

Ecosystem assembly and terrestrial carbon balance under elevated CO₂

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Research aimed at understanding how the global carbon balance will change with elevated CO₂ has largely ignored the responses of individual species and genotypes. Yet, plant traits strongly influence the biogeochemical cycling of carbon. Here, we illustrate how differences in inter- and intraspecific responses to elevated CO₂ affect not only physiology and growth, but also higher order biotic interactions and lifetime fitness, ultimately leading to new ecosystem assemblages. We assert that the unique combination of inter- and intraspecific traits in these ecosystem assemblages ultimately determine how ecosystems respond to elevated atmospheric CO₂. Thus, the identity of species and genotypes in an ecosystem is a crucial element to consider in forecasts of global carbon balance.

Plant species and genotypes mediate ecosystem responses to rising atmospheric carbon dioxide

The goal of this review is to emphasize how elevated carbon dioxide (CO₂) can directly affect plant physiology, growth and fitness, causing changes in the assembly of terrestrial plant communities and, ultimately, ecosystem carbon cycling. Using the conceptual model in [Box 1](#), we examine the cascading influence of intra- and interspecific variation under forecasted atmospheric CO₂ conditions on biotic interactions, microevolution, ecosystem assembly and their consequences for carbon cycling. A variety of current studies are used to illustrate how changes in the distribution and abundances of individual species and genotypes within an ecosystem (referred to as species and/or genotype shifts throughout text) would have significant consequences for the carbon cycle.

Owing to human activity, current atmospheric concentrations of CO₂ are at their highest levels in more than 650 000 years [1]. Most research has focused on understanding the response of net primary production to elevated atmospheric CO₂ [2,3], rather than attempting to understand how the physiology and population biology of genotypes, species and communities respond to changes in the composition of the atmosphere of the Earth. For example, existing global climate–carbon cycle models are generally assumed to have little sensitivity to species identity [4]. Yet, plant species traits affect most ecosystem properties, including hydrology [5] and biogeochemistry

[5,6]. Other lines of research on species-specific responses to climate change have documented changes in plant phenology and distribution [7], but here we address how the rapid and continued rise in atmospheric CO₂ will directly affect the rearrangement of species and genotypes in ecosystems, which, in turn, can affect carbon cycling.

Cascading effects of species and genotype shifts on terrestrial carbon cycling

Elevated CO₂ has been shown to alter ecosystem-level productivity and decomposition [1], but we assert that the direction and magnitude of the response of an ecosystem to CO₂ [8] depends on the assemblage of species and intraspecific variation present in the system [9,10]. This is because the influence of CO₂ on ecosystem processes is

Box 1. Cascading effects of elevated CO₂ on ecosystem assembly and carbon cycling: a conceptual model

Although elevated atmospheric carbon dioxide (CO₂) has been shown to affect ecosystem carbon fluxes [1,9,23], we argue that its influence must cascade through an ecological hierarchy that begins with the physiological responses of individual plant species and genotypes. Here, we present a conceptual model of this cascade ([Figure 1](#)). Different shapes are used to symbolize species; genotypes are represented by different colors. Total ecosystem carbon (represented by 'C' triangles at bottom of figure) is a balance between ecosystem productivity (P) and decomposition (D). Empirical examples corresponding to different steps in the cascade are presented in three subsequent boxes and the main text. We focus on elevated CO₂, but other global change factors, such as trophospheric ozone, could be substituted for CO₂ in this conceptualization, because their influence would cascade in a similar manner.

Photosynthetic responses to increased CO₂ concentrations are determined primarily by genetically determined thresholds, which vary among species and genotypes. Net increases or decreases in photosynthesis translate into altered patterns of growth and often, changes in plant tissue biochemistry (black unbroken arrows). Altered growth and biochemistry can affect plant–plant ([Box 2](#)), plant–herbivore and other biotic interactions (broken arrows), as well as fitness ([Box 3](#)). Differential responses in growth, survivorship and reproduction to elevated CO₂ between species and genotypes will affect their abundance and persistence in communities, leading to new ecosystem assemblages.

New ecosystem assemblages will have consequences for terrestrial carbon balance because species and genotypes vary widely in many traits important for the carbon cycle, including photosynthesis, tissue quality, wood density, growth form and timing of growth. Temporal and spatial shifts in the combination of traits present in an assemblage will affect carbon fixation (photosynthesis). Carbon release (decomposition) depends on microbial decay of dead plant tissues and soil organic matter; rates of decay are

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controlled by feedbacks between plants and soil microorganisms. The net flux of CO₂ between the biosphere and atmosphere could increase, decrease or remain unchanged depending on the species and genotypes present. Ultimately, this flux will determine total

terrestrial carbon accumulation. However, the influence of species and genotypes is likely to be transient (Box 4), making it important to understand both the short- and long-term dynamics of new ecosystem assemblages.

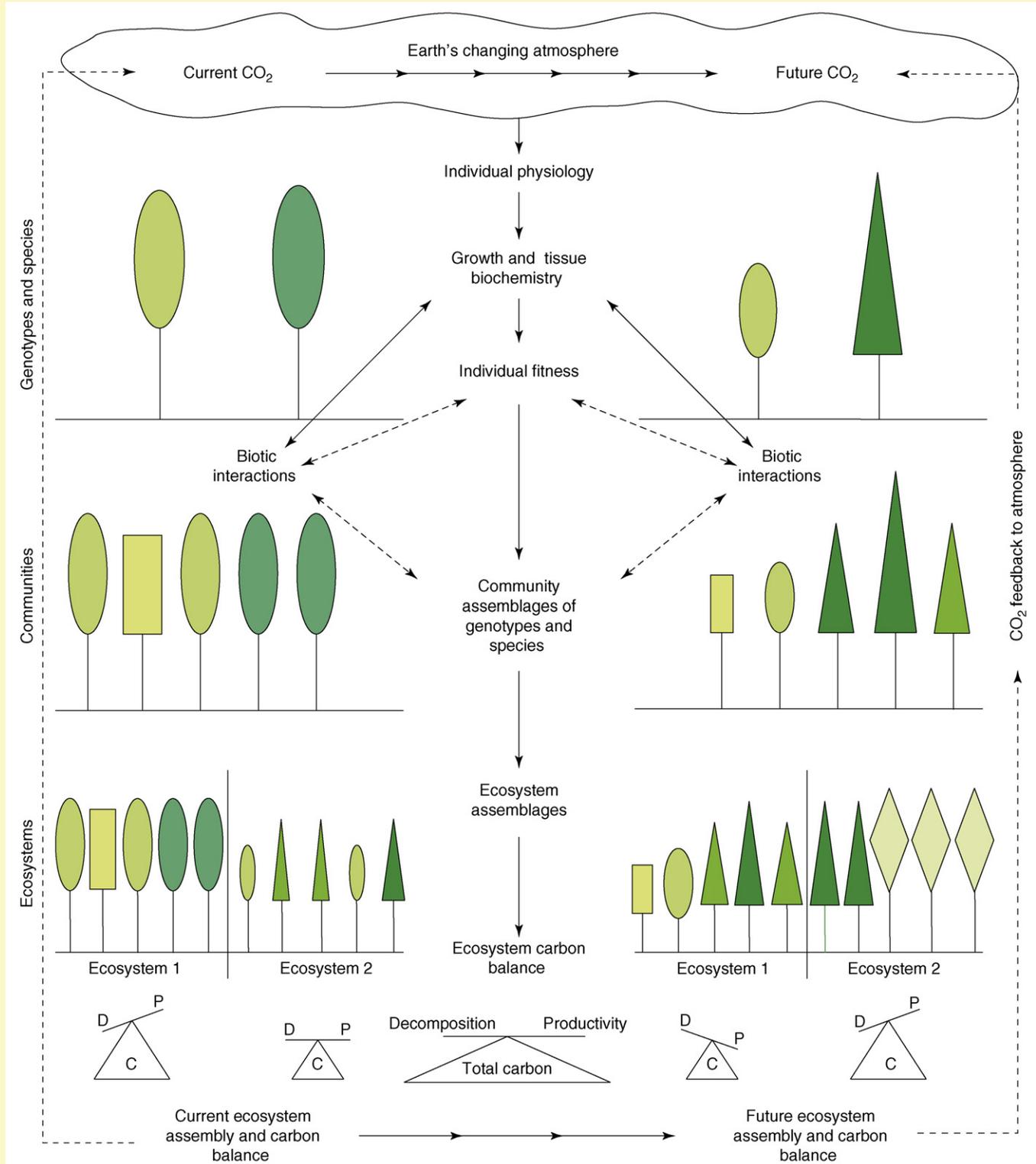


Figure 1.

manifested through an ecological cascade that begins with the physiological responses of individual plants (Box 1). Physiologically, species can respond to changes in CO₂ concentrations only within their genetically determined limits, which vary among and within species.

Plant physiology affects individual above- and below-ground growth, biochemistry, and inter- and intraspecific interactions, which, in turn, determine individual fitness. The role of microevolutionary responses [11] and biotic interactions [12] are often ignored in bioclimatic

models [13], yet differences in fitness affect which species and genotypes will persist, go extinct or migrate to assemble new communities [14]. These ecosystem species assemblages are highly dynamic through time, resulting in transient influences on ecosystem processes [15–17].

Plant responses to elevated CO₂ and the resulting species shifts can be strongly affected by interactions with other important environmental [1,12,18] and global change factors, including tropospheric ozone [19], nitrogen [18,20,21], temperature [7,16] and water [22]. We highlight examples of these interactions, but our main focus is to present the best available evidence demonstrating that intra- and interspecific variation in plant responses to elevated CO₂ has significant effects on ecosystem assemblages and ecosystem carbon balance.

Plant physiology links the terrestrial carbon cycle to the atmosphere

Changes in ecosystem-level productivity are, in part, driven by the differential physiological responses of species and genotypes to increased CO₂ (Box 1). Such species- and genotype-specific responses could alter the balance between above- and belowground biomass production and decomposition, which determines total ecosystem carbon accumulation. Extensive work from the global series of free air CO₂ enrichment (FACE) experiments has shown that elevated CO₂ triggers a physiological cascade in plants, enhancing photosynthesis [20,23] but decreasing stomatal conductance [20] and concentrations of Rubisco, the enzyme responsible for CO₂ capture in leaves [23].

Two reviews of FACE sites found that, under elevated CO₂, rates of photosynthesis were enhanced, but the relative change in assimilation rate varied from 0% to 60% depending on the species [20,23]. Photosynthetic responses depended on leaf-level nitrogen content, species and environment [20,23]. Similarly, at one FACE site with five genotypes of trembling aspen, *Populus tremuloides*, intraspecific responses to elevated CO₂ ranged from 0% to +40% for net photosynthesis and from 0% to –20% for stomatal conductance [24]. The genotypes at FACE represent only a small proportion of the genetic diversity in *P. tremuloides*, meaning that the sampled variation in physiological responses could be underestimated.

Too few genotypes have been studied in the FACE system to draw conclusions about intraspecific influences on ecosystems, but a synthetic assessment of FACE research concluded that species identity, rather than functional group classification, was an important determinant of ecosystem responses to elevated CO₂ [20]. A more detailed study of 16 species from four of the FACE sites showed that the maintenance of leaf-level carboxylation at elevated CO₂ depends on canopy nitrogen, which is determined by each species, genotype and/or assemblage of species and site factors [25]. Photosynthesis bridges the atmosphere and biosphere by transferring oxidized carbon, CO₂, to reduced forms utilized by plants [6]. Although net photosynthetic rates were enhanced by an average of 26% across FACE sites, this increase translated into smaller than expected gains in ecosystem net primary productivity (observed: +12%, predicted: +20%) [20]. Predictions for productivity enhancement based on functional groups alone did not accurately capture productivity responses; species identity and its interaction with the environmental conditions strongly mattered [20].

Genotype and species growth patterns vary under elevated CO₂

Species growth responses to elevated CO₂ can vary depending on their genetic identity and environmental conditions [18,26] (Box 2). Intra- and interspecific growth rates vary widely between species and can be enhanced, decreased or remain unchanged under elevated CO₂ [20,24,27,28]. This variation can result from differences in genotypes [29], competition [29] and environmental conditions, particularly nutrient [30] and water availability [20]. Despite large variation in shoot biomass responses (–44% to +90%) across 14 genotypes exposed to elevated CO₂, *Dactylis glomerata* exhibited only a weak genotype by CO₂ interaction over two years of growth. By contrast, *Bromus erectus*, the competitor of *Dactylis glomerata*, did not exhibit any genotype by CO₂ interactions [31]. Similarly, Ward and Kelly [11] showed that elevated CO₂ had no effect on the biomass production of six *Arabidopsis thaliana* genotypes.

Plant growth affects the accumulation of carbon in living plant biomass and soil organic matter, which includes decaying plant leaves, stems and roots. Although growth strongly affects net primary productivity, the cumulative

Box 2. Elevated CO₂ alters competitive interactions with consequences for ecosystem assembly

Changes in competitive outcomes under increasing CO₂ are likely to have a large role in the redistribution of species and genotypes [59] within and between ecosystems. Here, we present data from two experiments to illustrate how elevated CO₂ can change competitive interactions between species and result in an ecosystem dominated by a different species with unique traits. Our first example is from Aspen FACE, an experiment designed to address ecosystem scale questions about how species and genotypes mediate the responses of northern hardwood forest ecosystems to elevated atmospheric CO₂ [9,24]. Using mortality and growth rates of 600+ individual trees, Kubiske *et al.* [9] calculated a relative importance (RI) index for each species from 1997 to 2004 (Figure 1). RI values indicate the importance of each species compared with the total number and volume of trees in the community. Values were standardized (SRI) using 1997 RI

values [9]. SRI values indicate that elevated CO₂ enhanced the competitive ability of aspen, *Populus tremuloides* (Figure 1b modified with permission from [9]), whereas at ambient CO₂, the shade-tolerant maples, *Acer saccharum* (Figure 1a modified with permission of [9]), were able to increase in importance between 2000 and 2002.

Extrapolating results from one site to another within an ecosystem can be difficult as responses to elevated CO₂ depend on environmental conditions. This is evident in the experimental biomass responses of two co-occurring species – beech, *Fagus sylvatica*, and spruce, *Picea abies* (Figure 1c modified with permission from [18] based on data from [26]). They were grown for four years on an acidic soil and a calcareous soil at low and high nitrogen (N) availability and at ambient and elevated CO₂ ($n = 4$; CO₂ × N × soil × species) [26]. Elevated CO₂ enhanced spruce biomass in both soils, but beech

biomass was decreased on the acidic soil at elevated CO_2 [26]. The addition of N significantly enhanced both species performance on the acidic soil but not the calcareous soil [26]. Overall, spruce out-competed beech on the acidic soil at ambient and elevated CO_2 , whereas beech might outcompete spruce on the calcareous soil at

elevated CO_2 through time [18]. Switches in species assemblages triggered by elevated CO_2 and mediated by environmental context have the potential to alter forest carbon cycling particularly through their effects on root production [27,46], root decomposition [41,46] and plant–soil feedbacks [6,70].

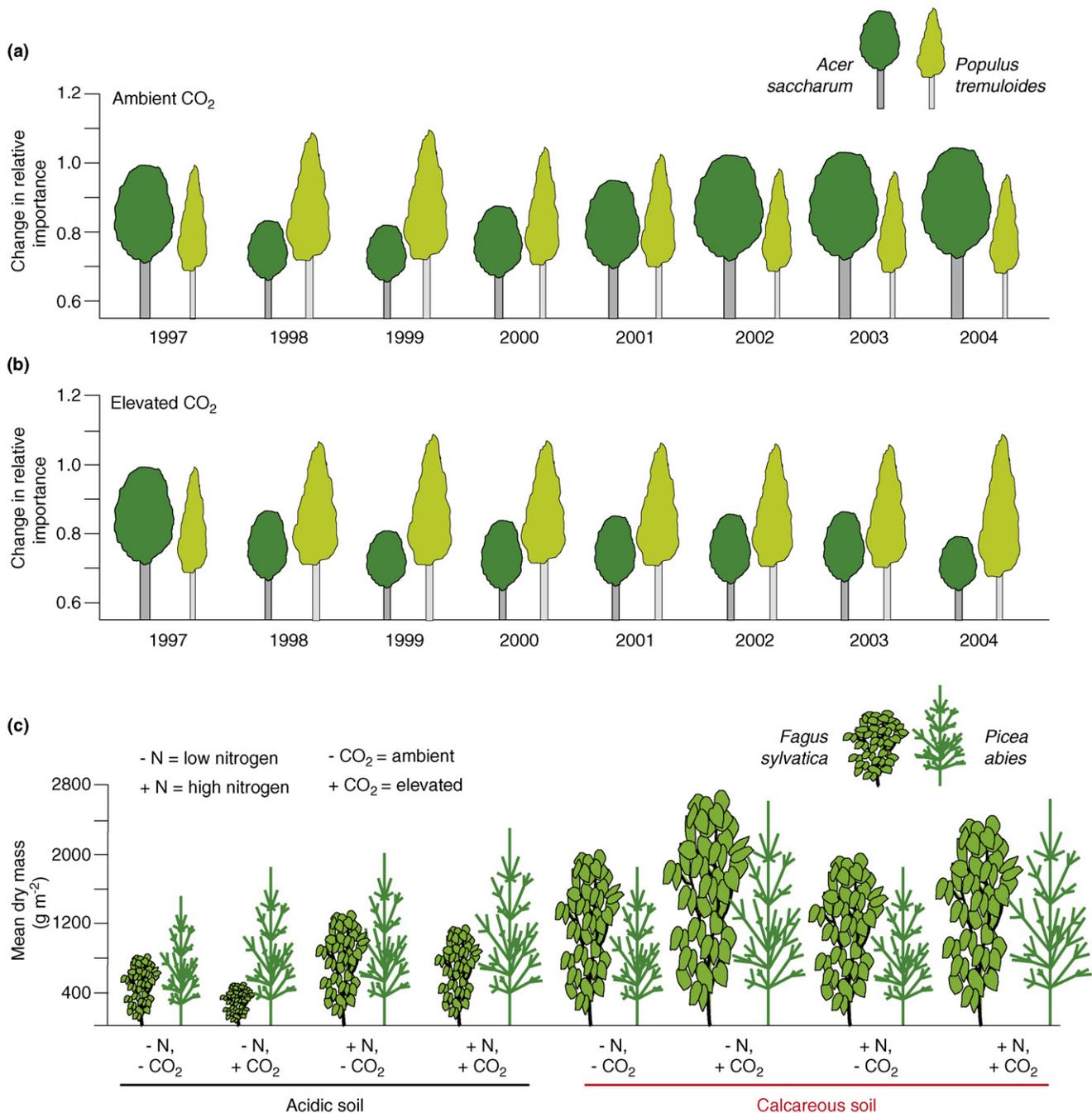


Figure 1.

balance between productivity and decomposition ultimately determines ecosystem carbon storage [18]. In forest ecosystems, carbon storage depends on stand age and not simply its growth rate [18]. Species with enhanced juvenile growth under elevated CO_2 will not necessarily have more biomass as adults [18], although they might have higher rates of survivorship [32] or reach maturity sooner, thus replacing slower growing species. Replacement of one forest species by

another could lead to increased carbon storage if, for example, wood volume increased. However, if the wood, roots or leaves of the new species decomposed more quickly than the previous species total ecosystem carbon could remain unchanged. Ultimately, the balance between productivity–decomposition at elevated CO_2 will be determined by the traits of the species and genotypes in an ecosystem assemblage (Box 1).

Inter- and intraspecific differences in biochemistry outweigh CO₂-induced effects on plant decay

Species vary widely in their biochemistry [5,33], and genotype is an important determinant of foliar [34–37] and wood [24,38,39] chemistry in many species. Inter- and intraspecific variations in biochemistry affect leaf [33,40], root [41] and wood [42,43] decomposition. In particular, rates of carbon loss (decomposition) are affected by concentrations of nitrogen, lignin, soluble sugars and secondary metabolites [40,44], whereas the loss of nitrogen from litter primarily depends on initial nitrogen concentrations [44]. Elevated CO₂ can dilute litter (dead plant tissues) nitrogen concentrations [20] and increase lignin concentrations; it has also been shown to increase wood starch and sugar concentrations in some genotypes of *Populus* [38] and silver birch, *Betula pendula* [39]. However, a majority of studies have concluded these slight changes in biochemistry resulting from elevated CO₂ have negligible effects on rates of litter decomposition [45,46].

Instead, the most significant effects of biochemistry are likely to result from ecosystem-level shifts in genotype and species composition rather than CO₂ effects on the biochemistry of leaves, roots or stems [44–46]. Elevated CO₂ increased the range of existing genotypic differences in leaf concentrations of condensed tannins and phenolic glycosides in *Populus* [35,36], which determine susceptibility to attack by insects, pathogens and mammals [35]. CO₂-mediated changes in these concentrations might affect the survivorship of individual genotypes [35] and their stand level distribution, with consequences for ecosystem-level decomposition rates and nutrient loss [37]. Elevated CO₂ increased net primary productivity but did not affect root turnover in pine, *Pinus taeda*, or sweetgum, *Liquidambar styraciflua*, forests [46]. Root turnover depended on the species and the size of the roots [46]. Similarly, elevated CO₂ has led to stand increases in paper birch, *Betula papyrifera*, which has more slowly decomposing roots than those of its co-competitor aspen, *P. tremuloides* [41]. This shift could increase ecosystem carbon storage (Box 1), but changes in ecosystem carbon storage will depend on how the competitive interactions of all the species (Box 2) and genotypes in this forest ecosystem will play out at elevated CO₂ [41].

Biotic interactions under elevated CO₂ will drive ecosystem assembly

Changes in the physiology, growth and biochemistry of individual species will probably affect biotic interactions, including competition [28], herbivory [36], pollination [47] and root–rhizosphere dynamics [6]. This can lead to shifts in the dominance of species and/or genotypes, affecting their influence on ecosystem properties [10,48]. An experiment by Grandos and Körner [49] has shown that liana growth can be enhanced under elevated CO₂, leading to increased liana abundance and reduced tree productivity [50]. Although the ecosystem would remain a lowland tropical forest, ecosystem carbon storage would decrease because lianas store much less carbon than do trees [10,50].

Species and genotypes exhibit wide variation in their individual responses to elevated CO₂, which is likely to change competitive interactions [11,31,32]. Baruch and Jackson [22] showed that changes in water use efficiency at elevated CO₂ improved the competitive ability of two invasive grass species and might increase their establishment in arid tropical savannas. Results of a FACE experiment have shown that elevated CO₂ affects the inter- and intraspecific competitive ability of aspen genotypes [9] (Box 2). Outcomes of competitive interactions depend not only on the direct physiological response to CO₂, but also nutrient availability [30], water availability [20,22], and the composition and diversity of the surrounding community [9,12]. For example, competitive interactions between juvenile beech, *Fagus sylvatica*, and spruce, *Picea abies*, varied depending on CO₂ concentrations [51,52], soil type [18,26] and nitrogen availability [18,26] (Box 2). The effects of CO₂ can cascade to affect other higher trophic level interactions [53].

Modeling has shown that increases in productivity resulting from increased CO₂ might reduce interaction strengths between trophic levels, reduce herbivore population sizes owing to poor food quality and increase recovery time of populations following disturbances [53]. In a FACE experiment, Agrell *et al.* have observed that elevated CO₂ can alter feeding preferences of tent caterpillars between species and between genotypes [54]. Greenhouse and FACE studies have shown that CO₂ can affect the herbivore-induced chemical defense responses in both *Arabidopsis* and aspen trees [19,55]. Conversely, a greenhouse experiment demonstrated that herbivores could modify plant responses to elevated CO₂ (Box 3). A recent literature

Box 3. Herbivory modifies *Arabidopsis thaliana* fitness responses to elevated CO₂

Quantifying lifetime fitness is the most direct way to measure plant performance, assess the effects of elevated CO₂ as a selective pressure, and make predictions about the future performance of a species or genotype [58]. Elevated CO₂ can have positive, negative or neutral effects on lifetime fitness, depending on the species or genotype [57,58]. However, these responses can be modified or even reversed when measured under conditions that include plant–plant [12,28] or plant–herbivore interactions [58]. Here, we present one of the few published studies that examines the interactive influence of CO₂ and herbivory on lifetime fitness.

Although research often measures the interaction between CO₂ and other abiotic factors (e.g. nitrogen, water or ozone), it is also important to consider plant responses in the context of the biotic interactions that are already known to strongly affect lifetime fitness. Herbivory can limit fitness through its negative effects on growth,

survivorship and reproduction, depending on the species involved [58]. In some annuals, biennials and short-lived perennials, herbivory limits seed production, and the quantification of seed production in these species and genotypes accurately reflects their lifetime fitness. In a recent study by Bidart-Bouzat [58], three genotypes of the annual, *Arabidopsis thaliana* (Figure 1a–c) were grown at two CO₂ concentrations; the genotypes differed in their flowering phenology and chemical defenses (i.e. glucosinolates). Second instar larvae of the diamondback moth, *Plutella xylostella* (Figure 1c), were added to the plants when they reached the early bolting stage (growth of flowering stalk) [58].

In the no-herbivore treatment, all three genotypes had increased seed production (Figure 1a–c). Individual *A. thaliana* plants with larval feeding had ~20% less leaf area and 20–50% lower seed production (Figure 1a–c). This work demonstrates that herbivory by

the diamondback moth reduced or cancelled the positive effect of elevated CO₂ on seed production in *A. thaliana*. Further, herbivory eliminated the genotype-specific responses to elevated CO₂. These

results suggest that without consideration of important biotic interactions, such as herbivory, species and genotype fitness will be poorly estimated. Figures 1a–c were modified with permission from [58].

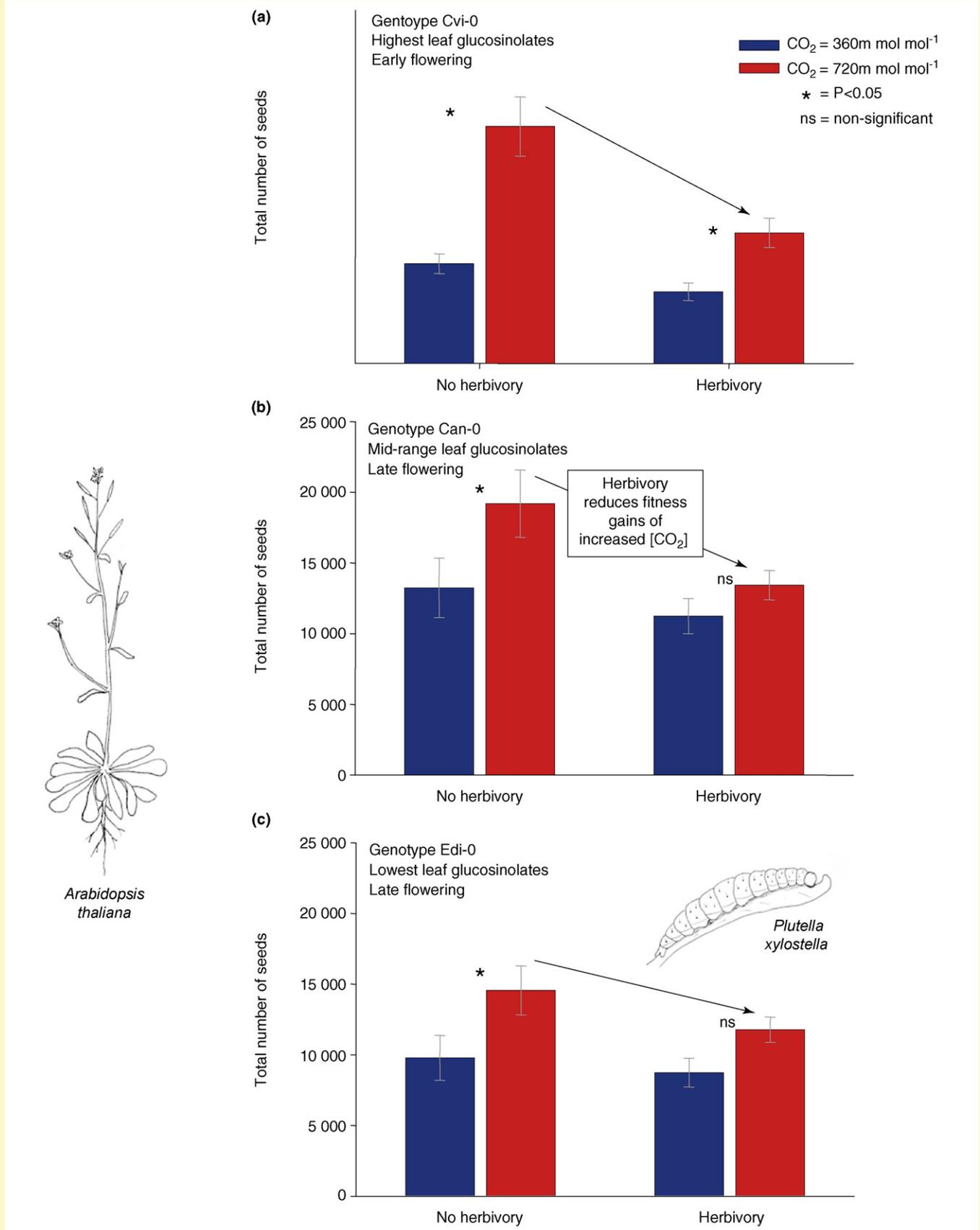


Figure 1.

review has shown that elevated CO₂ could affect flower–pollinator relationships by altering nectar production, which was increased in five species and decreased in four species [47]. Thus, without consideration of biotic interactions, effects of elevated CO₂ on plant performance might be over- or underestimated.

Elevated CO₂ can affect interactions with soil microorganisms, which are responsible for a majority of the soil carbon transformations affecting nutrient supply and ecosystem carbon storage [6]. For example, Chung *et al.* showed that elevated CO₂ altered soil fungal metabolism by increasing the production of extracellular enzymes that decompose plant-derived carbon compounds [56]. Plant responses to elevated CO₂ cascade into the soil and drive the activity of soil microorganisms; in turn, soil microorganisms influence plant growth by regulating nutrient supply, which could feedback to affect species and genotype assemblages [6]. Together, changes in biotic interactions and feedbacks triggered by elevated CO₂ are likely to affect distribution of individual species and genotypes, thus altering ecosystem assemblages and major flows of carbon through ecosystems.

Variation in intra- and interspecific responses to elevated CO₂ has consequences for lifetime fitness

Lifetime fitness is the relative number of offspring that an individual contributes to the next generation, and is determined by the combined influence of reproduction and survivorship. A review of 79 crop and wild species responses to elevated CO₂ showed average increases in flower, fruit and seed production across all species of 19%, 18% and 16%, respectively [57]; interspecific differences among the 55 wild species in the response to CO₂ were large (–25% to +30%) [57]. This variation indicates that some species will become more abundant with elevated CO₂, whereas others will decline or go extinct. Although seed production increased, seed nitrogen concentrations declined in most wild species, which could affect germination success, seedling size and survivorship [57].

Many plants also exhibit genotypic variation in fitness responses to elevated CO₂ [11,32]. A study of six *A. thaliana* genotypes found significant genotypic differences in survivorship at high CO₂ concentrations without significant intraspecific differences in seed production [11]. However, another study of *A. thaliana* found significant genotypic differences in seed production at elevated CO₂ but the addition of herbivory reduced those differences [58] (Box 3). There were no interactive effects of CO₂ and genotype on seed production for two perennial grass species, although the authors concluded that there was potential for some adaptive responses of *Dactylis glomerata* shoot biomass to elevated CO₂ [31]. A greenhouse study examining the response of *Acer rubrum* to different CO₂ concentrations, found that plant growth, germination rates and survivorship responses to CO₂ depended on maternal family and geographic origin [32]. Similarly, mortality rates for two of five *P. tremuloides* genotypes in a FACE experiment increased under elevated CO₂, reducing their relative importance in the stand [9].

Given that few genotypes of any species, relative to the total amount of existing intraspecific variation, have been evaluated at elevated CO₂, our understanding of the importance of genotypic variation in short- and long-term responses to a rapidly changing atmosphere is extremely limited. Overall, the evidence suggests that at high CO₂ concentrations the fitness of species is differentiated by their reproductive abilities, whereas the fitness of genotypes is separated by differential survival rates [11]. The differential effects of elevated CO₂ on fitness could influence the adaptive response of species and/or genotypes, but they could also alter ecosystem properties [48], depending on which traits are responsive [14]. For example, increases in tree height could improve survivorship and alter above-ground carbon stocks [59].

Evolutionary responses to a changing climate have had an important role in species persistence, migrations and extinctions during the past 25 000 years [14,60]. Although the current period of rapid climate change represents an episode of intense selection pressure, adaptive responses might be limited as gene flow from one population to another is restricted by species-specific rates of migration and land-use changes [14]. However, lags in evolutionary responses are likely to affect ecosystem responses through their interaction with growth and survivorship [14,59], generating phenotypic differences in lifetime fitness. Species and/or genotypes that grow faster at elevated CO₂ might competitively exclude other individuals, thus changing the ecosystem carbon balance (Box 1).

New species assemblages and the cascading effects on ecosystem processes

Given the different species and genotype responses to CO₂ documented in numerous studies outlined above, we argue that the direct effects of elevated CO₂ will contribute to the species shifts already resulting from climate change [7] with consequences for ecosystem carbon cycling (Box 1). Experimental evidence suggests that the cascading effects of elevated CO₂ on individual species and genotypes trigger the reassembly of communities (Box 2). For example, at one FACE site, elevated CO₂ altered community composition and productivity through its differential effects on two predominant, invasive species, honeysuckle, *Lonicera japonica*, and Japanese stilt grass, *Microstegium vimineum* [61]. However, the responses of the two species were transient and influenced by soil moisture [61].

Work at another FACE site has shown that CO₂ can alter the composition of forest stands, with the decline or expansion of a species depending on the identity of the competitor species (Box 2) [9]. The changes in the overstorey communities in this experiment altered the assembly of understorey communities through canopy differences in light transmission [62], affecting nitrogen acquisition and total biomass [62]. These species shifts have potentially larger consequences, because the responses of dominant forest species to elevated CO₂ can cascade through the entire ecosystem, affecting soil microbial communities [56,63], and the transformation and accretion of soil carbon [64].

In addition to species shifts, a growing body of work has demonstrated that genotypic variations in *Populus*

angustifolia, *P. fremontii* and their hybrids strongly affect ecosystem processes, including litter decomposition, energy flow and nutrient cycles [34,48,65]. Genotypes of a related species, *P. tremuloides*, also vary in their genetic, biochemical, physiological, growth and competitive properties [24]. Furthermore, the expression of these traits vary between genotypes under elevated CO₂ [24], which have led to increases in some genotypes and diebacks of others; however, the consequences for ecosystem carbon cycling are not yet apparent [24]. Modeling work by Rehfeldt *et al.* [59] has shown that the redistribution of the widely occurring *Pinus sylvestris* genotypes in response to a changing climate will result from intraspecific differences in growth rates and height, leading to the competitive exclusion of some genotypes and changing the volume of wood production, and thus carbon storage, across the landscape.

Research on global warming [15], invasive species [22,66] and biodiversity [1] has demonstrated that changes in plant species composition can affect ecosystem carbon cycling through their effects on productivity and decomposition (Box 4). Although shifts in the growth and predominance of existing species can alter the ecosystem carbon cycle [10], the influence of these species shifts vary through time [15,16], making it difficult to predict ecosystem-level responses to global changes such as elevated CO₂ [15–17] (Box 4).

Box 4. Plant species shifts induce transient changes in soil carbon

Changes in the species and/or genotype composition of an ecosystem can strongly affect rates of soil carbon accumulation and loss over short and long periods of time. Making predictions about how shifts in species identity and elevated CO₂ will affect soil carbon requires the consideration of transient responses of the soil and vegetation. An excellent example of such transient responses comes from a long-term study examining the effects of ecosystem warming on a montane meadow system in the Colorado Rocky Mountains [15,16].

Warming treatments were initiated in 1991 and have continued to the present [15,16]. After ten years, warmed plots experienced a loss of carbon stored in soil organic matter (200 g ± 150 g C m⁻²) in the top 10 cm of soil [15,16]. However, warming was not the only cause for this loss of soil organic carbon (SOC). Soil warming triggered a decline of shallow rooted forbs and increased sagebrush biomass (Figure 1a; with permission from [15]). Initially, these vegetation changes reduced SOC [15,16], but SOC losses are predicted to be partially offset by decreases in the rate of litter decomposition owing to the recalcitrance of sagebrush litter [16].

Using a simple, first-order, linear model that considers productivity, decomposability of litter and soil microclimate, Saleska *et al.* estimated that the SOC would recover to pre-warming levels, but recovery could take decades (Figure 1b; with permission from [16]). The unbroken line follows the observed changes in SOC, whereas the broken line represents the modeled recovery. Although shrub productivity was less than forb productivity, the estimated forb litter decay constant (0.0054 day⁻¹) was 2.25 times higher than the shrub litter decay constant (0.0024 day⁻¹), hence forb litter decomposed faster than shrub litter [16]. Essentially, shrub litter reduced soil respiration (loss of CO₂), and pushed the system toward the slow accumulation of soil carbon over a long time period. The model makes several, important simplifying assumptions but effectively illustrates the dynamics of a large, complicated system, the SOC pool.

Understanding long-term, ecosystem level consequences necessitates a modeling approach

Models represent the best available tool to tackle these large-scale, transient responses in ecosystem species assemblages. Some existing global climate–carbon cycle models include competition between plant functional groups, rather than species, using a Lotka–Volterra approach [4]. Results from numerous competition studies performed under elevated CO₂ (reviewed in [28]) could be used to develop competition coefficients for considering species and genotypes more explicitly in existing models, such as the Hadley terrestrial carbon cycle model; this dynamic global vegetation model incorporates the growth and respiration of five plant types, broadleaf tree, needle-leaf tree, C₃ grass, C₄ grass and shrub, but does not explicitly include species or genotypes [4]. Another approach would be to link gap-dynamics [67] or statistical models [68], which incorporate species-specific interactions to global climate–carbon cycle models.

Given the extensive body of bioclimatic research [68], it is reasonable that this information could be coupled to global climate–carbon cycle models that consider the effects of ‘new’ ecosystem assemblages on regional and global carbon cycling. However, any bioclimatic model utilized in these endeavors should explicitly incorporate plant–plant interactions, because these can vary widely

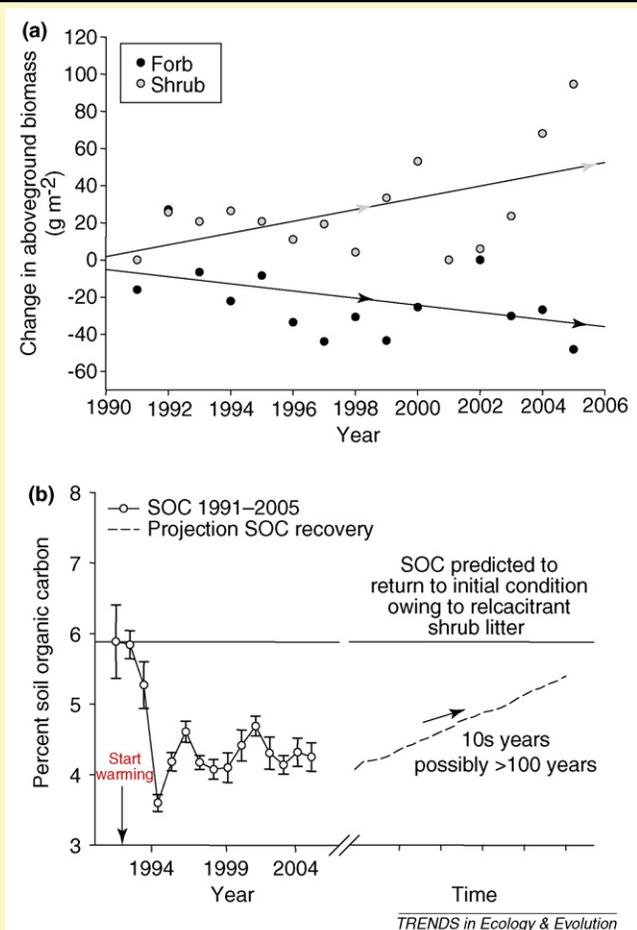


Figure 1.

through time and space [12]. Adding species or genotype specific responses to already complex models is a considerable challenge. Further, tackling gene–ecosystem or species–ecosystem linkages experimentally is complicated by the staggering diversity of species and genotypes.

Which species and genotypes should be included in models and experiments?

One approach used in experiments [20,21] and models [4] to make generalizations about the influence of species on ecosystems is to categorize species by a single important attribute that confers similarity of function; this plant functional group concept does not capture important inter- and intraspecific influences highlighted here [20]. We think the newer concept of foundation species will improve upon the idea of functional groups. The foundation species concept can guide the development of models and field experiments to understand how variation within and between species regulates ecosystem functions. Foundation species are defined by Whitham *et al.* [48] as ‘species which structure communities by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes’.

For example, the development of spruce forest ecosystems, *Picea sitchensis*, on deglaciated landscapes in Glacier Bay Alaska is strongly shaped by the presence or absence of the nitrogen fixing alder, *Alnus sinuate* [69]. At sites without the long-term alder dominance, the resulting spruce forests have different densities and growth rates; ecosystem carbon pools are up to 80% smaller than sites once dominated by alder [69]. Intraspecific influences on community and ecosystem processes have not been as well studied, but Whitham *et al.* have shown that heritable variation in tannin production in *Populus angustifolia*, *P. fremontii* and their hybrids can affect arthropod community composition and leaf litter decomposition [48].

A focus on foundation species in a given assemblage where sufficient information exists will enable scientists to better tackle gene–ecosystem linkages. Many of the FACE sites have deliberately incorporated multiple, common species in these large-scale experiments designed to understand how whole ecosystems will respond to elevated CO₂, and one, the Aspen FACE experiment has incorporated both inter- and intraspecific variation. Results from this global network of experiments have demonstrated that both species [20,61,62] and genotype [24] identity affect ecosystem level responses, and highlight the importance of understanding the feedbacks between individual plant responses and ecosystem-level responses to elevated CO₂ for ecologists and modelers alike.

Conclusions

The influence of elevated CO₂ on ecosystem processes is transmitted through an ecological cascade mediated by the unique combination of species and genotypic specific traits present in a given ecosystem assemblage [6,9] (Box 1). Substantial evidence is mounting to suggest that increasing atmospheric CO₂ will directly and indirectly alter the composition of plant communities [7,15,17] leading to new ecosystem assemblages (Box 2). However, ecosystem assemblages are highly dynamic through time, making

their influence on ecosystem productivity and decomposition transient [15–17] (Box 4). To accurately predict how carbon cycling in different terrestrial ecosystems will respond to elevated CO₂, it is important to consider the responses of individual species and genotypes, their interactions with other organisms (Box 3), and resulting feedbacks. Future research should aim to: understand linkages between species and/or genotypes, ecosystems and the atmosphere [8], with emphasis on characterizing and understanding the responses of foundation species from different ecosystem assemblages; and should address how elevated atmospheric CO₂ will interact with other global changes, including altered temperatures and precipitation, increased nitrogen deposition and increased tropospheric ozone, to shape ecosystem assembly.

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