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Review

Elevated CO_2, nutrition dilution, and shifts in Earth's insect abundance

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Declining insect populations are concerning, given the numerous ecosystem services provided by insects. Here, we examine yet another threat to global insect populations — nutrient dilution, the reduction in noncarbon essential nutrients in plant tissues. The rise of atmospheric CO_2, and subsequent 'global greening', is a major driver of nutrient dilution. As plant nutrient concentrations are already low compared to animal tissues, further reductions can be detrimental to herbivore fitness, resulting in increased development times, smaller intraspecific body sizes, reduced reproduction, and reduced population sizes. By altering herbivore populations and traits, nutrient dilution can ramify up trophic levels. Conservation of Earth's biodiversity will require not just protection of habitat, but reductions in anthropogenic alterations to biogeochemical cycles, including the carbon cycle.

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Introduction

The commercial use of fossil fuels for energy began in the early 1800s, rising from levels consistently below 300 ppm for the previous 20 million years [1] to >420 ppm today [2]. Given that emissions have yet to peak [3], Earth is likely to continue to face numerous consequences of humanity's ongoing combustion of fossil fuels. But what are the consequences? The phrase 'climate change' emphasizes the warming temperatures, altered patterns in precipitation, and increasing intensity of storms that are becoming ever more severe across the globe [4]. Rising sea levels and ocean acidification are further frightening outcomes [5]. We examine yet another effect that is not directly visible to the human observer and far less studied — nutrient dilution — the reduction in the concentrations of essential elements in plant tissues that can result from carbon fertilization due to increasing levels of atmospheric CO_2 [6,7].

These reductions in noncarbon elements are bad news for the plant consumer. Human deficiencies in iron, nitrogen, and zinc are all expected to increase over the next few decades in response to elevated CO_2 (eCO_2) [8]. Nutrient dilution also has repercussions for Earth's insects with variable fitness predictions expected among taxa, trait groups, and under different habitat conditions. Altered herbivore populations and traits are further expected to have repercussions for higher trophic levels but responses of predators and parasitoid to eCO_2 have rarely been empirically tested. Here, we examine repercussions of increasing levels of atmospheric CO_2 on plant nutrient concentrations and the expected consequences for these shifts across plant and insect food webs.

How does eCO_2 affect plants?

Increases in CO_2 are expected to have effects on plants from cellular to community levels of organization. Individually, plants under eCO_2 increase photosynthesis and growth [9] and vary in phenology [10]. They are also built differently, exhibiting increased levels of carbon-based herbivore defenses, including structural carbon-based defenses, phenolics [11], and leaf toughness [12] but decreased nitrogen-based secondary compounds [13]. Plant communities under eCO_2 can experience shifts toward greater dominance of invasives, crop weeds [14], fast growers, nitrogen fixers, angiosperms over gymnosperms [13], woody plants over grasses [15], C3 over C4 grasses [16], and prevalence of specific taxa such as poison ivy [17].

Rising atmospheric CO_2 can further cause reductions in the concentrations of noncarbon elements in plant tissues (e.g. nitrogen, phosphorus, potassium, magnesium, iron, and zinc). When plants under CO_2 fertilization displace these elements that are essential for life with more carbohydrates, this can result in nutrient dilution. Other hypotheses for the mechanism behind this ubiquitous plant response to eCO_2 have also been proposed

Box 1 Why does eCO_2 reduce plant nutrient concentrations?.

Reductions in the elemental concentrations of plant tissues under increasing atmospheric CO_2 may be a response of *H1.1)* nutrient dilution — i.e. increased growth of plants resulting in the reduction of concentrations of essential elements in plant tissues. CO_2 fertilization can generate nutrient dilution of noncarbon elements, assuming it generates growth and the availability of other elements for uptake remains constant [29]. Additionally, several other hypotheses for reductions in plant tissue elemental concentrations have been proposed. None of these hypotheses are mutually exclusive to nutrient dilution via additional plant growth.

Three hypotheses suggest mechanisms of plant physiology, predicting that plants under eCO_2: *H1.2)* have less demand for other nutrients due to reductions in RuBisCo levels, resulting in increased leaf C:N [65], *H1.3)* reduce photorespiration, inhibiting assimilation of some soil nutrients [66], and may also *H1.4)* reduce the amount of time that stomata are open, reducing uptake of nutrients due to reduced transpiration flux [67] and further suggesting effects on global water balances [68].

Two hypotheses implicate additional anthropogenic effects on plant quality: *H1.5)* Selection for high-yielding crop genotypes has unwittingly selected for nutrient-poor varieties [69]. This is unlikely a full explanation of the phenomenon of plant tissue nutrient concentration declines, given these are also occurring in natural systems [23,28,29] and in eCO_2 experiments [70]. *H1.6)* Reductions in atmospheric deposition of nitrogen due to reduced use of nitrogen fertilizers and air quality regulations within specific global geographies and are causing reduced concentrations of plant tissue nitrogen concentrations [71]. However, this hypothesis does not account for reductions in other nutrients [6,29], nor does it fully account for reductions in plant tissue nitrogen concentrations [72].

Finally, *H1.7)* eCO_2 may reduce litter decomposition rates, reducing the flow at which nutrients are recycled back into the system [73]. This scenario could be catalyzed by other mechanisms causing reductions in forage quality and resulting in a positive feedback loop toward continuous declines.

(Box 1). Early studies reporting reduction in plant tissue nutrients with eCO_2 came from crop systems [7,18] and have since been verified by meta-analyses [6,13,19–21] and long-term studies [22,23]. Plant tissue carbon is also affected by eCO_2, with increases in starch and total nonstructural carbon, especially for slow-growing plants, and decreases in structural carbon [12,13]. Such shifts in nutrient concentrations of plants, including availability of nitrogen, carbon, and other macro- and micro-nutrients — occurring at the global scale — have large potential to reshape Earth's food webs [7].

Which plants are exhibiting nutrient dilution and where?

Declines in essential elements in response to increasing atmospheric CO_2 vary in magnitude with plant taxa, geographies, and ecosystem type. Across taxa, C_4 grasses may not have as large of declines in nutrient concentrations as C_3 grasses [24]. Legumes, with their symbiotic nitrogen-fixing rhizobium bacteria, exhibit reduced declines in tissue nitrogen concentrations under eCO_2 [6], including leguminous trees [21]. Across abiotic geographies, plant tissues reflect environmental nutrient availability, especially soil nutrient gradients [25]. Plant consumers are more likely to be limited by a given essential nutrient in times and places where that nutrient is in short supply, such as in areas with old soils, inland geographies, and flat topographies [26]. This is further magnified for nutrients that cannot be stored in the body, such as cobalt and sodium [26]. Across ecosystem type, systems under annual production cycles such as temperate grasslands may exhibit greater nutrient dilution as a greater proportion of standing green plant biomass production represents recent growth. However, evidence of long-term nutrient dilution is ubiquitous, spanning croplands [27], grasslands [22,23,28], forests [29], and even marine systems [30].

Herbivore responses

The assimilation of elemental building blocks into food webs starts with primary producers. As primary producers are generally nonmobile, adaptations including modular growth/senescence, dormancy, and the ability to turn off DNA repair, allow them to survive under variable conditions and result in reduced but highly variable nutrient concentrations in their tissue compared with homeostatic animals [31]. Herbivores face the challenge of building their own tissues from this often low-quality food source and can be limited by a number of essential elements [32], many of which are diluted in plant tissues with CO_2 fertilization [6].

In a meta-analysis of insect herbivore responses to eCO_2, herbivores declined in growth rate (–4.5%) and pupal and adult weight (–5.5%) and increased in consumption rate (+14%) and development time (+3.5%) [13]. However, not all herbivores respond the same, and herbivore abundance responses are particularly variable [13]. For example, phloem feeders consuming plants under eCO_2 have reduced development times and increased fecundity and abundances, whereas folivores exhibit increased development times and decreased fecundity. Chewing herbivores decline under eCO_2 with the most studied order of Lepidoptera averaging severe (–65%) reductions in abundance, especially within leafminers [13,33].

Why do phloem feeders do better under eCO_2? Benefits may be related to their endosymbionts or changes in the quantity and/or quality of plant carbon, but few studies have evaluated changes in the chemistry of phloem.

Alternatively, sap feeders may have more access to essential nutrients through consuming dynamic phloem and their efficient filtering abilities, whereas chewing herbivores must consume more nutritionally static tissues and have no mechanism to excrete excess carbon [7].

But chewing herbivores are hardly a monolithic group and vary greatly in nutrient needs. Within grasshoppers, optimal diets can range from needing nearly double protein versus carbohydrates (*Melanoplus femurrbrum*) to 2.5 times more carbohydrates than protein (*Schistocerca cancellata*) [34,35]. Locusts are generally more carbohydrate limited compared with other chewing insect herbivores, including other grasshoppers, and eCO_2 is predicted to promote increasing locust outbreaks [36]. In addition to taxonomic variation, body size can affect nutritional needs. Smaller insect herbivores have greater concentrations of nutrients per unit mass, both interspecifically [37,38] and in earlier ontologies [36,39]. This means smaller herbivores *ceterus paribus* require more protein-rich food than larger herbivores and may be less able to adapt to reduced concentrations of nitrogen [26]. Finally, specialist herbivores are more negatively affected by nutrient dilution than generalists with the ability to host-switch to more nutrient-dense plant taxa [13].

The abiotic drivers of temperature, precipitation, and biogeochemistry interact in ways we are just discovering (Kaspari and Welti 2024). Herbivore protein limitation can both increase [40] and decrease [41] with rising temperatures. Herbivores may be more limited by carbohydrates in dry conditions [36] and more protein limited in wet habitats [42], suggesting greater potential for nutrient dilution effects on herbivore populations with increasing moisture and plant biomass. Other aspects of the herbivore environment are also worthy of study. Both pathogen infection [43] and predation pressure [44] can generate herbivore diet switches to more carbohydrate-rich food sources, suggesting top-down controls may mediate responses to nutrient dilution. Similarly, it seems plausible that herbivores, as predators of N-defended plants, could benefit from reductions in secondary compounds under eCO_2 could benefit herbivores. In sum, Earth's enormous diversity of insect herbivores — ontogenetically and within and between species — likely combine to generate a variety of responses to eCO_2-induced nutrient dilution (Figure 1).

Consequences across the food chain

Not just herbivores, but decomposers, and coprophagous insects — especially those that specialize on herbivore feces and carcasses — are likely to face similar declines in noncarbon essential nutrient concentrations in their food sources under eCO_2. Reduced populations of decomposers and coprophagous insects are additionally troubling as this can decrease nutrient cycling rates, creating a positive feedback loop toward increasingly lower nutrient availability.

Consequences for pollinators are likely mixed: plants under eCO_2 have reduced protein concentrations [23] but may increase nectar production [45] and increase nectar concentrations of glucose and fructose [46]. Insect visitation rates to flowers may also increase under eCO_2, potentially benefiting plants in the form of increased pollination and seed set [10]. We predict that predacious Hymenoptera, like wasps, that build colonies from nectar and animal prey will be less impacted by eCO_2 than bees that do so on a purely plant-based diet of nectar and pollen.

While omnivores, predators, scavengers, and parasitoids consume higher quality food and are not likely to be directly limited by altered plant quality, indirect effects due to altered populations and traits of their prey may affect their populations. For example, omnivorous ants may benefit from increased sugar availability from farmed aphids; one study found aphids grown on plants under eCO_2 exhibited a tripling of their production of honeydew, which doubled the frequency of visits by tending ants [47]. Increased development times of herbivores may increase the time window where vulnerable life stages are susceptible to parasitoids and predation. However, reductions in herbivore populations can result in reductions in populations of higher trophic levels through a 'dilution' of prey availability in space [48]. Differences in rates of insect declines by trophic level are explored in Box 2.

How do herbivores deal with nutrient mismatch?

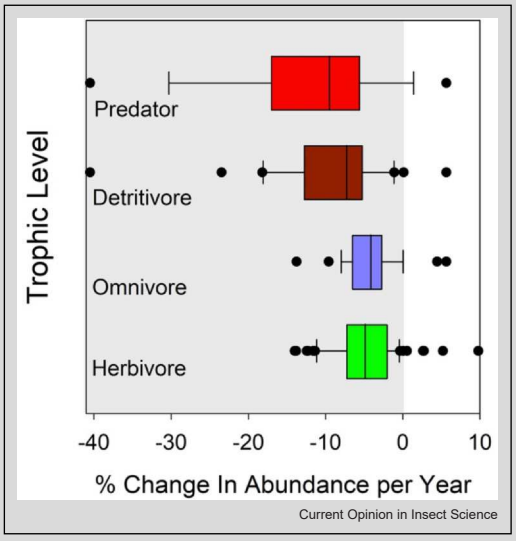
Fitness costs due to differences in nutrient densities in food and consumer requirements decrease as interactions move up the food web, with primary consumers likely to face the greatest nutrient mismatches of consumer guilds [49]. Herbivores can deploy several strategies to cope with variation in nutrient availability in relation to their needs. Strategies include:

1) movement, from patch selection to migration, to locate higher quality food,
2) diet switching, from selecting different parts of the same plant [50] to including scavenging and omnivory for 'herbivores' and detritivores,
3) using variation in microclimate to alter optimal digestion of particular nutrients [41],
4) compensatory consumption [7],
5) symbiosis with microbiota for increased extraction of nutrients from food,

Box 2 Insect declines magnify through the food web.

Herbivores uptake life's elemental building blocks from plant tissues and concentrate them in their flesh, passing this improved food quality onto their predators and beyond. Under nutrient dilution, this suggests two scenarios based on the balance of bottom-up and top-down forces regulating herbivore populations [74]. *H2.1)* '*Bottom-up*' predicts that nutrient dilution–caused declines in herbivore populations ramify upward to decrease predator abundance, whose rarity further puts them at risk of local extirpation [75]. *H2.2)* '*Rock and a Hard Place*' predicts herbivore declines will be higher, as they suffer from the consequences of malnourishment, longer development times, and the increasing susceptibility to predation that results.

The van Klink synthesis on global insect declines [76] gives an early clue of a strong bottom-up effect of herbivore declines on food webs (Fig. i). When each of the 130 insect families (12 007 species) for which species data are available are assigned to trophic groups [77] — herbivores, predators, omnivores (mix of plants and animals), and detritivores (dead plants and animals and the microbes that colonize them) — families of predatory insects have over twice the annual decline rate of the two groups eating live plants (General Linear Model, $p < 0.001$).



The magnitude of decline (% change per year) across 130 insect families varies with their diet. Data summarized from Ref. [76] with diet records compiled at the family level from a total of 12 007 records. Box and whisker plot reflect the median, 25 and 75th percentiles, 10th and 90th percentiles, and outlier points. The gray zone represents families that are declining in abundance over time.

6) nutrient storage, including storage in the body or external caching [37], and
7) taking a direct fitness hit such as through reductions in growth or reproduction [51].

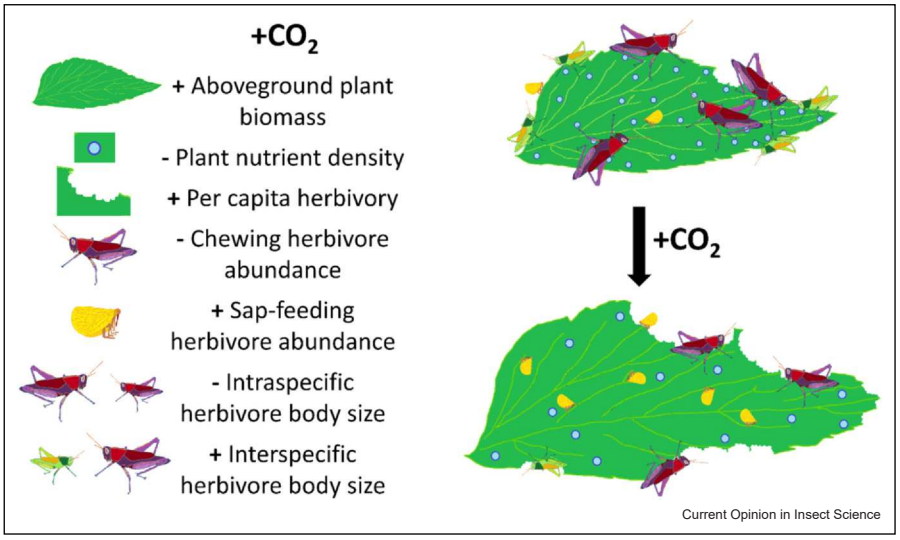
Some of these strategies may allow persistence of herbivore taxa under increasing CO_2 and subsequent reductions in essential elements such as nitrogen. However, strategies can be evolutionarily constrained and can come with fitness costs, resulting in reductions in herbivore populations [7].

Open questions

While it is established that eCO_2 alters plant nutrient concentrations [6] with clear implications for insect herbivores [13], long-term, distributed networks of studies that combine plant chemistry and consumer responses remain rare (US LTER sites can provide an exception) [28]. Such long-term studies require investment that take years to pay off in unique temporal signatures. Spatially, eCO_2 field experiments such as FACE have 1–30 m diameter footprints, adequate for plants and soils, but inadequate for mobile herbivores. For example, under eCO_2, herbivory is known to increase [13], but in small-scale field experiments, eCO_2 may be observed to reduce chewing insect herbivory as insects vacate these patches of less desirable forage [52].

Further unexplored topics include responses of predators, parasitoids, and plants to changes in herbivore populations, traits, and life histories. Herbivore-relevant compounds are rarely measured in studies of eCO_2 effects focusing on insects, including structural and nonstructural carbons, plant toughness, and plant-defensive compounds. These responses are likely co-occurring with other effects of eCO_2, complicating predictions. For example, tannins, which can increase with eCO_2 [13], can reduce nitrogen use efficiency through binding proteins [53], magnifying the effects of decreased nutrient availability. Finally, as global change is multivariate, more work is needed to test for interactions between nutrient dilution and other global change drivers [54]. For example, co-occurrent increases in eCO_2 and temperature may either offset plant nutrient density

Figure 1



Plant and insect herbivore responses to eCO_2. Rising CO_2 can increase aboveground plant biomass through carbon fertilization, leading to declines in the densities of other essential elements (i.e. nutrient dilution). Altered nutrient availability in plant tissues and phloem is detrimental to chewing herbivores but can benefit sap-feeding herbivores. Reduced forage quality can reduce individual body size of developing insect herbivores but may also have the highest fitness costs for the smaller herbivores interspecifically, as smaller taxa generally use and require diets containing higher nutrient concentrations in comparison to larger herbivore taxa.

declines [55] or not [56], and carbohydrate availability can constrain insect thermal maxima [57].

Conservation in a world of altered biogeochemistry

Threats to biodiversity span biological hierarchies from organisms to populations, communities, and ecosystems. Addressing the biodiversity crisis will require integrative approaches that span these hierarchies [49]. In particular, while altered biogeochemistry is often listed as a major threat to Earth's planetary boundaries [58], within ecology, it is often studied in the context of abiotic, ecosystem-level change and is less often considered in the context of conservation [59]. However, effects of altered nutrient availability may be particularly relevant for declines in insects that are ubiquitous even within protected areas [60].

At the local scale, efforts to ameliorate altered nutrient availability with the goal of insect conservation are limited. One positive example is the use of riparian buffers around streams to limit diffuse nutrient runoff [61]. A second proposed strategy is the incorporation of species with variable nutrient profiles in seed mixes for restoration [49]. We caution against more direct approaches to 'correct' for altered nutrient availability. For example, the use of mineral licks in wildlife reserves may inflate herbivore populations beyond their carrying capacity [62]. Additionally, while changes in plant biomass and concentrations in carbon and nitrogen under eCO_2 are ameliorated under increased nitrogen availability [13], fertilizer addition has downsides, including creating increasing imbalances in the availability of yet other elements essential for life [26], favoring fast-growing plants, and the creation of eutrophic conditions with negative downstream effects on insect biodiversity [63].

At national to larger scales, legislation can be an effective tool to reverse biodiversity declines caused by altered nutrient cycles, as has been the case for freshwater macroinvertebrates following regulation of water and air quality in Europe and North America [64]. As a first step, we believe that to slow nutrient dilution and other consequences of eCO_2 — like the acidification of oceans — global action is required to reduce anthropogenic emissions. Until then, the contribution of nutrient dilution to shifts and biodiversity declines of Earth's insects provides yet one more reason why these efforts are increasingly critical.

Data Availability

The authors do not have permission to share data.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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