

REVIEW AND  
SYNTHESIS

## Global change and species interactions in terrestrial ecosystems

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**Abstract**

The main drivers of global environmental change (CO<sub>2</sub> enrichment, nitrogen deposition, climate, biotic invasions and land use) cause extinctions and alter species distributions, and recent evidence shows that they exert pervasive impacts on various antagonistic and mutualistic interactions among species. In this review, we synthesize data from 688 published studies to show that these drivers often alter competitive interactions among plants and animals, exert multitrophic effects on the decomposer food web, increase intensity of pathogen infection, weaken mutualisms involving plants, and enhance herbivory while having variable effects on predation. A recurrent finding is that there is substantial variability among studies in both the magnitude and direction of effects of any given GEC driver on any given type of biotic interaction. Further, we show that higher order effects among multiple drivers acting simultaneously create challenges in predicting future responses to global environmental change, and that extrapolating these complex impacts across entire networks of species interactions yields unanticipated effects on ecosystems. Finally, we conclude that in order to reliably predict the effects of GEC on community and ecosystem processes, the greatest single challenge will be to determine how biotic and abiotic context alters the direction and magnitude of GEC effects on biotic interactions.

**Keywords**

Climate change, CO<sub>2</sub>, competition, disease, food web, global warming, interaction effect, land-use change, mycorrhiza, nitrogen deposition, parasite, pollination, seed dispersal.

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**INTRODUCTION**

“It would not be surprising to see entire patterns of community organization jumbled as a result of global change” (Kareiva *et al.* 1993, p. 1).

The world and its ecosystems are undergoing rapid change (MEA 2005). The ecological impacts of the main drivers of global environmental change (GEC) – increasing atmospheric CO<sub>2</sub> levels and associated climatic changes, deposition of anthropogenically fixed nitrogen (N), loss and fragmentation of natural habitats, and biotic invasions – are all predicted to become more important as human exploitation of the environment increases over short time scales (Sala *et al.* 2000). Despite the large body of research demonstrating effects of GEC on population abundances, community composition, and organismal physiology (Sala *et al.* 2000), GEC may cause less obvious alterations to the networks of

interactions among species (Janzen 1974; Tylianakis *et al.* 2007). Yet, complex networks of biotic interactions such as predation, parasitism and pollination play an important role in the maintenance of biodiversity (Bascompte *et al.* 2006), mediation of ecosystem responses to GEC (Brooker 2006; Suttle *et al.* 2007), and the stability (resilience and resistance; Ives & Carpenter 2007) of those ecosystem services on which human well-being is dependent (Dobson *et al.* 2006). The historical lack of research into GEC effects on biotic interactions probably stems from difficulties in quantifying changes in interactions compared with changes in biodiversity (McCann 2007). Nevertheless, interactions may be more susceptible to GEC, as they are sensitive to the phenology, behaviour, physiology and relative abundances of multiple species (Suttle *et al.* 2007; Tylianakis *et al.* 2007).

Our goal in this review is to unite various subdisciplines of population, community, and global change ecology,

which have traditionally focused separately on specific GEC drivers such as climate change (Walther *et al.* 2002), or on specific interactions such as animal-mediated pollination (Aguilar *et al.* 2006). While several review articles have considered how specific global change drivers may affect biological communities, and explicitly recognized that biotic interactions can be highly responsive to global change (e.g. Parmesan 2006; Stiling & Cornelissen 2007), this review is focused more on identifying the extent to which the effects of global change drivers on biotic interactions can be generalized across a wide variety of interaction types and across all global change drivers. To achieve this, we synthesize broad trends in the impacts of GEC on over 1000 biotic interactions from 688 separate published studies (see Supporting information). We emphasize that these studies are highly heterogeneous, and that for each global change driver they include a wide range of organisms and ecosystem types. As such, we focus on the total numbers of interactions in the data set that show positive, negative or neutral responses in the strength or frequency of interactions to GEC. This is conceptually the same approach as that recently taken by Ives & Carpenter (2007) when dealing with a similarly heterogeneous data set (on diversity–stability relationships), because as they note ‘it would be incautious to perform a meta-analysis (on such a data set) to try to derive broad conclusions’.

Through our literature search, we show that the five GEC drivers regularly cause: (i) reduced interaction strengths of

several mutualisms involving plants (e.g. pollination and seed dispersal), (ii) multitrophic effects in the soil food web that can affect different taxa, trophic levels and ecosystem process rates depending on the environmental context, (iii) shifts in the relative dominance of coexisting plant and animal taxa, (iv) increases or decreases in natural enemy attack on herbivores and frequent increases in the intensity of herbivory, and (v) increased frequency and severity of pathogen influences on plants and animals (Fig. 1). However, for each GEC driver, we find great variability across studies and systems (Figs S1–S5). This may result partly from frequently observed higher order effects among multiple GEC drivers, whereby the effects of one driver may be exacerbated or mitigated by another driver (Box S1). We discuss this possibility, and then highlight the implications of recent work on complex interaction networks for interpreting community and ecosystem responses to global change. Finally, we evaluate areas of new research that may help to better predict future consequences of GEC for biotic interactions, as well as facilitate prioritization of conservation efforts. Biodiversity loss is often cited as a form of GEC, but as it can both affect and respond to biotic interactions, and because the effects of diversity on ecosystem processes and species interactions have recently been reviewed in depth (Hooper *et al.* 2005), we do not include biodiversity loss explicitly as one of our five global change drivers. However, we do discuss effects of other drivers mediated via biodiversity loss when appropriate.

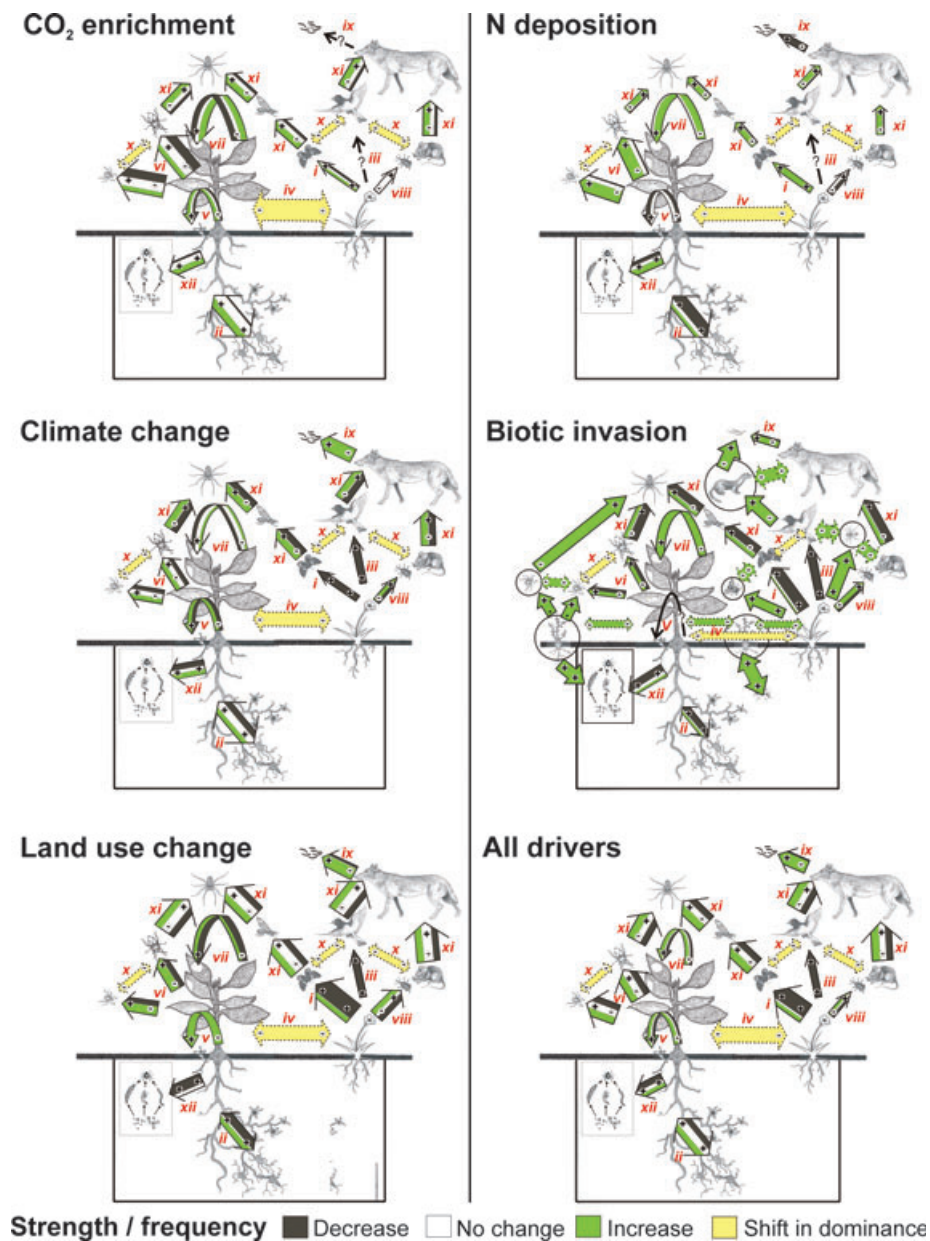
**Figure 1** Responses of key biotic interactions to each global environmental change (GEC) driver. The figure presents the results of a synthesis of 688 separate published studies (Table S1) that have each examined the effect of at least one GEC driver on at least one interaction type (Figs S1–S5), totalling over 1000 specific species interactions. The number of specific pairwise interactions (or entire communities, when interactions were measured at the community scale) showing a decrease, increase, or no effect in the strength or frequency of the interaction, under that specific global change driver was recorded, and this number of interactions was the basis for quantifying changes to interaction frequencies in Fig. 1 and Figs S1–S6. This essentially gave extra weighting to studies that examined a greater variety of pairs of interacting species. Arrows with solid outlines indicate nutrient and energy flow, while double-headed arrows with dotted outlines indicate resource competition. + and – symbols within arrows indicate benefit or cost to each participant (e.g. ++ within an arrow is a mutualism). The proportion of colours within each arrow indicates the proportion of published pairwise interactions of a given type affected by each of the GEC drivers present in our database (Table S1) showing increases (green), no effect (white), or decreases (dark grey), respectively, in the strength or frequency of the interaction following each of five major GEC drivers. Yellow arrows indicate a change in dominance between competing species. Width of arrows represents the number of studies considered in this review for each individual driver (small: ≤ 10; medium: 11–40; large: > 40 cases) and all drivers in combination (bottom right, small: ≤ 40; medium: 41–100; large: > 100 cases). In the Biotic Invasion panel, invasive species are depicted within circles, and the new interactions between invasive and native biota are depicted as an interaction (block arrow) with increasing strength. A table of the studies on which these trends are based (Table S1) is provided in the supporting information, with details regarding specific treatments and response variables. The final (bottom right) panel represents the summation of the individual effects of each driver (i.e. the number of pairwise interactions showing an increase, decrease, or no effect when studies of all GEC drivers are combined). Although we acknowledge that this ‘vote-counting’ approach can only give general indications of trends in the literature, it has been argued that a quantitative meta-analysis of such a large number of different response variables and specific treatments would give a false sense of confidence in the trends (see Ives & Carpenter 2007). We therefore emphasize that these are broad generalizations based on current literature, rather than predictions for any single system. Roman numerals describe the interactions as follows: (i) Plant–pollinator, (ii) Plant–fungal mutualism, (iii) Plant–seed disperser, (iv) Plant–plant competition, (v) Plant–hemiparasite, (vi) Plant–herbivore, (vii) Plant–pathogen, (viii) Plant–seed predator, (ix) Host–pathogen, (x) Animal–animal competition, (xi) Predator–prey, (xii) Soil food web. Enlargements are presented in the Figs S1–S6.

Additionally, it should be noted that these direct GEC drivers are themselves the result of indirect socioeconomic drivers of global change (Carpenter *et al.* 2006a), which we do not address here.

**Direct drivers of global environmental change**

Increasing concentrations of CO<sub>2</sub> and anthropogenic N can directly increase short-term plant growth rates and alter plant chemistry (C : N ratio and concentration of carbon-based compounds often increase), and these physiological

changes can affect a range of biotic interactions involving plants (Fig. 1; Figs S1, S2, Box S2). In contrast, the effects of climate and land use change on interspecific interactions pervade across multiple trophic levels, rather than being mediated solely by plants (Fig. 1; Figs S3, S5, Box S2). Whereas other GEC drivers have direct effects on species interactions, invasive species are themselves involved in the community web, making their impact on the pairwise interactions among other species by definition indirect (Fig. 1; Figs S4, Box S2). Each of these GEC drivers can have a variety of effects on different types and measures of



species interactions. Here, we summarize broad trends in these findings (see Methods S1 for literature search criteria, and Table S1 for the literature used in this review) across all GEC drivers, and refer the reader to the Figs S1–S6, for some specific examples that underlie these trends. Although effects vary greatly across studies and individual drivers, certain overall patterns emerge.

*Mutualisms involving plants are generally negatively affected*

Although CO<sub>2</sub> and N enrichment may in some instances have positive effects on nectar quality (Davis 2003a) and abundance of flowers (Muñoz *et al.* 2005), climate-induced phenological shifts (Walther *et al.* 2002; Visser & Both 2005; Parmesan 2006) and frequent negative effects of competition with invasive plants and pollinators (Lopezaraiza-Mikel *et al.* 2007; Aizen *et al.* 2008) may outweigh these benefits, producing a net reduction in pollination (Fig. 1; Fig. S6). Even very small shifts in the phenology of individual plant species may have large impacts on community-wide pollination mutualisms (Mummott *et al.* 2007). Further, land use change and habitat fragmentation have nearly always been found to have negative effects on pollination, with the strongest effects observed on native pollinator species (Aguilar *et al.* 2006). The effects of habitat modification on pollination mutualisms can be mediated through a loss of pollinator diversity (Chacoff & Aizen 2006), shifts in pollen quality transferred by different species (Chacoff *et al.* 2008) or altered pollinator behaviour (Cheptou & Avendano 2006). Further, different pollinator species may respond to land use changes at different spatial scales (Steffan-Dewenter *et al.* 2001). Reduced pollination may in turn have cascading effects on seed dispersal by frugivores (Harrison 2000). Additionally, direct effects of climate on the timing of fruiting (Jordano 2000), displacement of native mutualists by invasives (Traveset & Richardson 2006), and impaired dispersal among habitat fragments (Cordeiro & Howe 2003; Garcia & Chacoff 2007) have frequent negative effects on seed dispersal, potentially compounding the effects of reduced pollination on plant reproduction. A study of hawthorn (*Crataegus monogyna* Jacq.) in Spain found that plant reproduction could be affected by reduced pollination and seed dispersal, as well as increased seed predation in fragmented habitats (Garcia & Chacoff 2007), indicating that even a single GEC driver can affect plant fitness via three different mechanisms involving mutualisms and antagonisms.

Effects of GEC on plant–fungal mutualisms are more variable, but mycorrhizal community composition is often altered by land use intensification or biological invasion (Mummey & Rillig 2006; Opik *et al.* 2006). Colonization of (particularly native) plants by arbuscular mycorrhizal and ectomycorrhizal fungi (AMF and EMF) tends to decline with N deposition, although this effect is highly dependent

on P levels and plant growth form (Egerton-Warburton *et al.* 2007). Elevated CO<sub>2</sub> has the reverse effect, often increasing colonization by AMF (Hu *et al.* 2005) and EMF (Lukac *et al.* 2003), but having variable or no effects on other aspects of this mutualism, such as nutrient uptake (Table S1). Increased temperatures sometimes increase root colonization and mycorrhizal hyphal production (Staddon *et al.* 2004), but the effects of climate on plant–fungal mutualisms are highly variable. However, direct effects of CO<sub>2</sub> or N enrichment on the fungi and the mutualistic interaction *per se*, are difficult to separate from indirect effects via plant growth, and there is considerable variation across species.

*Soil food webs show multitrophic responses that are strongly context-dependent*

Enrichment of CO<sub>2</sub> and climate change can influence both the quality and quantity of resources that plants return to the soil through a number of mechanisms; some of these have positive effects on plant-derived resources while others have negative effects (Wardle 2002; Bardgett 2005). Because different mechanisms dominate in different contexts, several studies have revealed both positive and negative effects of CO<sub>2</sub> enrichment and climate change on multiple trophic levels of the soil food web (Klironomos *et al.* 1996; Ruesch *et al.* 1999; Wardle 2002). Nitrogen deposition often improves the quality of resources that plants return to the soil, with generally positive indirect effects on soil biota. However, N deposition also exerts direct effects on soil biota that can be either positive or negative depending on context (Wardle 2002). Further, N deposition can be an important determinant of how CO<sub>2</sub> enrichment affects the soil food web (Klironomos *et al.* 1996; Lutze *et al.* 2000).

Invasive organisms including plants, herbivores, predators, and detritivores such as earthworms can greatly influence decomposer food webs (Yeates & Williams 2001; Fukami *et al.* 2006; Van der Putten *et al.* 2007), and the magnitude and direction of these effects depends on both the type of invader and environmental context. For example, Wardle *et al.* (2001) found invasive deer in New Zealand native forests to have positive, negative, or neutral effects on each of three consumer trophic levels in the soil food web (i.e. microbes, microbe-feeding nematodes, and top predatory nematodes), depending on site conditions. In contrast, it is well established that land use intensification has consistently adverse effects on many components of the decomposer food web (Hendrix *et al.* 1986; Wardle 1995). These arise mainly through enhanced disturbance, changes in the nature of organic and inorganic inputs, and altered basal resource levels in the soil (Hendrix *et al.* 1986). Further, there is much evidence that different components of the soil food web respond very differently to each of the five global change drivers, because the relative importance

of top-down and bottom-up forces differs for different components of the soil web (Klironomos *et al.* 1996; Ettema *et al.* 1999; Wardle 2002). For example, Yeates *et al.* (1997) found higher but not lower trophic levels in the soil food web responded to CO<sub>2</sub> enrichment because the upper levels were regulated by resource limitation (bottom-up control) while the lowest level was regulated by predation (top-down control).

*Competitive interactions are frequently altered by changes in the dominance of plant and animal species*

The nearly ubiquitous differences in responses of different plant and animal species to GEC drivers can shift competitive balances to favour certain plant species or growth forms over others, and this was the most consistent pattern found by our literature review (Supporting information). For example, C3 plants often derive a competitive advantage following N deposition (Tilman & Lehman 2001) and C4 plants can derive a competitive benefit from increased temperatures (Zavaleta *et al.* 2003). Changes in the competitive balance among plant species may also be mediated by changes in herbivore pressure (including by invasive mammal or insect herbivores; Callaway & Maron 2006) or altered pathogen infection rates (Malmstrom *et al.* 2006) under GEC.

Similar competitive shifts frequently occur among animals, with high variability in the responses of different herbivore species to climate change, CO<sub>2</sub> elevation and N deposition potentially altering competitive balances among them (Figs S1–S3). Temperature increases may affect seed dehiscence times, thereby shifting the competitive balance between invertebrate seed dispersers and mammalian seed predators (Ness & Bressner 2005). Invasive animals can outcompete native species through more effective exploitation of prey, or by enhancing populations of a shared natural enemy (Snyder & Evans 2006). However, introduced species are more likely to cause extinctions of native species through trophic, rather than competitive interactions (Davis 2003b). Habitat modification has also been shown to shift the competitive balance between different insect (Elzinga *et al.* 2007) and vertebrate species (Attum *et al.* 2006).

*Antagonistic interactions involving plants often intensify, but predator–prey interactions can be positively or negatively affected, depending on the GEC driver*

Higher trophic levels are often disproportionately affected by drivers such as climate change, competition from invasives, and habitat modification (Bascompte & Solé 1998; Tscharrntke & Brandl 2004; Voigt *et al.* 2007), although effects of warming on predator and parasitoid physiology are variable (Supporting information). Loss of consumers at higher trophic levels could potentially benefit herbivores, but this effect is highly dependent on the

mechanism of operation and specialization of the predator or parasitoid species involved (specialists may be more severely affected than generalists; Rand & Tscharrntke 2007). For example, generalist predators frequently benefit from resource subsidies in modified landscapes (Rand *et al.* 2006), so land use change may have either positive or negative effects on different predator taxa (Fig. S5). Parasitoids in particular benefit frequently from increased host quality under elevated N (Moon & Stiling 2000), and increased parasitism rates under elevated CO<sub>2</sub> may result from slowed herbivore development providing a longer period of vulnerability to attack (Johns & Hughes 2002; Asshoff & Hättenschwiler 2005). Effects of GEC on plant–herbivore and seed predator interactions are highly variable, and depend on the driver and mechanism of the plant-mediated response. Herbivore performance often declines under increased CO<sub>2</sub>, although consumption rates often increase or remain unaffected, and there is great variability across taxa and feeding modes (Table S1, Fig. S1). Different herbivore guilds were suggested in an early review to respond differently to CO<sub>2</sub> enrichment (Bezemer & Jones 1998), but this remains to be tested empirically and across different GEC drivers. Reduced herbivore performance under elevated CO<sub>2</sub> may be offset by positive effects of other GEC drivers such as frequent increases in herbivory with added nitrogen (Fig. S2), and less consistent effects of increased temperature (Logan *et al.* 2003; Zvereva & Kozlov 2006; Stiling & Cornelissen 2007; Box S1).

Invasive plants and exotic crop species in agricultural habitats may subsidize herbivore and seed predator populations, and lead to increased attack rates on native plants (Rand & Louda 2004). Plant–hemiparasite antagonisms may be enhanced as a result of reduced competition with the host plant following land use intensification (Ameloot *et al.* 2006), but CO<sub>2</sub>- and temperature-mediated changes to parasite and host physiology (Phoenix & Press 2005) have variable effects (Table S1). Hemiparasites can be favoured by higher growth rates, thereby increasing the demand for host mineral nutrients and competition with the host for N. Although there may be no direct effect of N deposition on plant–hemiparasite antagonisms, variability in the effects of other GEC drivers with soil nutrient status suggests that N deposition may moderate the effects of other drivers (Hwangbo *et al.* 2003).

As with plant–animal mutualisms, plant–herbivore and herbivore–predator antagonisms can be altered by phenological changes following climate change (Visser & Both 2005; Parmesan 2006). Slight differences in the physiological responses of plants, herbivores and predators to temperature cues may positively or negatively affect their synchrony, with important consequences for herbivore population sizes (van Asch & Visser 2007) and predator population growth (Durant *et al.* 2007).

*Pathogen infection of plants and animals generally increases*

Climate change, land use change and biotic invasions (usually of disease vectors) have all been shown frequently to promote transfer of diseases and parasites to native fauna (Figs S3–S6). The frequency and severity of plant pathogen infection generally increases under elevated N, although responses to other drivers are more variable. Elevated leaf amino acid concentrations following N deposition may be a mechanism promoting fungal infection, and many pathogens of plants and animals are currently increasing in incidence and range following climate warming (Parmesan 2006). ENSO events have been shown to promote the growth of animal disease vector populations (Stapp *et al.* 2004), and facilitation of pathogen outbreaks by temperature shifts has been implicated in widespread amphibian extinctions (Pounds *et al.* 2006). Invasive plants and animals can indirectly influence virus incidence in native species by increasing populations of vectors or by acting as source populations for pathogens themselves (Hampton *et al.* 2004; Malmstrom *et al.* 2005), although they have also been shown to act as a sink for pathogens in some cases. Effects of habitat modification on pathogen attack are generally more variable (Fig. S5), but vectors that benefit from modified habitats can also spread diseases to rarer wildlife or to human populations (Yanoviak *et al.* 2006). Increases in plant infection under elevated CO<sub>2</sub> can occur because of decreased water stress or increased leaf longevity and photosynthetic rate (Mitchell *et al.* 2003).

**Caveats**

Inevitably, our review and literature synthesis is subject to several caveats. First, there is likely to be a publication bias toward studies showing significant effects of GEC on species interactions, so the outcomes presented here should not be expected to be universal. Similarly, interactions that have received little research attention (e.g. seed dispersal and plant–hemiparasite antagonisms) may potentially have different responses to those that we have described; therefore early conclusions regarding specific interactions must be made with caution. Nevertheless, the mere fact that severe alterations to species interactions have been observed in some cases should serve as a warning of future changes to pairwise interactions that may result from GEC.

Despite the broad patterns we have synthesized, a recurrent feature of the available literature is the great variability across species and studies. While strong generalizations can be made regarding the effects of some GEC drivers on certain types of interactions, there are many interactions for which there has been little research, or for which the effects of GEC (in terms of both magnitude and direction) are heavily dependent on environmental context and on the species involved (Table S1; Figs S1–S5). This

suggests that expanding the spatio-temporal scale of studies may influence the generality of the patterns we present. Progress in GEC research therefore requires studies that focus on a broad suite of species or environments, and that explicitly evaluate context dependency in the effects of each driver. Scaling of ecosystem processes in time and space is a key determinant of ecosystem resilience (Carpenter *et al.* 2006a), and the extent to which interactions are propagated across a community web may amplify or buffer the effects of GEC on individual interactions.

**Webs of interacting species**

The above sections (and Supporting information) have detailed numerous effects of GEC on a variety of species interactions and simple food chains. However, the nuances of individual interaction responses under specific conditions can obscure overall patterns within communities. All species are embedded in complex networks of interactions with other organisms, and the crucial ways in which changes to pairwise interactions combine across the entire community remain opaque, largely because of difficulties in quantifying such complexity (McCann 2007). Nevertheless, the myriad of indirect effects that are potentially susceptible to global change (Willis & Memmott 2005), and the complex feedbacks that exist among species (Suttle *et al.* 2007), mean that species-specific projections are not necessarily consistent with those of their communities (Tylianakis *et al.* 2007). Therefore, a full understanding of the effects of GEC on communities and ecosystem services inevitably requires some kind of scaling from pairwise interactions to whole interaction networks (McCann 2007).

Quantitative interaction webs (Memmott *et al.* 1994; Bascompte *et al.* 2006) provide a framework for empirical community-scale analyses, and replicated community webs may be compared to address questions regarding global change (Lopezaraiza-Mikel *et al.* 2007; Tylianakis *et al.* 2007; Aizen *et al.* 2008). Recent work on interaction networks involving plants and pollinators has found them to be highly susceptible to GEC. Phenological shifts caused by climate change may affect up to 50% of pollinator species within a network (Memmott *et al.* 2007), and the presence of invasive plant and pollinator species can affect flower visitation and pollen transfer to native species (Memmott & Waser 2002; Lopezaraiza-Mikel *et al.* 2007; Aizen *et al.* 2008; Bartomeus *et al.* 2008). Similarly, habitat modification and fragmentation have been shown to significantly affect parasitoid–host food web structure (Albrecht *et al.* 2007; Tylianakis *et al.* 2007). However, these studies only compared two-trophic levels, whereas trophic skew resulting from the differential susceptibility of different trophic levels to GEC (Tscharrntke & Brandl 2004) implies that future research on interaction webs could benefit from incorporating multiple trophic levels.

Although empirical research on the responses of interaction networks to GEC is in its infancy, recent theoretical work has explored how the structure of large ecological networks influences community-wide responses to GEC (Box S3). For example, networks of mutualistic interactions between plants, pollinators and seed dispersers were found to be heterogeneous, nested, and built upon weak and asymmetric links among species (Bascompte *et al.* 2003, 2006). These network patterns may confer robustness to the loss of interactions because a core of redundant interactions brings cohesion to the whole network (Memmott *et al.* 2004; Bascompte *et al.* 2006; Fortuna & Bascompte 2006; Okuyama & Holland 2008). Similarly, metacommunity models have shown that the architecture of mobile mutualistic networks affects their response to habitat loss. Although some mutualists go extinct sooner than expected at random, the network as a whole withstands higher levels of habitat loss (Fortuna & Bascompte 2006). These network patterns seem to be widespread irrespective of community composition, geographic location and other factors (Bascompte *et al.* 2003, 2006), suggesting that the effects of removing links or species should be general across different types of mutualisms among free-living species. However, potential effects on sessile, obligate mutualists such as mycorrhizae are less clear, as they have distinct physiological roles that cannot be substituted by other species.

As discussed above, the strength of mutualistic networks is likely to affect network stability (Bascompte *et al.* 2006; Okuyama & Holland 2008). Our literature synthesis (Fig. 1; Figs S1–S6) revealed that the strength of mutualistic pairwise interactions involving plants is likely to decline considerably from GEC. Therefore, even though the structure of mobile mutualistic networks makes them relatively robust to losses of particular species, GEC may directly or indirectly alter specific interaction pathways within networks (Lopezaraiza-Mikel *et al.* 2007; Memmott *et al.* 2007). Further, if phylogenetically related species have similar ecological roles in interaction networks, a high frequency of co-extinctions among related species may be observed (Rezende *et al.* 2007), which translates into a biased pruning of the evolutionary tree and increased loss of species diversity for specific taxa. In the case of plants, the negative consequence of reductions in their mutualists is likely to be further exacerbated by a frequent enhancement of their antagonists (Fig. 1).

Antagonistic networks appear to be more compartmentalized than mutualistic networks (Lewinsohn *et al.* 2006; but see Thebault & Fontaine 2008), which may translate into differential susceptibility to GEC. Some studies suggest that food webs, like mutualist networks, are structured in ways that promote community stability (Neutel *et al.* 2002; Bascompte *et al.* 2005; Rooney *et al.* 2006; Otto *et al.* 2007), but their resilience to GEC may depend strongly on top predators (Bascompte *et al.* 2005). For example,

intact communities controlled by top predators (such as wolves in Yellowstone National Park; Wilmers & Post 2006) are more resistant to the effects of climate change. Without these predators, the community as a whole may change through the amplification of perturbations. In this example, conservation of top predators would serve to make the entire community more resistant to climate change.

### Multiple interacting drivers of global environmental change

The vast majority of studies have examined effects of a single GEC driver on species and their interactions, but researchers have recently begun to test for higher order effects among multiple drivers. Evidence for these higher order interactions has emerged so frequently that their effects may be almost as important as those of each driver in isolation (Didham *et al.* 2007). For example, plant biomass production under elevated CO<sub>2</sub> becomes increasingly limited by N (Reich *et al.* 2006), so N deposition may affect community and ecosystem responses to elevated CO<sub>2</sub>. Similarly, a recent meta analysis found that concentrations of non-structural carbohydrates and phenolics increased with elevated CO<sub>2</sub> treatments, decreased under elevated temperature and did not change when elevated CO<sub>2</sub> and temperature were combined (Zvereva & Kozlov 2006). Interactions among GEC drivers (Box S1) may help explain variable responses to CO<sub>2</sub> of interactions involving herbivores or soil biota across studies (Table S1).

Carbon dioxide-induced changes in the decomposer food web can also vary according to climatic factors (Yeates *et al.* 1997) and availability of soil nutrients, particularly N (Klironomos *et al.* 1996; Sticht *et al.* 2006). In particular, responses of decomposer organisms to CO<sub>2</sub> enrichment are often greater when N is not limiting, so N deposition may promote the responsiveness of soil food webs to elevated CO<sub>2</sub> (Klironomos *et al.* 1996). Similarly, the positive effects of elevated temperature and atmospheric CO<sub>2</sub> on microbial decomposition can interact synergistically, such that their combined effect is greater than when these factors operate alone (Fenner *et al.* 2007). This can create an even stronger positive feedback on carbon loss from soil.

Although interactions between CO<sub>2</sub> and N deposition have received the most attention, there is mounting evidence that higher order effects among all the major GEC drivers can affect biotic interactions (Didham *et al.* 2007). For example, species invasions and habitat modification so frequently occur in combination that there can be real difficulties in separating the individual effects of each driver (Didham *et al.* 2007). Climate change (Walther *et al.* 2002) and elevated CO<sub>2</sub> (Brooker 2006) or N (Siguenza *et al.* 2006) can also promote species invasions, and the interplay between land use (grazing) and N deposition can drastically

alter plant competitive interactions (van der Wal *et al.* 2003). Similarly, habitat fragmentation may affect the ability of habitat specialists to track climatic change (Walther *et al.* 2002), with potential consequences for the mutualisms and antagonisms in which they are involved.

Theoretical ecologists are beginning to incorporate interactions between multiple GEC drivers into models of biotic interactions. For example, recent models have shown that the combined effect of two drivers (CO<sub>2</sub> and climate) on predator–prey population responses could be less extreme than expected based on the effects of the two drivers considered separately (Hoover & Newman 2004), and that vegetation change could be affected by interactions between management, climate and N deposition (Britton *et al.* 2001). Adequate prediction of the future effects of GEC on biotic interactions hinges on understanding the higher order effects of multiple drivers, in order to avoid seriously under- or overestimating the net effects of GEC.

### The way forward

Our review has shown that global environmental change has significant effects on a multitude of interactions between species, and that seemingly minor changes to individual interactions can combine to exert important effects on the structure of entire communities. Although there have been substantial recent advances in understanding the direct effects of GEC drivers, we highlight three broad research priorities that are beginning to receive attention from the scientific community, but which could be further emphasized to better predict the consequences of GEC for communities, ecosystems, and the provision of ecosystem services (Carpenter *et al.* 2006a).

#### *Quantitative scaling from pairwise species interactions and networks to ecosystem responses*

Variable responses of species interactions to specific GEC drivers (Table S1; Figs S1–S5), along with the dearth of studies that have investigated non-additive effects of GEC across multiple trophic levels, point to the need for caution in predicting community-level responses to global change. Existing analytical frameworks and metrics allow quantitative examination of interaction networks across multiple trophic levels (Fortuna & Bascompte 2006; Tylianakis *et al.* 2007), paving the way for research on the mechanisms of community-scale responses to GEC. However, some major questions regarding food web responses to GEC remain unanswered. First, the relative importance of external perturbations (e.g. GEC) vs. local and regional factors (e.g. diversity, species pool) in structuring interaction webs is largely unknown, and null models of network structure are required for comparison with perturbed systems. It is now widely appreciated that biodiversity and linear interaction

chains may be strongly affected by processes occurring at the landscape scale, as well as at local scales (Tschamntke *et al.* 2005), and a comparable framework is needed to scale food webs up to landscape scale interaction networks. The presence of weak interactions has long been known to promote web stability (McCann *et al.* 1998; Neutel *et al.* 2002; Bascompte *et al.* 2005), and recent theoretical work has shown that weak interactions can promote the stability of metacommunities at landscape scales, although the mechanism underlying regional stability is contingent on local dispersal regimes (Maser *et al.* 2007). If other local network attributes and processes have similar regional effects on networks of interacting species, a critical challenge for theoretical and empirical ecologists will be to develop tools to expand the spatiotemporal scale of food web research. Intrinsically, food webs comprise a static representation of a dynamic interacting community, and it remains unclear how the accuracy of this representation, and the variability in structure (Olesen *et al.* 2008), is affected by external environmental drivers.

Second, the mechanistic link between food web structure and ecosystem function has yet to be made. Interaction networks have structural properties that affect their stability (Rooney *et al.* 2006), but their relationship to ecosystem services and human wellbeing (Carpenter *et al.* 2006a) remains poorly understood. Future theoretical and empirical examination of the connections between web architecture and function has the potential to inform management strategies that prioritize the conservation of network structure (McCann 2007), rather than particular species or biodiversity *per se*, thereby connecting structural attributes to ecosystem outcomes (Carpenter *et al.* 2006b).

#### *Understanding the higher order effects of multiple GEC drivers*

As discussed above, growing recognition of strong higher order effects among GEC drivers is leading to a greater mechanistic understanding of ecosystem responses (Reich *et al.* 2006), even though relatively few studies have manipulated multiple GEC drivers (but see Peters *et al.* 2006). Interactive effects among multiple drivers therefore remain poorly understood, and a fruitful area for future research would be to test explicitly for non-additivity among multiple drivers (Didham *et al.* 2007), allowing more robust predictions of changes to species interactions under specific scenarios. Work on individual drivers has produced highly variable results (Fig. 1), and this variability highlights the context-dependency in the effects of each GEC driver. Simultaneous analysis of multiple drivers will provide a greater breadth of conditions under which to test the effects of each driver, and a more realistic approximation of future conditions. At the local level, conservation efforts could benefit by addressing interactions between drivers, and recognizing that sustained reduction in the effects of one



GEC driver (e.g. species invasions) could require management actions targeted at another driver (e.g. habitat loss; Didham *et al.* 2007). Whereas current global initiatives such as the Kyoto protocol focus on single GEC drivers, recognition of the role of interactions among drivers requires that future global initiatives adopt a multilateral approach. For example, it has been suggested that a policy mechanism akin to the Intergovernmental Panel on Climate Change (IPCC) could utilize scientific expertise to inform governments, policy makers, NGOs and the general public about matters involving biodiversity (Loreau *et al.* 2006). Such an initiative could explicitly address the threat of multiple interacting GEC drivers, utilizing the efforts of existing initiatives such as the IPCC and Millennium Ecosystem Assessment (MEA 2005; Carpenter *et al.* 2006a).

#### *Mitigating catastrophic regime shifts in ecosystems*

In most instances, community and ecosystem responses to GEC are incremental (Scheffer *et al.* 2001) and scale in direct proportion to the magnitude of external forcing. However, a slow decrease in ecological resilience following seemingly minor changes in GEC drivers can push ecosystems to a critical threshold, beyond which normal stochastic events can trigger rapid ecosystem state change (Scheffer *et al.* 2001; Carpenter & Brock 2006). Such catastrophic regime shifts are unpredictable, frequently large in magnitude, and often expensive or impossible to reverse (Scheffer *et al.* 2001). Alternative regimes are maintained by positive feedback mechanisms between species and environment, yet the shift in interaction network structure underlying community state changes is rarely investigated. Recent exceptions are the studies by Memmott & Waser (2002), Olesen *et al.* (2002), Aizen *et al.* (2008) and Bartomeus *et al.* (2008). In particular, Aizen *et al.* (2008) identified structural changes to plant–pollinator mutualist webs following community invasion by exotic species. Structural changes to the network associated with the invasion process (reduced interaction strength and high interaction asymmetry) can promote persistence of community structure (Bascompte *et al.* 2006), and suggest that invaders may cause a positive feedback promoting further invasion. The effects of network structure on ecological stability (May 1973; Bascompte *et al.* 2006; Rooney *et al.* 2006; Okuyama & Holland 2008) suggest that a focus on the alteration of interaction structure may help to explain the loss of ecological resilience that precedes major regime shifts. We suggest that deriving generalities from the biotic interactions underlying feedback mechanisms will improve predictive understanding of ecosystem change.

#### CONCLUSIONS

Ecologists are increasingly charged with translating complex changes in communities and ecosystems into the

unconditional probabilities (Carpenter *et al.* 2006a) required for policy decisions. The frequent focus on uncertainties in projecting future scenarios for the biodiversity of Earth's ecosystems should not obscure the relevance and utility of the information that is already at hand. The vast majority of published studies we synthesized that tested GEC effects on biotic interactions (Table S1, Figs S1–S5) found these effects to be important. Further, the few recent studies that have examined multiple interacting drivers or changes across entire interaction networks have found significant unanticipated effects. Despite this, most scenarios predicting the future impacts of GEC do not yet incorporate effects on interaction networks, or their explicit relationship to ecosystem services, resilience and human wellbeing (Carpenter *et al.* 2006a). Finally, our analysis highlights substantial variability among studies in both the magnitude and direction of effects of any given GEC driver on any given type of biotic interaction. If we are to reliably predict the effects of future GEC on community and ecosystem processes, then the greatest challenges lie in determining how biotic and abiotic context influences the direction and magnitude of GEC effects on individual biotic interactions, and in determining how the varying responses of multiple pairwise interactions translate into altered interaction structure of entire communities.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Box S1** Higher order effects of multiple GEC drivers on species interactions.
- Box S2** Effects of Global Environmental Change (GEC) drivers on biotic interactions.
- Box S3** The consequences of interaction network architecture for the effects of GEC on two different species interaction types.

**Table S1** Spreadsheet (Excel format) containing list of studies and their results on which to this synthesis is based.

**Methods S1** Description of methods and search terms used for literature review.

**Figure S1** CO<sub>2</sub> enrichment.

**Figure S2** N deposition.

**Figure S3** Climate change.

**Figure S4** Biotic invasions.

**Figure S5** Land use change.

**Figure S6** All drivers combined.

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