Biological invaders in a greenhouse world: will elevated CO$_2$ fuel plant invasions?

Jake F Weltzin[1], R Travis Belote[1], and Nathan J Sanders[2]

Climate change and biological invasions, two of the hottest topics in ecology, both have ecological and societal implications, but they have developed on separate and parallel paths. Both are likely to have global impacts, yet researchers seldom explicitly consider their interaction. We argue that changes in atmospheric concentrations of carbon dioxide (CO$_2$) and subsequent climate change may facilitate biological invasions, both directly and indirectly, and that our research agenda to date has left us poorly prepared to predict the consequences for communities and ecosystems. Forecasting the impact of biological invaders or elevated CO$_2$ is a challenge for ecologists, and it is therefore prudent and timely to investigate the greater challenge, namely predicting the combined effects of invaders and elevated CO$_2$ on native ecological systems.

In the 1930s, the US Soil Conservation Service grew 85 million kudzu (*Pueraria lobata*) seedlings and encouraged farmers to plant them to control soil erosion. By 1950, kudzu had escaped cultivation and was creeping across the American landscape at about 0.25 m per day. The plant began enshrouding trees and native vegetation across the southeastern United States (Mitich 2000; Figure 1). Seventy years later, the "miracle vine" covers an estimated 1–3 million ha and has been dubbed "the vine that ate the South". Kudzu can be controlled, but the efforts require the strength of Hercules, the wealth of Midas, and the patience of Sisyphus.

Biological invaders such as kudzu threaten global biological diversity, the integrity of natural ecosystems, and the goods and services that ecosystems provide (Mack *et al.* 2000). Specifically, plant invaders have displaced native species, altered disturbance regimes, and changed the rates and patterns of nutrient cycling in terrestrial ecosystems ranging from deserts to tropical forests to wetlands (Vitousek and Walker 1989; D'Antonio and Vitousek 1992; Cronk and Fuller 1995). Because of the worldwide threat to ecosystems, biological invasions are considered

Figure 1. Kudzu covers an abandoned cabin near Dahlonega, GA in one growing season.

Courtesy of Jack Anthony

In a nutshell:
- Considerable research has focused on changes in CO$_2$ concentrations, climate, and biological invasions, but the interactions between these factors have seldom been considered
- Combined changes in CO$_2$ and climate may facilitate invasions by non-native plants, by affecting growth rates, resource availability, and other biological and physical variables
- It is important to be able to forecast the potentially powerful effect this could have on community and ecosystem structure and function worldwide

[1]*Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville, TN 37996 (jweltzin@utk.edu)* [2]*Department of Biological Sciences, Humboldt State University, Arcata, CA*
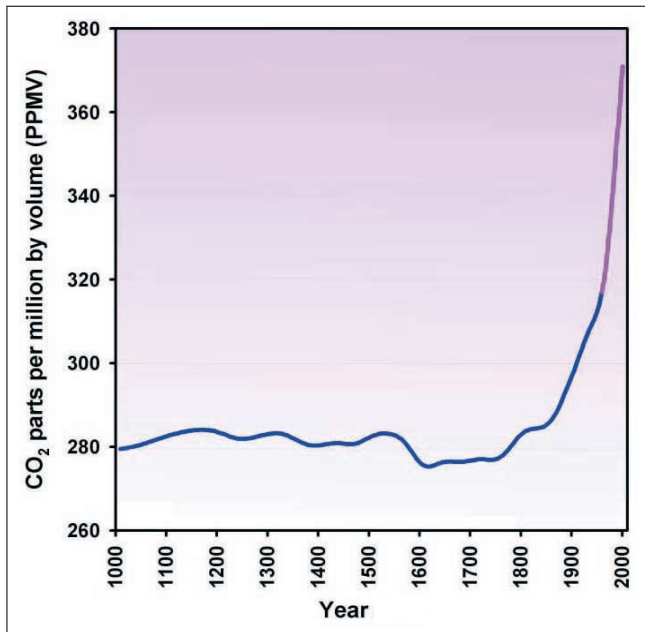
one of several important and interacting components of global change (Vitousek 1994). Global changes in climate, nitrogen (N) deposition, disturbance regimes, and habitat fragmentation are all expected to exacerbate non-native invasions (Dukes and Mooney 1999).

The prognosis worsens with ongoing changes in atmospheric chemistry – particularly the increase in atmospheric carbon dioxide (CO$_2$) and its by-product, global warming – that may facilitate the spread and impact of non-native plants. For example, when kudzu is grown under conditions of elevated CO$_2$, it produces more and longer stems and more biomass (Sasek and Strain 1988). Furthermore, as global temperatures rise, the plant's range may extend northward because its growth is no longer limited by cold weather (Sasek and Strain 1990). Hard data for other plant invaders are scarce. Nevertheless, the response of kudzu shows that elevated CO$_2$ and climatic changes could promote, and may have already contributed to, the spread and environmental impact of other non-native plants, exacerbating the threat to native ecosystems (Dukes and Mooney 1999).

Figure 2. *Levels of global atmospheric CO_2 for the last 1000 years, derived from measurement of CO_2 in air bubbles in layers of ice extracted from a core drilled in Antarctica (blue line: Etheridge* et al. *1998) and from atmospheric measurements at Mauna Loa, Hawaii, since 1958 (purple line: Keeling and Whorf 2002).*

■ Increases in CO_2

One undeniable aspect of global change is the alteration of atmospheric gases, particularly CO_2 (Houghton *et al.* 2001), which has increased from a pre-industrial level of 280 parts per million (ppm) to 370 ppm in 1997 (Figure 2), and is now rising faster than at any other time during the past 20 000 years. Depending on scenarios of global rates of fossil fuel consumption, CO_2 levels are expected to increase to 540–970 ppm by the end of this century (Houghton *et al.* 2001).

Atmospheric CO_2 is the primary source of carbon (C) for all terrestrial ecosystems, and is fixed by primary producers through photosynthesis (Panel 1). Consequently, increases in CO_2 may directly affect vegetation by increasing the rates of photosynthesis and C sequestration, which may ultimately affect the patterns and processes of native communities (Figure 3). Moreover, changes in atmospheric chemistry may alter the radiative transfer of energy in the atmosphere and at the earth's surface, resulting in global warming, changes in atmospheric and oceanic circulation, and changes in precipitation patterns (Houghton *et al.* 2001). These changes are the indirect effect of increases in CO_2 and they may interact with CO_2 to alter the spread, establishment, and impact of non-native plant species (Dukes and Mooney 1999).

■ Biological invasions and changing CO_2

In addition to the recent scientific scrutiny of plant responses to elevated CO_2, much research has focused on

### Panel 1. Plant responses to elevated CO_2

Research results to date have indicated that increasing CO_2 levels have direct and important effects on plants (Koch and Mooney 1996; Körner and Bazzaz 1996). The most common response is the "fertilization effect", whereby the growth rates of individual plants increase by approximately 37% (Poorter 1993). Other plant responses include increases in aboveground and belowground production, increases in the optimal temperatures for photosynthesis, increased efficiency in the use of water and N, reduced photorespiration, and decreased stomatal conductance (Körner and Bazzaz 1996; Norby *et al.* 1999).

However, not all plants respond the same way to increases in CO_2, in part because their response is directly mediated by their particular photosynthetic pathway or physiology. Generally, plants that use the C_3 photosynthetic pathway (most common plants) tend to respond positively, especially if they have symbiotic relationships with N-fixing microorganisms. On the other hand, plants such as corn and sugarcane that use the C_4 photosynthetic pathway, which is more efficient at capturing CO_2, respond in less predictable ways (Poorter 1993; Reynolds 1996). Although resource limitations (eg water and N) typically reduce plant responses to elevated CO_2 (Poorter and Pérez-Soba 2001), the differences between plant species or functional groups growing in complex natural communities may be accentuated (Owensby *et al.* 1999).   ■

understanding and predicting biological invasions. Two important questions for those studying contemporary invasion biology are (1) which species will invade, and (2) which ecosystems are vulnerable to invasion? Although theoretical and experimental research has intensified, answers remain elusive (Panel 2). They may become even more elusive as the climate continues to change because of unexpected interactions with other aspects of global climate change (Dukes and Mooney 1999).

An underlying tenet of contemporary ecology is that resources ultimately constrain the distribution and abundance of organisms (Tilman 1982). Generalizing the important role of resources in controlling invasibility, Davis *et al.* (2000) proposed a theory of fluctuating resource availability. They argued that, given adequate dispersal and an absence of herbivores or pathogens, resources are the most critical factor in the establishment and spread of invading populations into new habitats. Resources become available to new plants, either native or non-native, when those normally used by native species increase in relative availability as a result of increases in supply (through disturbance, eutrophication, or changes in weather or climate) or decreases in demand (disturbance, pathogen outbreaks, timing shifts of resource use relative to availability).

Shea and Chesson (2002) expanded on this idea, sug-
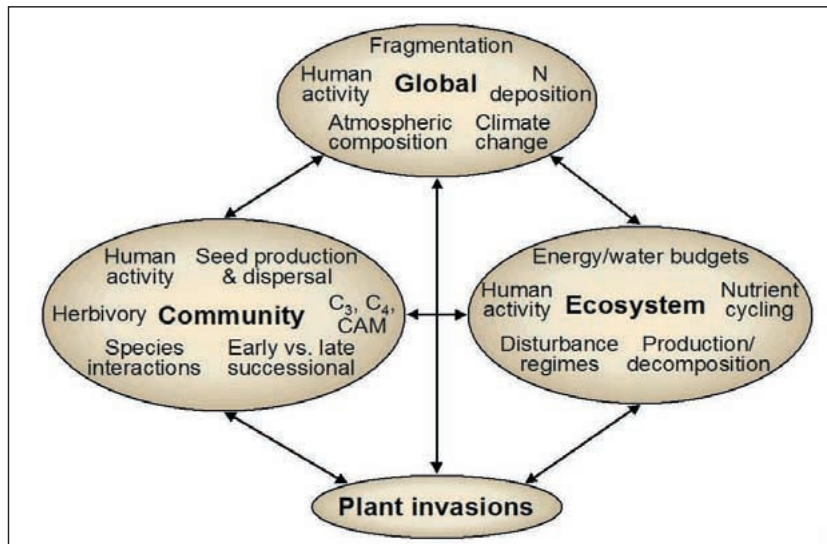
Figure 3. *Conceptual model of direct and indirect effects of elevated atmospheric CO$_2$ on plant invasions.*

respond strongly to increased CO$_2$. Dukes (2000) compared the mean weight gain ratios of native and non-native plant species grown under ambient and elevated CO$_2$ and found that the responses were statistically indistinguishable. He argued that there is nothing intrinsically special about invasive plants that would make them more responsive to increases in CO$_2$ when grown in monoculture. Invasive species may possess novel traits that allow them to invade native ecosystems, however (Cronk and Fuller 1995; Panel 2), and elevated CO$_2$ might give them an added advantage when invading new habitats.

■ **Indirect effects of CO$_2$ on plant invasions**

Increases in CO$_2$ may also indirectly affect the availability of resources. Although temperature is not usually considered a resource, changes in mean or extreme temperatures caused by increased CO$_2$ may make more resources available to plants by thawing frozen soil or changing rates of nutrient cycling, and allowing non-native species to grow faster than they would otherwise (Figure 4). Changes in when and where precipitation falls (caused by global warming and changes in atmospheric circulation) may facilitate the invasion of regions where normal soil moisture regimes keep new species from establishing. Furthermore, most models used to predict climate in a CO$_2$-enriched world suggest a continued increase in extreme weather events (Easterling *et al.* 2000) which
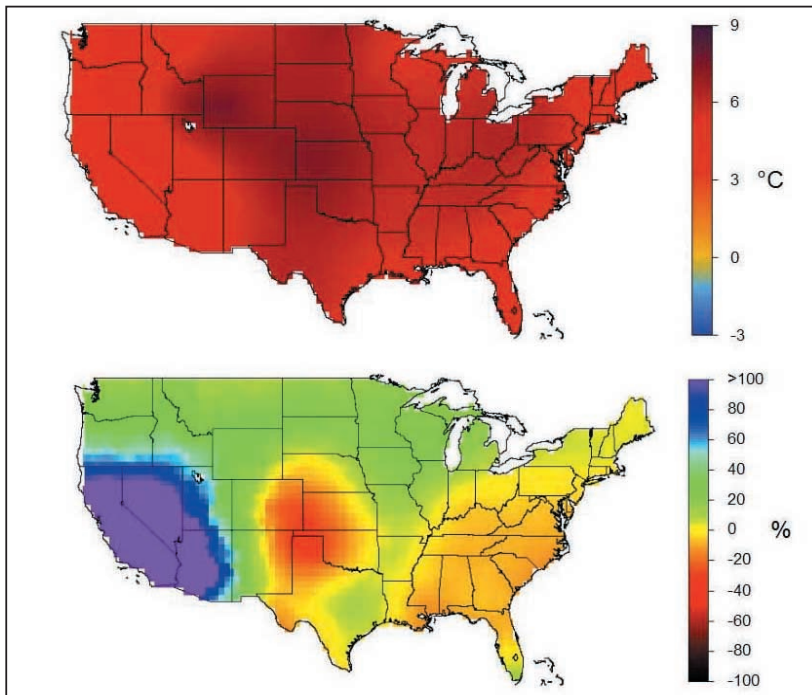
gesting that "resource opportunities" may arise when invaders have lower thresholds or maintenance requirements than resident species, when invaders acquire resources faster than resident species do, or when resources are distributed either in space or time. Sher and Hyatt (1999) adopted a slightly different perspective, suggesting that, although individual disturbance events may not facilitate invasions per se, changes in historic disturbance regimes may contribute to plant invasions.

■ **Direct effects of CO$_2$ on plant invasions**

Carbon dioxide is itself a resource that directly affects plant growth and production (Panel 1). All plant species

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Panel 2. Invaders and invasibility

Identifying invasive plant species

Few generalities have emerged in predicting which introduced species will become invasive, in part because each species has characteristic traits that make it invasive only in particular habitats. One challenge has been to find common attributes among invaders, which requires researchers to examine individual species traits to understand how genetics, physiology, and life history may affect a species' ability to invade (Kolar and Lodge 2001; Sakai *et al.* 2001). Understanding these attributes also requires knowledge of how the physical or biological environment may influence the genetic composition of populations. It is necessary to know the effects populations have within a community in order to understand how non-native plants may invade. Investigators must also consider the possibility that an invader might shape its own environment (Vitousek and Walker 1989).

Identifying communities vulnerable to invasions

Some ecologists have focused on the features of communities that make them vulnerable to invasions. Researchers need to consider processes that occur on multiple scales and levels of organization, in order to determine the traits that render an ecosystem vulnerable to invasion (Parker *et al.* 1999). Global changes will probably affect the availability of resources, yet genetic shifts in invader populations (Sakai *et al.* 2001) will act on very different spatial and temporal scales. Lonsdale (1999) suggests that a region's climate and disturbance regime, together with the competitive abilities of resident species and the presence or absence of pathogens and herbivores, determine the general invasibility of an area. Historically, areas of high species diversity were thought to be more resistant to invasions (Elton 1958). However, Stohlgren *et al.* (1999) suggested that areas rich in species are actually more vulnerable to invasions, which may be directly related to resource availability, habitat diversity, and the scale of the investigation. ■

Figure 4. Predicted mean change in surface temperature (top) and precipitation (bottom) for the US in 2060–2090 relative to 1960–1990. Data are from the HADCM2 model, UK Meteorological Office, Hadley Center for Climate Prediction and Research, National Assessment Synthesis Team (USGCRP 2002).

be studied. Hungate *et al.* (1996) suggested that elevated CO_2 can increase N uptake by invasive species (possibly because of differences in absolute growth rates and seed size), which may give them an advantage over native species. Enriched CO_2 often decreases the concentration of N in plant tissues, which may slow decomposition and decrease the availability of soil N (Norby *et al.* 2001). Alternatively, elevated CO_2 could increase the C content of soil by slowing the decomposition and increasing production and turnover of fine roots (Norby and Jackson 2000). This process may affect soil C:N ratios, alter soil water holding capacity, and affect soil microbial populations, including symbiotic N-fixers (Hu *et al.* 2001). Several N-fixing plants, including kudzu, Scotch broom (*Cytisus scoparius*), and fire tree (*Myrica faya*), are notorious invaders. These species can have a substantial effect on ecosystem properties – particularly N cycles – that favor subsequent invasions by a range of non-native species (Vitousek and Walker 1989). This could lead to the "invasional meltdown" envisioned by Simberloff and Von Holle (1999).

◼ Community and ecosystem structure and function

Plant community structure

A great deal of research is focused on plants grown individually or in monoculture (Panel 1). In contrast, relatively little research targets the responses of plants within more complex communities to elevated CO_2, particularly under realistic field conditions. Ironically, where community-level research exists, the results suggest that the responses of individual species grown in pots or greenhouses with elevated CO_2 tell us little about how entire communities would respond (Lawton 2000). Although ecologists have begun to manipulate entire systems, the results to date have not always been predictable (Smith *et al.* 2000; Shaw *et al.* 2002). Under natural field conditions, plant responses to elevated CO_2 are often constrained by biotic (eg competition) and abiotic (eg soil nutrients and water) factors that interact with each other and with changing CO_2 levels.

Interspecific variation in the plant responses may lead to community-level changes in species dominance, composition, and diversity. For example, Arp *et al.* (1993) found that elevated CO_2 increased total biomass and favored the sedge *Scirpus olneyi* in salt marshes, but the total response of the community varied from year to year. In tallgrass prairie, elevated CO_2

may facilitate invasions by changing disturbance regimes, altering resource availability, and increasing habitat fragmentation. Changes in resources could also affect the growth or spread of native species, which may make non-native species more or less competitive than they currently are and affect the invaders' relative success.

Ecosystem water budgets

Increases in CO_2 may affect the availability of soil moisture by affecting plants' physiological processes. Plants need less water in conditions of elevated CO_2 because they can keep their stomatal apertures smaller, which decreases water loss, while still being able to take in the same amount of CO_2. This reduction in water loss may lead to increases in soil moisture (Owensby *et al.* 1999; Dukes 2002), which, in turn, may alter community composition by favoring the establishment of either native or non-native species. For example, Polley *et al.* (1996) suggested that the combination of elevated CO_2 and consequent changes in soil moisture regimes may have contributed to the encroachment of woody plants into many of the world's former grasslands and savannas. Alternatively, Archer *et al.* (1995) argued that the spread of woody plants is more likely affected by grazing, fire, and climate change than by elevated CO_2.

Nutrient cycling

Increases in CO_2 and invasions may also change terrestrial N cycles, although their combined effect has yet to

favored C$_4$ grasses over C$_3$ grasses, particularly in drought years, and increased the contribution of broad-leafed C$_3$ species to total community biomass (Owensby *et al.* 1999).

Plant invasions and community composition

Although elevated CO$_2$ can alter community composition by favoring individual species or functional groups, the effects of CO$_2$ on plant invasions and the impacts of those invasions on native communities are mostly unknown (Dukes 2000). Nevertheless, several recent studies provide evidence that increased CO$_2$ favors invasions. For example, Smith *et al.* (2000) determined that red brome (*Bromus madritensis*), a non-native annual grass that has invaded many areas of the Mojave and Sonoran deserts, increased its density and production of aboveground biomass and seeds under elevated CO$_2$ during a wet El Niño year. These attributes may make it a more successful invader, facilitating its spread into fragile arid and semiarid ecosystems.

At Oak Ridge National Laboratory, we are tracking the response of approximately 30 understory plant species to increased CO$_2$ (Figure 5) as part of an ongoing investigation of the response of a closed-canopy deciduous forest to raised CO$_2$. Most of these understory plants have shown little response, but the two dominant plant species, both of which are non-native and invasive, are much more sensitive. Japanese honeysuckle (*Lonicera japonica*), a C$_3$ woody vine that is considered a threat to native plant communities throughout the southeastern US, showed a threefold increase in annual production (Belote unpublished). This result, coupled with other research (Sasek and Strain 1990), suggests that this species may become even more abundant, and may pose additional threats to native habitats as CO$_2$ levels continue to rise. In contrast, Japanese grass (*Microstegium vimineum*), a C$_4$ annual grass that has spread across much of the eastern US in less than 70 years, produced half as much biomass when CO$_2$ levels were increased. Although the underlying mechanism has not yet been determined, the data suggest that when CO$_2$ concentrations increase, the interaction between invasive species (a factor seldom considered by invasion biologists) may produce unexpected and non-intuitive results.

Succession

Other research suggests that elevated CO$_2$ may slow secondary succession by giving early successional species, which tend to be fast-growing and short-lived, an advantage over later-successional species, which are generally slow-growing and longer-lived (Potvin and Vasseur 1997; Niklaus *et al.* 2001). In particular, increased CO$_2$ promoted the coexistence of early- and late-successional species, which could delay the sequential turnover of species that characterizes the process of succession. Although these studies did not consider plant invasions per se, non-native

Figure 5. *An experimental stand of sweetgum* (Liquidambar styraciflua) *trees at Oak Ridge National Laboratory, Oak Ridge, TN, exposed to elevated atmospheric CO$_2$. (top) Twenty-four vertical vent pipes encircling each 25-m diameter plot emit CO$_2$ into the 15-m tree canopy to maintain canopy CO$_2$ at about 565 ppm. (bottom) The understory plant community within the sweetgum stand is dominated by Japanese honeysuckle* (Lonicera japonica), *a C$_3$ woody vine, and Japanese grass* (Microstegium vimineum), *a C$_4$ annual grass, both considered problematic plant invaders in the southeastern United States.*

plant invaders often possess traits common to early-successional species (Panel 2). Thus, if elevated CO$_2$ slows succession, non-native plants would have a greater opportunity to invade and dominate communities, further slowing or halting succession in some areas.

Fire regimes

The combined effects of increases in CO$_2$ and plant invasions could potentially change fire regimes in many ecosystems. For example, non-native species such as red brome and cheatgrass (*B tectorum*) respond positively to increases in CO$_2$ (Smith *et al.* 1987; Smith *et al.* 2000). These annual

grasses produce substantial quantities of fine fuels that may increase the frequency and extent of fires in plant communities that are not adapted to fire, such as the Mojave Desert or the shrublands of the Great Basin. This may facilitate plant invasions in many ecosystems (D'Antonio 2000). Alternatively, changes in CO$_2$ that increase the growth rates of woody plants may make them less susceptible to fire by raising vulnerable tissues above the flames (Bond and Midgley 2000).

Feedback mechanisms

Changes in CO$_2$ that facilitate plant invasions may set in motion positive feedback mechanisms that further entrench invasive species in their new habitats. For example, as suggested above, changes in fire regimes may favor the continued dominance of a particular invader by reducing competition from neighboring plants, or by encouraging establishment by preparing seedbeds or directly affecting germination rates (Anable *et al.* 1992). Simberloff and Von Holle (1999) suggested that synergistic interactions between non-native species may contribute to an "invasional meltdown", although their review of published research found limited evidence for this, and even less on the significance of such interactions for populations and communities. We clearly have much to learn, therefore, about the patterns and processes of non-native invasions, especially the role of elevated CO$_2$ in facilitating or constraining invasions.

■ The ripple effect

Changes in the composition and structure of plant communities caused by increased CO$_2$ and plant invasions are likely to have direct and indirect impacts on the insects that depend on the plant community. However, no studies to date have examined the interactive, cascading effects of plant invasions and elevated CO$_2$ on insect communities.

The direct impact of rising CO$_2$ on insect populations is probably mediated by the response of individual plants to CO$_2$ – in other words, herbivorous insects are affected because the quality of their host plants has changed (Lindroth 1996; Díaz *et al.* 1998). For example, because the C:N ratio of leaf tissue is generally higher under elevated CO$_2$, some insect herbivores may compensate by increasing their leaf consumption to maintain their rate of N intake (Bezemer and Jones 1998). Other species may not be able to compensate; larvae of the butterfly *Junonia coenia* exhibit higher rates of mortality and longer devel-

Courtesy of Mark Camara

Figure 6. *Buckeye caterpillar* (Junonia coenia) *feeding on a plant.*

opment times when fed on plants grown at increased CO$_2$ concentrations (Fajer *et al.* 1991; Figure 6). If herbivore populations are influenced by changes in plant quality, higher trophic levels (ie predators and parasitoids) will also be affected.

Elevated CO$_2$ may indirectly affect insects by facilitating invasions of plants with lower-quality leaf tissue, regardless of CO$_2$ levels, which will have implications at higher trophic levels. Furthermore, because the diversity of plant and insect communities is often positively correlated, plant invasions that reduce diversity within the recipient plant community may also influence the diversity or composition of the insect community.

Most studies involving plants, insects, and increased levels of CO$_2$ have been performed in settings without insect predators, parasitic insects, detritivores, and competitors. It is nearly impossible, therefore, to predict how entire insect assemblages will respond. More work is clearly needed at the community level under field conditions, because the responses of single-species systems are not likely to translate to complex, multi-species systems (Díaz *et al.* 1998). Most species do not respond to changes in driving variables in isolation from other organisms, so interactions between species may also be mediated as CO$_2$ increases.

■ Conclusions

There are two certain and predictable aspects of global change: increasing atmospheric CO$_2$ and the spread of species into new habitats. Each of these has the demonstrated capacity to alter community composition or ecosystem-level processes. When combined, they may have unexpected and dramatic effects.

Very few investigations currently target the effects of atmospheric CO$_2$ enrichment on intact natural communities. Even fewer studies have examined the effects of

elevated CO$_2$ on invasive species within communities, the invasibility of these communities (Panel 2), and the impacts of the invaders on the structure or function of the recipient community and ecosystem. More community-level studies need to be conducted under natural field conditions to better understand the effects that elevated CO$_2$ will have on both invasive and native species and their habitats. Where possible, research should focus on the mechanisms that drive observed responses and should attempt to rank the relative importance of direct and indirect effects of CO$_2$ on species, communities, and ecosystems.

Field experiments are one way to improve our understanding of the mechanisms that drive invasive species' responses in natural communities. However, the effects of increases in CO$_2$ are likely to be accompanied by other aspects of global change, including N deposition, rising temperatures, changing precipitation regimes, and habitat fragmentation, each of which may increase the success of invasive species. Thus, in addition to community-level experiments, multifactor and cross-site studies are needed to reveal the mechanisms that will influence future invasions. These should incorporate multiple trophic levels and focus on how trophic structure changes under elevated CO$_2$.

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