

Opinion

Nutrient dilution and the future of herbivore populations

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Nutrient dilution (ND) – the decrease in the concentration of nutritional elements in plant tissue – arises from an increase in the mass of carbohydrates and/or a decrease in the 20+ essential elements. Increasing CO₂ levels and its promotion of biomass are linked to nutrient dilution. We build a case for nutrient dilution as a key driver in global declines in herbivore abundance. Herbivores must build element-rich animal tissue from nutrient-poor plant tissue, and their abundance commonly increases with fertilization of both macro- and micronutrients. We predict the global impacts of nutrient dilution will be magnified in some of Earth's most biodiverse, highly productive, and/or nutrient-poor ecosystems and should favor specific traits of herbivores, including sap-feeding and ruminant microbiomes.

Wait, the 'greening of the Earth' has a downside?

Decades ago, the 'greening of the Earth' was a meme used to temper fears about burning fossil fuels and the subsequent rise in atmospheric CO₂ [1]. The logic is clear enough: the vast majority of plant biomass is carbon, hydrogen, and oxygen (henceforth **CHOs**) (see [Glossary](#)) built from CO₂ and H₂O. The **CO₂ fertilization hypothesis** posits that **Anthropocene** CO₂ emissions promotes photosynthesis and the accumulation of CHOs in plants [2]. It is now seen as a remedy, evoking immense tree-planting projects to scrub CO₂ from the atmosphere [3]. However, a tiny fraction of that biomass consists of 20+ chemical elements, all **essential elements** for life [4]. This relative increase in CHOs compared with other elements – from nitrogen to phosphorus, from boron to zinc – underlies a global downside to the increasing plant biomass in the Anthropocene (+31% during the 20th century) [5]: the dilution of **nutrients** in the food supply of plant eaters. Here we argue that increasing CO₂ levels threaten human and natural ecosystems by producing 'green deserts': fields and forests that have ample energy, but are less and less adequate to meet the elemental quotas necessary for animal life.

Nutrient dilution (ND) occurs when plant tissues are depleted in one or more of the elements essential to build organisms. A defining feature of ND is the decrease not in the total nitrogen and zinc per plant but in their concentrations, bite by bite, in plant tissue. Plants vary in their elemental recipe (particularly the big three – C:N:P – of ecological stoichiometry) [6]. The first warnings about ND in the human food supply emerged 20+ years ago [7]. Evidence now extends beyond these macronutrients to electrolytes such as potassium and sodium, and metal ions such as copper and iron essential to enzyme function [8]. Complementing the work of agronomists and human health advocates, ecologists are revealing the critical role of both macro- and micronutrient shortfalls in the health, performance, and abundance of **herbivores** [9–13]. Herbivore bodies contain a higher proportion of nutrients than the plants they eat [4,6,11]. This has created a unique and fundamental challenge for a herbivore in an ND world: making up that difference for all its essential elements, from carbon to cobalt.

Highlights

Global declines in animal populations suggest global causes.

Herbivores are uniquely vulnerable to declines in the nutrient density of the plants they consume.

CO₂ pollution is a global agent of nutrient dilution: the impoverishment of plant tissue, bite for bite, of the elements essential for herbivore survival. As plants assimilate higher levels of CO₂, nutrient dilution can create flammable 'green deserts' of low-quality food for herbivores already limited by elements from nitrogen to sodium to zinc.

We posit that nutrient dilution is a key driver – rich in testable predictions – of global declines in herbivore abundance. Its impact should be highest in productive and/or nutrient-poor ecosystems like tropical forests and the open oceans. It is reversed by fertilization. It acts regardless of habitat size or pesticide use. It thus complements these and other agents of herbivore decline.

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At the same time, there is extensive evidence for recent, substantial decreases in animal populations [14,15]. Insect declines are widely documented, with a consistent (mean -1.5% /year) decrease in abundance [16]. While a recent review of the likely causes [17] lists 12 potential agents, we build the case for adding ND to that list as a widespread agent of animal decline acting in diverse ecosystems around the world. Indeed, we argue that ND could be a major agent of the 'insect apocalypse' [16] due to both its ubiquity and its targeting of the most abundant animal niche, the herbivores (that represent the highest fraction of threatened species in the vertebrates) [18]. In this synthesis we explore ND, its mechanisms, likely ubiquity in a $+CO_2$ Earth, and implications for the abundance and traits of its herbivores.

ND reduces the quality of food, bite by bite

ND occurs at the level of the whole plant, as leaves absorb CO_2 and release O_2 , roots take up elements in compounds and ions from the soil, and stems distribute elements and glucose via phloem and xylem throughout the plants' roots, leaves, and reproductive structures. A plant's concentration of a given essential element, R (measured as mg R/kg plant or ppm), reflects ND over time or space. The concentration of R can decline if (total) R declines in the plant, or if total R remains constant as plant mass increases, or by a combination of both. ND can occur for any of the one or more of the 20+ elements that make up plant tissue, including those essential to both plants and their consumers (e.g., nitrogen and phosphorus), and those essential to consumers only (e.g., sodium and cobalt) [4,19].

While multiple hypotheses have been floated for patterns of ND [12,20–24], there is a long record of ND arising through the uncompromising math of mass-balance outlined earlier. One is the promotion of plant growth, and, at the ecosystem level, **net primary productivity (NPP)**. Structural carbohydrates such as lignins and cellulose increase as a percentage of the plant mass as plants grow and require more structural support. However, if plants pack on CHOs without matching their uptake of other essential elements, the proportion of nutrient-poor tissue will increase as plant size increases (Box 1).

The second way to promote ND is to impede a plant's access to pools of essential elements in the soil, detritus/excreta, and via aerosol deposition [11]. For example, as ecosystems age, rock-derived elements are gradually leached away; forest chronosequences of 600–600 000 years in duration regularly reveal ND in leaf phosphorus [25]. Water erosion is projected to account for 50% of the 4–19 kg/ha/year of phosphorus lost from the 5 billion ha of land in agriculture (38% of Earth's terrestrial surface), essentially, sending it to the bottom of the ocean [26]. A decline of leaf nitrogen in ecosystems since the 1900s [27] suggests a long-term loss in access to this macronutrient.

Increases in CO_2 have been posited to have a variety of other effects on nutrient availability. The microbial community below ground – built of roughly the same elements as plants [4] – are potential competitors for these shared building blocks [28]. Just as plant ecologists fertilize with sugar and sawdust (i.e., CHOs) to grow microbes and reduce available N [29], increased inputs of CO_2 absorbed by plants can make their way into the soil as labile carbon of fine roots or exudates [30]. Shortage of one element can have cascading effects: for example, insufficient concentrations of the essential plant electrolyte potassium [20] impedes the uptake of other elements from the soil [12]. In wheat cultivars, $+CO_2$ suppresses uptake of a variety of macro- and micronutrients through the same mechanism [21,22]. Finally, the transpiration that drives transport from roots to leaves is hampered if higher levels of CO_2 allow plants to conserve water by closing stomata [23]. Not surprisingly, many of these discoveries emerged from the study of crops and pastures.

Glossary

Anthropocene: the geological age in which human activity is the dominant influence on Earth's ecosystems.

CHOs: acronym for molecules built from carbon, hydrogen, and oxygen (e.g., carbohydrates).

CO_2 fertilization hypothesis: a fraction of post-industrial CO_2 emissions is used by plants to fix carbon as CHOs, reducing atmospheric levels of CO_2 .

Essential elements: elements required to build living organisms, a shortfall of any of which causes pathology.

Herbivores: animals whose diet consists exclusively of plants. Herbivores convert nutrient-poor plant tissue into nutrient-rich flesh.

Ionomics: the study of the elemental composition of life. This field of study is sufficiently new and far flung across scientific disciplines to have generated a number of names, from ecological stoichiometry, elementomics, and atomic ecology.

Net primary productivity (NPP): the rate of carbon fixed by plants in an ecosystem that is not used for metabolism by the plant and thus is available to consumers. NPP integrates over the growth of all the plants in a given area typically 1 square meter over 1 year ($gC/m^2/year$) and is a stand-in for CHO production.

Nutrient: an atom or compound that when ingested is used to build or fuel an organism.

Nutrient dilution (ND): the decline in the concentration of elements in plant tissue that are essential for survival of plant consumers.

ppm: parts per million: a measure of concentration that varies by six orders of magnitude for essential elements in tissues.

Stoichiometric mismatch: the deviation between the optimal ratio of nutrients in the diet of a herbivore (as determined by its metabolic requirements), and the actual nutrient densities.

Box 1. How building plant biomass can dilute available nutrients

All plants grow by building CHO-rich cell walls; the larger terrestrial plants invest in woody cores [24,86]. In larger plants, the metabolically active, element-rich tissues (e.g., leaves) make up a smaller fraction of its increasingly CHO-rich make-up. 'Dilution by growth' was first identified by agronomists watching CHO-rich stem tissue accumulate in taller plants, while concentrations of sugars, amino acids, and minerals declined (Figure I) [24]. This mechanism emerges along productivity gradients: across 54 North American grasslands, concentrations of 16 of 18 elements of herbaceous plants declined in high biomass sites, seven of 18 for grasses [19]. Across plant species and their many possible functional niches there is mixed evidence for mass-based interspecific ND. In one synthesis, an 11 orders of magnitude range in plant mass across 687 species, from herbs to trees, revealed an allometric decrease in % nitrogen consistent across two of the four compiled datasets [87].

Photosynthesis uses CO₂, H₂O, and solar energy to build CHOs. Abiotic controls of plant productivity – and hence standing crop biomass – should drive many gradients of ND. An early summary of CO₂ fertilization experiments with 130 species cultivars revealed an average 8% decrease in the mineral content of plant tissues, driven by the predicted increase in C content by 6% [31].

Precipitation and temperature variation across Earth's grasslands can generate a 10–100-fold variation in biomass from spring to summer, interannually with drought, and from arid shortgrass to mesic tallgrass prairies. Grasslands are thus laboratories for the study of ND and its effects [8,19,88]. Cattle ranchers report that high rainfall years leads to lush pastures of high biomass but low protein 'washy grass'. The digestibility of a mouthful of hay for a cow in Nebraska, USA, declines 52–63% from June to July [89]. Low precipitation years, by contrast, are linked to grasshopper outbreaks [90], especially following a year of high grasshopper abundance and a larger egg supply [91]. So, when herbivore outbreaks are linked to 'drought stress', this may have less to do with decreasing plant defenses and more to do with increased nutrient density [92]. In aquatic systems, temperature is a key constraint to productivity: warmed aquatic systems, from mesocosms [93] to kelp beds [37], can generate their own high-biomass 'green deserts' of low nutrient quality, to the detriment of their herbivores.

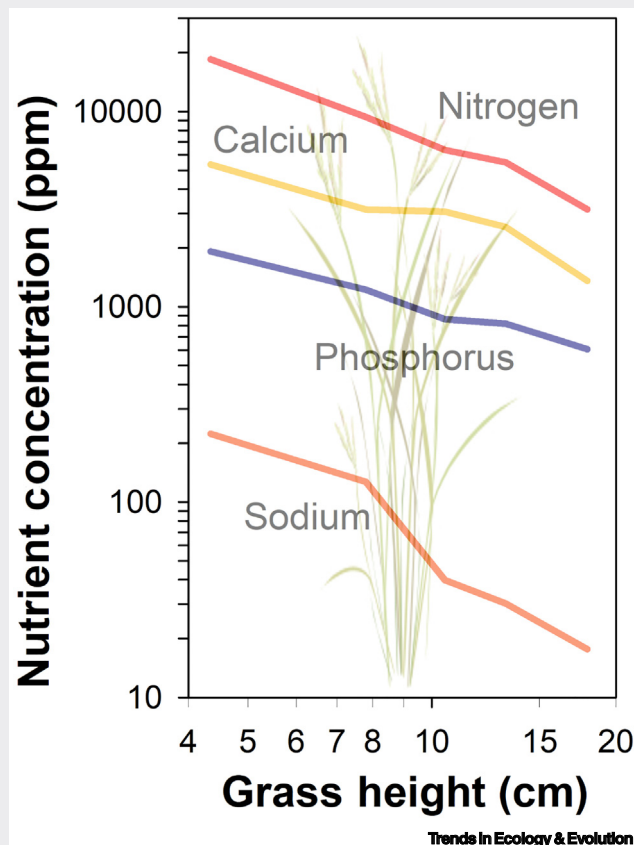


Figure I. Grass tissue from a tallgrass prairie in Kansas, USA, revealed nutrient dilution (ND) by growth from May through September. Data repurposed from [12].

Evidence that ND started with crops and has expanded to natural ecosystems

The early warnings about ND were linked to the food supply of humans and livestock [7,11,31]. In Rothamsted, UK, the total biomass of wheat cultivars under study since 1845 almost doubled since the 1940s, all against a background of stable or increasing soil nutrients [32]. However, as predicted by ND, the concentration of essential metals such as zinc, iron, copper, and magnesium in the grain, stable until about the 1960s, decreased even as grain yields remained relatively constant. Another 50-year record of cultivars grown throughout India found similar (ca. 30%) decreases in iron and zinc in wheat and rice grains [33].

Evidence for ND has more recently been found in ecosystems from forests, grasslands, and the oceans. Long-term forest monitoring plots, established to evaluate effects of air pollution and nitrogen deposition, have found widespread (but not universal) nutrient dilution in foliage. Against 17-year trends of increasing biomass production from six common European trees, 20 of 22 significant trends in foliage nitrogen and/or phosphorus revealed ND [34]. A similar study of 30-year trends for foliar nutrients in forests from 42 European states [35] revealed declines in nitrogen (5%), phosphorus (11%), potassium (8%), sulfur (6%), and magnesium (7%). Over 15–30 years in an undisturbed Ugandan tropical forest, leaves from ten tree species had become 13% more fibrous (i.e., increased levels of CHOs) and had 7% less protein (effectively, foliage nitrogen) [36]. A compelling picture of ND from an annually burned grassland in Kansas, USA, revealed a 30-year doubling of grass biomass production while nitrogen concentrations declined by 42%, phosphorus by 58%, potassium by 54%, and sodium by 90% [8]. In algae or aquatic macrophytes, a 19-year increase in biomass has been associated with an 18% decline in the nitrogen content of kelp forests in southern California, USA [37].

Given the rarity of long-term studies designed to measure **ionomics**, ecologists have artfully found other ways to get these data. One study used the persistent hay piles created by American pikas (*Ochotona princeps*) in a high-elevation grassland, and found a 30-year, 20% decline in nitrogen [38]. Three additional studies used herbarium records: the first observed declines in foliar nitrogen from 1926 in 24 species of North American grassland plants [39]; a second study of goldenrod (*Solidago* spp.) pollen revealed declines in protein content, with over 80% of variation accounted for by atmospheric CO₂ levels [40]. By contrast, a 90-year record of 12 tree species in southern China revealed no change in foliar nitrogen; however, this was against a background of increasing nitrogen deposition [41]. In the only such study aimed at parsing out the effects of +CO₂, 43 000 plant samples revealed a 9% decline in foliar nitrogen after accounting for 37 years of precipitation and temperature flux [42].

In an ND world, the knife-edge of nutrient limitation grows sharper

A herbivore eats foods that are CHO-rich and poor in other nutrients vital for herbivore health (Figure 1). To survive and reproduce, it must find and harvest plants that contain sufficient quantities of universally essential nutrients (e.g., nitrogen, phosphorus, potassium) as well as the handful of elements that are essential primarily to consumers, such as sodium and cobalt [4,11], each of which has its own geography [43]. For example, sodium, rare in Earth's continental interiors [44], constrains the development [10], activity [45], abundance [9,46], and trophic position [47] of herbivores. Cattle suffer from 'blind staggers' in Florida and 'bush sickness' in Australia due to shortages of copper and cobalt, respectively [6,48,49].

Given the ailments attributed to shortages of the 20+ essential elements [48], it is easy to imagine that nutrient shortfall is the global rule and not the exception for herbivores. A key synthesis [50] of plant and invertebrate responses to macro- and micronutrient fertilization gives credence to this working hypothesis: unlike the plants they eat, grassland herbivores show profoundly larger

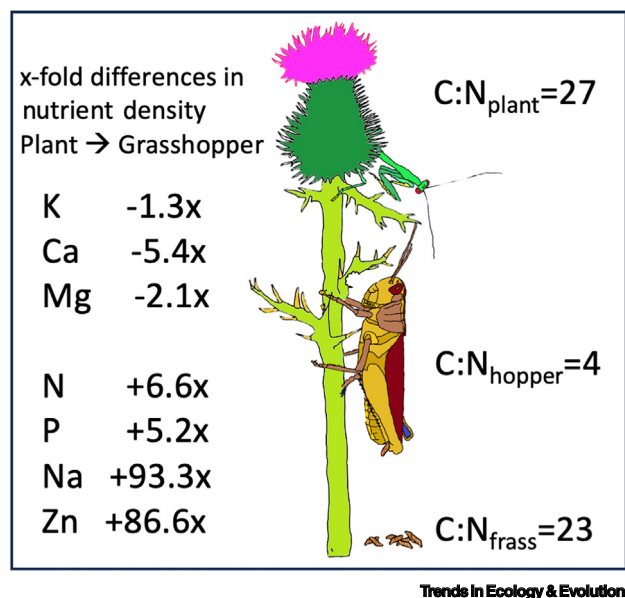


Figure 1. A herbivore faces many challenges in building new tissue and offspring from a plant-based diet. First, it must choose a diet that concentrates and replenishes the essential elements such as N and Zn found in lower densities in plant than animal tissue. Second, it needs to break down, pass through, and excrete surplus elements that occupy space and interfere with uptake of limiting nutrients. That means converting plant tissue (where a C:N of 27 means that carbon mass is 27x higher than nitrogen mass) to grasshopper tissue (4x) by creating carbon-rich (23x) frass (i.e., feces). And it needs to do this while allocating time and energy to other fitness-increasing activities, such as avoiding predators. All of this becomes more challenging as factors that increase plant growth and ecosystem productivity, or erode soil nutrients, dilute plant nutrients, bite by bite. Data repurposed from [19,97].

increases with the fertilization of both macro- and micronutrients than to macronutrients alone (e.g., nitrogen, phosphorus, potassium). The nutrient limitation of animal abundance by multiple combinations of elements [51,52] is already widespread and acute.

Not surprisingly, one response of herbivores under +CO₂-based ND is to eat more [53,54]. However, a pioneering 9-year +CO₂ experiment showed that despite a 117% increase in herbivory rates on three oak species, leaf miners had 20% less conversion efficiency, developed 14% more slowly, and decreased in abundance by 20% [55]. A comparison of herbivory on fossil leaves from the Cretaceous to the Pleistocene with recently deposited leaves in three New World forests suggests a doubling of average herbivory rates after controlling for temperature [56]. Syntheses of experiments with CO₂-fertilized plants show consistent increases in herbivory rates, but with a decrease in herbivore fecundity [57]. This raises the question: why are herbivores not able to eat their way out of ND? We suggest two reasons.

First, in a +CO₂ world, herbivores are not just challenged with securing enough essential elements that are in short supply. They are also burdened by consuming excesses of CHOs that take up space in the gut, interfere with the absorption of other nutrients, and must be broken down, passed through, and evacuated (Figure 1) [6]. This **stoichiometric mismatch** requires investment of time and energy. This is why herbivores, when given a choice, adopt a balanced diet, not just to avoid nutrient shortfalls, but to avoid the costs of dealing with excess [58].

Second, increased time spent eating is subtracted from other fitness-increasing activities. Foraging herbivores are vulnerable to predators and parasites (Figure 1), and ND demands longer consumption times and longer periods before the herbivore matures reproductively [57,59]. An elegant field experiment demonstrated this balance between nutrition and predation: grasshoppers which were fearful of innocuous spiders (their mandibles had been glued shut) foraged less and grew more slowly than controls. Importantly, increased access to macronutrient-dense food (i.e., reversing ND) removed the effect of predators on fitness [60].

The future of Earth's herbivores under ND

The widespread declines of the abundance of animals, and herbivores in particular, likely arise from a suite of agents, from habitat loss to pollution (including pesticides), from increases in temperature to changes in precipitation. Given the many possible causes for herbivore declines, how do we parse out the effects of ND? Clearly, more quantitative data are needed from monitoring and distributed experiments (e.g., [61]). But we suggest a rich variety of phenomena – from the geography of declines to their effects on functional traits – that test the working hypothesis that ND is reducing the abundance of Earth's herbivores (Box 2, Figure 3).

Look for ND-driven declines in highly productive and/or nutrient-poor ecosystems

ND occurs with either increasing plant biomass or loss of access to nutrients. Many of Earth's ecosystems are biogeochemically impoverished (e.g., open oceans, the continent of Australia, the Congo, and the Amazon Basin). This is especially true for herbivores from tropical rainforests that are already oligotrophic, productive, and among those ecosystems closest to the nutritional

Box 2. How to identify ND as a driver of herbivore decline

As in most higher-order ecological patterns, ND is complementary to other processes driving trends in abundance. What is the current status of the working hypothesis that ND is an important driver in herbivore declines, and how do we separate its effects from other hypothesized drivers such as habitat loss, pesticides, and the abiotic stressors of heat and desiccation [17]? Toward accelerating research, we rank predictions and assumptions of this hypothesis by the current evidence.

Strong support

Herbivore abundance is constrained by nutrient density of plants. Multiple field experiments and comparative data are given in [12,84], and some are summarized in [50].

Some support

Declines in plant nutrient density are common and global [7,8]; exceptions exist due, for example, to nitrogen pollution, and time series of plant nutrient density, especially for the complete plant ionome, remain uncommon. This is a top research priority.

Herbivore declines follow ND: experimental CO₂ additions (e.g., [55]) generally support herbivore declines with ND. So does co-occurrence of biomass increase and nutrient dilution [8,88,90]. However, the ubiquity of both long-term datasets – plant nutrients and animal abundance – are still rare. This is a top research priority.

Declines are less in sap feeders than in leaf chewers: this is supported by at least one meta-analysis [57].

Measuring multiple drivers and parsing their effects statistically: simultaneous measures of nutrient density, temperature, and precipitation (e.g., [8]) allows parsing multiple drivers.

Nutrient stressed herbivores become more omnivorous (e.g., [94]): when plant sources of nutrients are diluted, add nutrient-rich flesh to your diet.

Nutrient stressed herbivores become more geophagous (e.g., [95]): isolated mineral licks maintain herbivore abundance in low-nutrient areas.

Key predictions needing more definitive tests

Herbivore declines are stronger in high NPP and/or oligotrophic environments: since tropical forests and the open ocean represent a host of ecosystems services, this is a top research priority.

Decreases in abundance are preceded with declines in health of herbivores, through nutritional diseases: methods that diagnose herbivore health before ND-caused declines would be a useful forecasting tool.

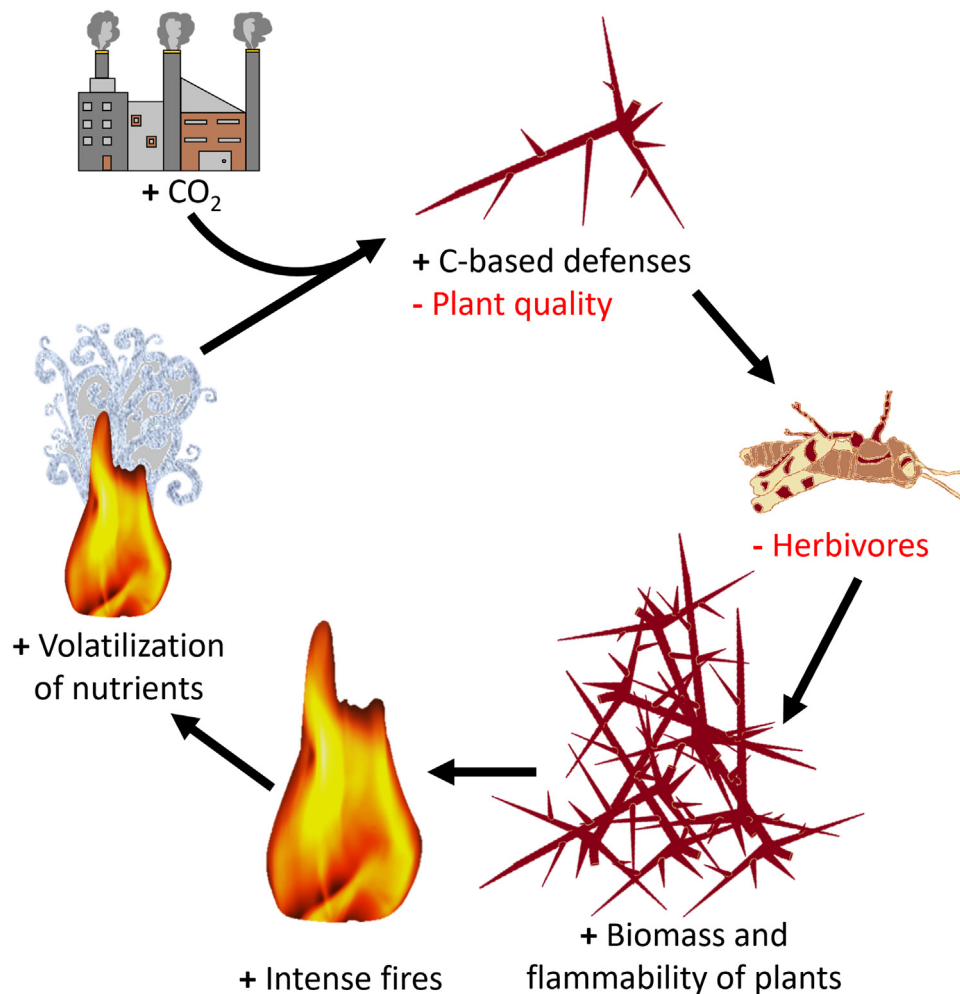
Herbivore declines are reversed by fertilization: large-scale fertilization experiments that use locally declining element mixtures would be a strong test for ND.

Dilution and declines occur in large protected areas (e.g., [8,16]): this prediction is contrary to declines through habitat loss.

Declines occur in the absence of pesticide residues (e.g., [96]): this prediction is contrary to declines due to pesticide/pollution.

knife's edge [62]. Two types of datasets, prioritizing these ecosystems, should be collected to test for ND. First, we need globally distributed, long-term datasets that combine the dynamics of plant ionomics and the abundance of animal populations. Second, and perhaps the highest research priority toward understanding the ubiquity of CO₂-based ND, are global, distributed experiments manipulating productivity and biogeochemistry [46,61,63].

In this vein, satellite resources suggest the CO₂ fertilization effect – relying on plants to absorb fossil CO₂ – has decelerated globally, with the greatest declines in regions with the lowest available foliar nitrogen and phosphorus [64]. This nutritional race to the bottom may be accelerated by well-meaning attempts to increase sequestration of CO₂. For example, forestation programs [3] may serve to produce more, increasingly nutrient-poor vegetation that reduces survivorship of local herbivores (and that regularly burns, rather defeating the purpose) (Figure 2). Similarly, in



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Figure 2. In the +CO₂ world of nutrient dilution (ND) and the subsequent decline in herbivore abundance and activity, the abiotic consumer fire steps up [74]. When carbon is in surplus relative to macronutrients such as nitrogen, plants may invest in carbon-based defenses such as thorns, phenols, and resins. Combined with +CO₂, rising temperatures, and droughts, the accumulation of carbon fuel increases the frequency and intensity of fires. While low-intensity fires can return minerals to the soil in the form of ash, high-intensity fires volatilize essential nutrients, further advancing ND [98].

the open, oligotrophic oceans, where iron and light co-limit production [65], models warn that iron fertilization to capture carbon risks sequestering other nutrients in algae that, when dead, bury essential elements in the ocean depths [66]. (See Figure 3.)

Herbivore functional traits will be constrained and promoted

Herbivores have several traits that facilitate survival on CHO-rich and mineral-poor plants; others are linked to particular ionic recipes [67] that will constrain their expression under ND. We predict that herbivores in ecosystems experiencing more ND will see the greatest changes in the following traits.

Abiotic tolerance: in a +CO₂ world, two grand ecological challenges are increases in temperature and increased variance in rainfall [68]. Thermal and desiccation tolerance are functional traits that must be built and maintained. For example, phosphorus content accounted for a third of the interspecific variation in thermal maxima in a rainforest ant assemblage [69]. By contrast, increased access to CHOs under ND can promote higher thermal tolerances [70,71]. In one tropical canopy ant, *Azteca chartifex*, a 10% sucrose solution raised thermal tolerance by 5°C compared with water only.

Sap feeders versus chewers: insects that feed on the phloem and xylem access sugary CHOs and minerals before their host plants trap nutrients in matrices of cellulose and lignins. Sap feeders like those of the Hemiptera may thus circumvent the worst of +CO₂-driven ND by increasing ingestion rate (e.g., [72]). In +CO₂ experiments, sap feeders showed 9% increases in fecundity, while leaf-chewing members of the Coleoptera, Lepidoptera, and Orthoptera suffered decreases of 13% or more [57].

The microbiome: herbivores can form a synergistic interaction with microbes to deal with a CHO-rich diet. For example, the large four-chambered foregut of ruminants (such as the American

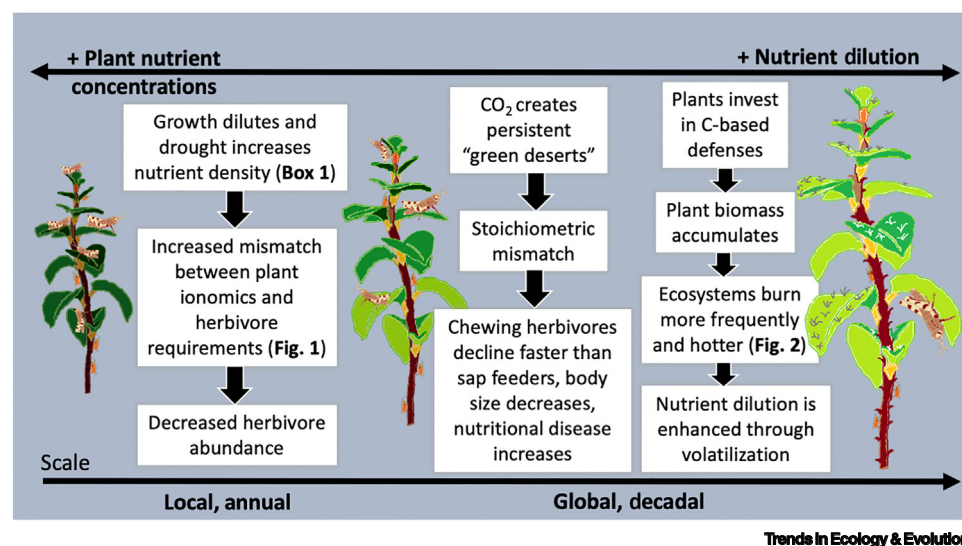


Figure 3. Mechanisms and predicted outcomes of nutrient dilution (ND). At annual time scales, plants become less nutrient-dense as they grow, and droughts serve to maintain richer tissues with less biomass. This variation shapes herbivore abundance. At decadal time scales, CO₂ pollution is shifting the ionic baseline downward, with multiple implications for herbivore functional traits. Long-term CO₂ pollution can shift plant communities toward those richer in carbon-based defenses, suffering less net herbivory, and shifting their ecosystem to one maintained by fire.

bison, *Bison bison*) means that they are able to survive better on low-quality forage than hindgut fermenters (such as horses and humans) [73].

Herbivores may be trapped in smaller bodies (though larger guts are more adaptive)

Building a large fermenting gut and a suite of bacterial symbionts, while one solution to a high +CO₂ high-CHO diet, requires a supply of essential elements to do so. Orians and Milewski [74] posit that Australian herbivores are stuck on a small, less-adaptive fitness peak for that very reason: namely, impoverished soils short on iodine (key for development and function of the nervous system) [11] and cobalt (essential for microbial conversion of CHO-rich fiber to energy) [48]. The result is small absolute size compared with other faunas, small relative brain mass, and reduced metabolic rate and fecundity [49].

Likewise, warmer temperatures can, with exceptions, generate faster development to a smaller size [75], a common occurrence at the edges of species distributions [76]. ND, which makes the herbivore do more work for the same quota of building materials, decreased the development rate, and ultimately the abundance, of grasshoppers on a Kansas tallgrass prairie despite a doubling of plant productivity [8,59]. Searing *et al.* [77] showed that the body size of 23 small mammal species across North America has declined over the past century, and almost all of these are herbivores [77]. Notably, these decreases are associated with both increases in temperature and NPP, consistent with both temperature and ND effects. Thus while protracted ND should favor larger herbivores with large, complex microbiomes (and the rapid digestion of high CHO, fibrous foods) [78], it can simultaneously decrease access to the elements in the diet required to make this happen [49].

Plant–herbivore interactions will enter a new phase of the arms race, sometimes to the bottom

In a productive ecosystem supercharged with CO₂, especially those on impoverished soils, plant communities often increase investment in relatively cheap carbon-based defenses (Figure 2). For example, in Australia, plants are characterized by carbon-based defenses thick with indigestible lignin, phenolics, resins, and oils, and physical defenses such as thorns [49,74]. The same was true for super-depleted white sand forests in Peru compared with tree species from richer clay soils [79]. +CO₂ experiments generate similar defensive shifts in a variety of ecosystems: pea plants (*Medicago truncatula*) use enriched CO₂ to build defensive trichomes, spike-like hairs that protect their leaves from herbivores [80]. When combined with +2°C warming, +CO₂ treatments decreased plant crude protein and increased plant toughening lignins in a tropical grassland [81]. A 30-year record of samples from a montane grassland revealed a twofold increase in defensive phenolics [38].

Within communities, where herbivores can choose among a variety of species, individual plants can benefit by diluting their own nutrients, especially nutrients essential to their herbivores, at the expense of tastier neighbors [11,63,82]. In a +CHO world, plants that can get by on the lowest nutrient quota (and the tradeoffs associated with this tactic, such as slower growth) [62] may benefit locally from decreased herbivory. In this vein, competition of humans with insect herbivores will likely increase under ND as herbivores ‘pick their patches’, and some of the richest patches may be agricultural fields.

Plants also exchange nutrient-rich pollen and nectar with pollinators [13,83,84]. ND can disrupt pollination by leading to poor/small/inviable pollen, and poor pollen transfer and performance [24]. We note that many studies of ‘nutrient limitation’, including our own, in plant communities use NPP/plant biomass as a proxy for fitness. With documented declines in pollen nutrient density [39], both pollinators and their mutualists will likely suffer lower reproduction, a parameter more challenging to document than biomass.

Concluding remarks

We make the case that in the Anthropocene, CO₂ fertilization and soil nutrient depletion are drivers of the ongoing decline of herbivores by reducing the quality of their food supply. At the same time, there is an abundance of opportunity for further work to clarify the where, how, and why of ND by combining mechanistic studies with long-term datasets (see [Outstanding questions](#)).

The global declines of herbivores, like those of insects in general, can be likened to a death by a thousand cuts [17]. If, as we propose, ND is a global phenomenon exacerbated by rising levels of atmospheric CO₂, it comprises a ‘wicked problem’: widespread, impactful, with many causes but no easy solutions [85]. Indeed, we recommend caution against ‘greening the earth’ to manage Earth’s CO₂ levels. Replacing grasslands with massive forests, and/or depositing those plants (and their nutrients) in anoxic ocean depths [3], have the potential for making ND worse. The reduction of anthropogenic CO₂ emissions and the concentration and sequestration of CO₂ in inorganic form seems, to us, the only true fix for ND.

Acknowledgments

We dedicate this essay to Dr Tony Joern and colleagues at the Konza Prairie LTER who have contributed so much to the long-term ecological study of herbivore ecology. Work was supported by an National Science Foundation (NSF) grant (DEB-1556280) to M.K.

Declaration of interests

The authors declare no conflict of interests.

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Outstanding questions

Where is the geography of ND? Global change biology requires distributed observatories for dedicated, standardized sampling of Earth’s ecosystems, including many most at risk from ND. Such long-term datasets are difficult to initiate and maintain.

What plants and plant tissues are most susceptible to ND? As herbivore niches range from specialists on plant tissues and plant species to generalists consuming whole plants or patches, understanding the ‘microgeography’ of ND will help predict which herbivores are most targeted by it.

When ND generates ecosystems with CHO-rich, nutrient-poor plants, what herbivore niches are most at risk of decline? How will a herbivore’s diversity of foods, its ability to thermoregulate, its microbial symbionts, and its optimal body size change as its food supply becomes less nutritious? Functional ionomics – the elemental recipes required to build and maintain traits – will help us link the changing environments driven by ND with herbivore performance.

How will the effects of ND cascade through populations and ecosystems, and what are the early-warning symptoms? Given the many roles plants and herbivores play in ecosystems, any perturbations are likely to generate a variety of outcomes, many less predictable.

How do we monitor herbivore populations to recognize early warning symptoms of ND? Nutrient deficiencies should manifest first as malnutrition, likely followed by decreased growth and fecundity, finally resulting in population collapse. How do we measure initial signs of this progression in wild populations, from aphids to elephants?

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