require grazing to prevent dominance of alien annual grasses[49].

Natural fertilization processes can also increase the invasibility of some systems. In a study of California coastal prairie, Maron and Connors[48] examined vegetation that regrew in gaps created by the death of yellow bush lupine (*Lupinus arboreas*), a nitrogen-fixing shrub. Soil in these gaps had higher N availability than soil in the surrounding grassland, and tended to support a simple community of weedy aliens, in contrast to the surrounding species-rich assemblage of native grasses and forbs. Invasion of this shrub into coastal areas outside its historical range might have concurrently increased the success of non-native weeds.

Invasions and global change: implications for ecosystems and prospects for future research

Integration of theoretical principles with the results of the few studies that have addressed how biological invaders respond to global change leads to the conclusion that most of the important elements of global change are likely to increase the prevalence of biological invaders (Table 1, Box 2).

Future research should directly test the general predictions presented here. Many critical questions, such as whether climate change will increase the susceptibility of ecosystems to invasion, have yet to be addressed. Other studies should examine the responses of the most devastating invasive species to relevant components of global change. This can be achieved either through extensive observational and experimental study, or by observing the performance of an invasive species in many different geographically isolated locations and correlating its performance with biotic and environmental variables in those areas. These approaches, both of which were employed by Richardson *et al.*[31] for South African invaders, help to describe the performance of a species under many different conditions. In addition to improving predictions of the potential ranges of invaders under global change, such methods can improve predictions of the potential ranges of invaders that are currently spreading[50]. In many cases, it should be possible to design experiments that simultaneously address questions about the impact of global change on specific alien species and general questions about invasion biology.

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