Trends in
Ecology & Evolution

CellPress

Review

Nitrogen deposition and climate: an integrated synthesis

Elizabeth T. Borer [1,*,@] and Carly J. Stevens [2]

Human activities have more than doubled reactive nitrogen (N) deposited in ecosystems, perturbing the N cycle and considerably impacting plant, animal, and microbial communities. However, biotic responses to N deposition can vary widely depending on factors including local climate and soils, limiting our ability to predict ecosystem responses. Here, we synthesize reported impacts of elevated N on grasslands and draw upon evidence from the globally distributed Nutrient Network experiment (NutNet) to provide insight into causes of variation and their relative importance across scales. This synthesis highlights that climate and elevated N frequently interact, modifying biotic responses to N. It also demonstrates the importance of edaphic context and widespread interactions with other limiting nutrients in controlling biotic responses to N deposition.

Highlights

Many biotic responses to nitrogen (N) vary with climate, suggesting that the intersection of climate and N inputs is a critical area to build understanding.

Elevated N often results in reduced grassland species richness, elevated foliar N concentrations, and more non-native species, but soil chemistry can control the direction and magnitude of these changes.

Plant aboveground biomass is often increased by N, but responses can take decades to emerge and can interact with climate; in addition, growth in many grasslands is co-limited by other elements.

Grassland consumers often increase with, and have increasing impact on, elevated N, but climate contributes, and mechanisms linking N via plants to consumers remain a key knowledge gap.

The relationship between carbon cycling and elevated N varies among locations, likely reflecting interactions with climate and co-limitation by other nutrients.

Reactive nitrogen and biotic responses

Reactive N impacts human health [1] and shapes the diversity, composition, and function of the biosphere [2–4]. Yet, in less than a century, human activities have more than doubled the reactive N supplied to Earth's ecosystems via atmospheric deposition [5], with some regions currently receiving more than 50 kg N ha^{-1} $year^{-1}$ [6]. The supply of reactive N deposition (N_{dep}) on Earth is regionally variable because it is associated with agriculture and fossil fuel emissions and can be transported long distances via weather systems [6,7].

Policies recognizing the threats of anthropogenic N to human health and ecosystem functioning have focused on regulating oxidized N, or NO_x, emissions, inducing new regional variability in N_{dep} trends. For example, N_{dep} is increasing rapidly in some regions, including East Asia and Brazil [7,8], while declining due to regulations in the USA and many European Union countries. Nonetheless, although N_{dep} in the USA, for example, declined following successes of the Clean Air Act, it remains five to ten times higher than preindustrial levels [8], and N_{dep} across the USA increased by 8% between 1984 and 2016, even with strong regulatory policies [6]. However, while some regional emissions have declined directly in response to NO_x regulation and indirectly via regulation of CO_2 [9,10], less regulated N forms (e.g., reduced N, or NH_x) have come to dominate N_{dep}, with some regions experiencing substantial net increases [6,11,12].

From the perspective of Earth's biota, N_{dep} is occurring in the context of many ongoing changes to ecosystems, including changing climate and atmospheric CO_2. Given that biotic responses to N_{dep} can vary widely depending on abiotic factors, such as temperature and precipitation, our ability to predict the effects of N supply on diversity and functioning from reviews of empirical studies remains a key challenge [13]. Furthermore, while syntheses and reviews of studies performed in different locations provide a powerful basis for summarizing published work, these approaches are limited in their ability to capture sources of variation in biotic responses across edaphic and climatic gradients because of differences in methods and heterogeneous reporting of environmental conditions among studies.

[1]Department of Ecology, Evolution, and
Behavior, University of Minnesota,
St Paul, MN 55108, USA
[2]Lancaster Environment Centre,
Lancaster University, Lancaster, UK

*Correspondence:
borer@umn.edu (E.T. Borer).
@Twitter: @e_borer

https://doi.org/10.1016/j.tree.2022.02.013

Reviews of N effects on biota also typically combine differing N sources, even though oxidized and reduced N forms can differ in their effects on species growing under the same conditions [14]. Thus, while existing reviews and syntheses have generated important insights into the threats posed by N_{dep} in some regions and to some components of the environment, this knowledge is patchy on a global basis and can provide only limited insight into causes of variation in biotic responses and their relative importance across sites, continents, and studies.

Here, we fill this gap with a focus on Earth's grasslands. We briefly review studies of multitrophic impacts of N_{dep} to summarize the current state of knowledge. We build from this by synthesizing the range of biotic responses to identical, experimental N addition across climatic gradients in the long-term, multicontinent NutNet[i] experiment (Box 1). While N_{dep} varies widely and is lower than

Box 1. The Nutrient Network

The Nutrient Network, or NutNet, a global change study begun in 2007, is currently replicated at 152 grassland sites in 29 countries, spanning Earth's climates (Figure I). The NutNet collaboration is generating three interoperable data sets [99]: (i) Observational data. Using identical methods at all sites, this project is generating a spatially extensive data set on grassland biodiversity and ecosystem characteristics; (ii) multinutrient experiment. At >100 sites, NutNet scientists are applying a factorial combination of N (10 g N m^{-2} $year^{-1}$ as slow-release urea, CH N O), phosphorus [P: 10 g P m^{-2} $year^{-1}$ as $Ca(H_2PO_4)_2$], and potassium (K: 10 g K m^{-2} $year^{-1}$ as K_2SO_4) with micronutrients (one-time addition in K treatment plots of a micronutrient mix, μ, containing calcium magnesium, sulfur, boron, copper, iron, manganese, molybdenum, and zinc); (iii) nutrient and herbivory experiment. At >100 sites, NutNet scientists are applying a factorial combination of large herbivore exclusion (via fences) and annual NPKμ addition.

At all NutNet sites, annual data on grassland plant species identity, cover, biomass, and light interception have been collected from a median of 30 plots per site using identical sampling protocols. Soil chemistry and texture data have also been collected from every plot around the world at regular intervals. Many sites have collaborated on collection of additional response data, including arthropods, foliar chemistry and damage, and soil microbial composition and functioning. Slow-release urea, released into the environment as a function of site-level precipitation, is an effective proxy for N deposition [100], and the experimental N supply rate, while high, is less than double some currently observed regional deposition rates [6]. High experimental addition rates are often used as a proxy for chronic, multidecadal nutrient inputs by pollution. Thus, NutNet's factorial experimental design provides directly comparable, integrated data on a range of biotic responses to identical inputs of a single form of N (CH N O) across a range of global climate regimes.

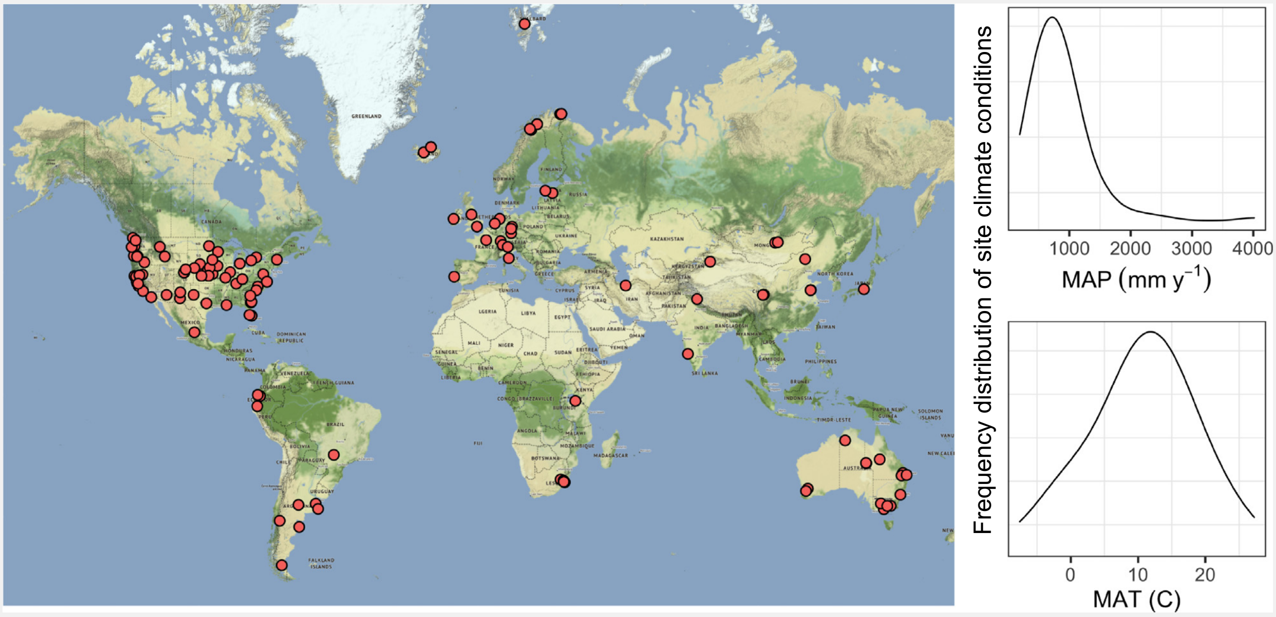

Figure I. Nutrient Network (NutNet) site locations represent a wide, globally relevant range of mean annual precipitation (MAP) and mean annual temperature (MAT).

NutNet addition rates in most locations [6], even under future scenarios [15], this synthesis provides novel insights into the types of biotic responses most likely to simultaneously depend upon N inputs and climatic conditions. Using this approach, we fill knowledge gaps about N impacts on grassland populations, communities, and ecosystem processes, including in the context of climate, and we point to future opportunities for understanding N impacts to support ongoing development of environmental standards (Box 2).

Plant diversity and species traits

One of the most widely reported responses to N_{dep} across the ecological literature is the loss of species from plant communities, with abundance declines and local extinction even at low rates of N input [14,16,17]. Across experiments, climate can determine species loss rates, which can continue for years [14]. While the responses of individual species to N_{dep} vary among sites and studies [8,16], compositional changes frequently result in reduced species richness [17,18]. N_{dep} can favor grasses over forbs, with shorter-statured, low tissue N species at greatest risk of local extinction [8]. Invasive species often increase with elevated N_{dep} [8]. While competition for light may underlie N-induced changes in species composition and biodiversity loss [19], soil acidification can exacerbate biodiversity loss in unbuffered soils [18]. Long-term simulated N_{dep} can even deplete seed banks, reducing the capacity for recovery [20].

Diversity trajectories and N

Results from the NutNet experiment (Box 1) are concordant with this literature, showing that grassland plant diversity responds similarly to identical rates of N addition across continents and conditions, with continued losses over a decade of chronically elevated N [21]. These directly comparable data further demonstrate that this diversity loss trajectory is exacerbated by high background rates of other soil elements [22] and is compounded when other elements, such as phosphorus, which arrives in many locations via long-distance transport [23], are also added. These results corroborate consistent N impacts on grassland plant diversity across conditions, and advance understanding by demonstrating that the magnitude of N impacts on diversity loss through time depend on edaphic conditions and input rates of other elements (Figure 1 and Table 1). Although herbivory can maintain grassland diversity at sites where it increases ground-level light, herbivores do not consistently counteract the effect of elevated N on diversity [24].

Box 2. Standards for the control of nitrogen emissions and deposition

Following the United Nations Conference on the Human Environment, the Convention on Long-Range Transboundary Air Pollution (CLRTAP) was signed in Geneva in 1979. This was the first multilateral convention addressing air pollution, signed by 51 primarily European parties, and supported by several protocols, including the Gothenburg Protocol, focused on reducing acidifying pollutants, including N. The CLRTAP introduced the critical loads concept, defined as ‘a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge’ [101]. Empirical critical loads are based on evidence from studies [102] and are subject to routine review.

The USA has National Ambient Air Quality Standards for NO_x, introduced in 1971, and is a signatory of CLRTAP. National critical loads for N_{dep} into ecosystems were published in 2011 [103]. Due to lower levels of background N deposition in the USA, critical loads are often lower than European equivalents and may be accompanied by lower protective target loads.

China is one of the dominant emitters of reactive N. In China, N_{dep} peaked around the year 2000 and declined dramatically between 2010 and 2018, as NO_x emission controls came into effect [104]. Critical loads in China are largely based on the steady-state mass balance approach [105], although empirical evidence that could be used to create empirical critical loads is growing [106].

In other regions of the world, there is increasing awareness of the need to control N emissions, but emissions policies must be balanced with food security. For example, regions in Africa and Latin America have considerable shortages of agricultural N, while other regions are experiencing unwanted impacts of N deposition [107,108].

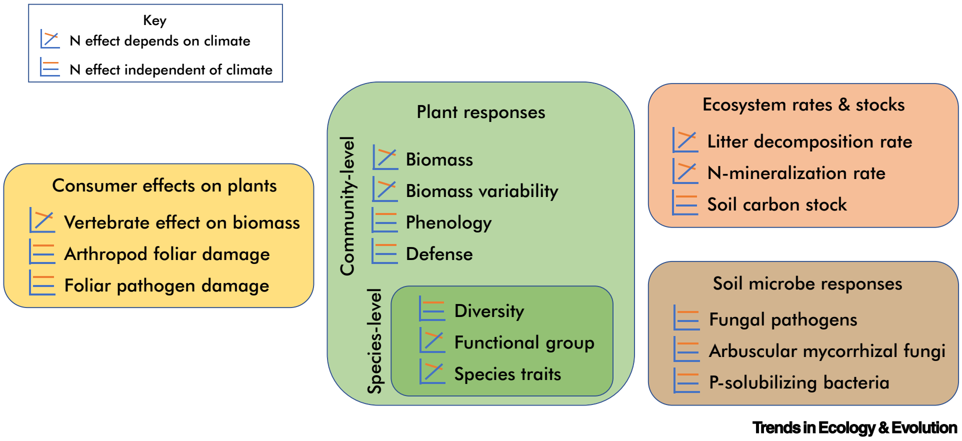

Figure 1. Many biotic responses to elevated nitrogen (N) depend on climate. In the Nutrient Network experiment replicated across global climates, N supply affects biotic responses, and climate modifies some, but not all, biotic responses to elevated N supply. Icons indicate whether climate modifies a response to N; they do not imply magnitude or direction of effect. See Table 1 and the main text for effect direction and additional details.

Plant trait responses to N

Leaf N concentrations in 243 species of dominant plants in NutNet plots spanning four continents increased with a consistent rate of N addition due to elevated within-species N content (via e.g., luxury uptake [25]) and increased domination by N-rich species [26]. Non-native graminoids in sites around the world also tend to have more N-rich foliage compared with their native counterparts [27], and native abundance and richness decline while non-native dominance and richness increase with N addition [28,29], suggesting a likely trait advantage under increasing N_{dep}. This shift induced by elevated N alters community trait distributions, favoring grasses and annual plants [28] and causing widespread declines in legumes [30] (Figure 1 and Table 1). Plant community trait shifts induced by N supply can arise from, and impact, consumer communities (see 'Consumer responses' section). For example, the supply of nutrients, including N, can interact with usually unmeasured traits, such as foliar sodium, to alter trait abundances as a function of herbivory [31].

Traits, N, and climate

Whereas elevated N across NutNet sites tends to increase the local richness (m^2 scale) of non-native species, this effect is reversed with increasing interannual precipitation variability, such that, at sites with highly variable precipitation, added N tends to cause non-native species losses. By contrast, native species tend to persist with N addition when interannual precipitation is variable [29]. Added N also reduces legume abundance, particularly at sites with high mean annual temperatures, suggesting that N deposition is increasingly detrimental to biological N cycling with increasing annual temperatures [30] (Figure 1 and Table 1).

Plant live biomass

Increased aboveground biomass is a frequently reported response to elevated N across the literature, both via N_{dep} and experimental fertilization [32]. However, increasing N_{dep} shifts communities toward limitation or co-limitation of biomass production by other elements, including phosphorus [33] or micronutrients [34,35]. Precipitation can interact with N to constrain biomass production [36]. Plant diversity can also constrain biomass production, and biomass can have a reciprocal effect on diversity [37], with chronically elevated nutrient supply potentially reducing biomass gains via species extinctions over the long term [38] and reducing temporal stability [39].

Table 1. N and climate impacts in the NutNet experiment[a]

Response category	Response variable	N effect direction	Climate interaction with N	Refs
Plant species	Plant diversity	↓		[21,22]
Plant species	Foliar nitrogen	↑	Herbivores reduce plant community foliar N at low precipitation sites	[26,61]
Plant species	Plant provenance (non-native species)	↑	Precipitation variability increases native plant species despite elevated N	[28,29]
Plant species	Functional group (legumes)	↓	Elevated temperature increases legume loss with N	[30]
Plant species	Functional group (grasses, annuals)	↑		[28]
Plant community	Plant biomass	↑ Most consistently with addition of other nutrients	Strongest effect of N at high latitude, cool sites	[21,42]
Plant community	Plant biomass variability	↑	Stability is further reduced with drought and aridity	[47–49]
Plant community	Plant community phenology	N can change community phenology in some regions		[62]
Plant community	Plant community defense	↓		[63]
Consumers	Arthropod foliar damage	↑	Damage increases with precipitation, but this is independent of N addition	[64]
Consumers	Vertebrate impacts on plant biomass	↑	Large herbivores most strongly reduce N-fertilized biomass at low precipitation sites	[31,61,65]
Consumers	Foliar pathogen damage	↑	Infection increases with site-level precipitation independent of N supply	[64]
Soil microbes	Soil pathogenic fungi diversity	↑		[75]
Soil microbes	Arbuscular mycorrhizal fungi	↓		[74]
Soil microbes	P-solubilizing bacteria	↓		[76]
Ecosystem	Soil microbial growth	↓		[77-79]
Ecosystem	Soil microbial respiration	↓		[78,80]
Ecosystem	Litter decomposition	↑ Early, ↓ late-stage decomposition	Likely interacts with climate and other factors (vegetation, microbial community)	[21,87,109]
Ecosystem	N-mineralization		Highest at sites with a warm, wet growing season	[93]
Ecosystem	Soil carbon stock	Losses and gains across sites	Varies with precipitation, particularly when other elements are added in addition to N	[90,91]

[a] In the NutNet experiment, climate modifies many of the biotic responses to experimental N supply. Response categories relate to Figure 1 in the main text.

Although aboveground biomass is often reported to increase with added N, this is reported less often for belowground biomass, leading to reduced root:shoot ratios [40]. However, reviews across studies are limited in their ability to uncover climatic and edaphic interactions with N that may control biomass production.

Biomass and N_{dep}

While most work in NutNet has focused on experimentally added N, the network has also quantified impacts of N_{dep} on grassland biomass around the world. Directly comparable NutNet data spanning five continents demonstrate that, for every 1 kg N ha^{-1} $year^{-1}$, standing plant biomass increased by 3%. N_{dep} was a better predictor of plant biomass than was site-level climate or even plot-scale edaphic properties [41].

Nutrient effects on above- and belowground biomass

NutNet experimental N supply increased grassland aboveground biomass at only ~24% of sites after 3 years [42], but this effect amplified at most sites over a decade [21]. However, the availability of other elements determines the strength of this response [43]. When N is supplied with other elemental nutrients, peak season biomass increased rapidly at ~66% of sites [42], and biomass at most sites increased in response to a chronic supply of multiple nutrients after a decade [21], demonstrating widespread nutrient co-limitation and impacts that can take years to manifest. Root allocation increased in response to N supply at grasslands spanning four continents [44], but canopy density determined site effects. Root mass declined with N addition at sites with dense aboveground canopies but increased at sites where canopies were sparse [44].

Nutrient effects on diversity, production, and stability of biomass

After a decade of chronic N addition at NutNet sites spanning continents, biomass continued to increase despite widespread diversity loss [21]. N supply reduced the temporal stability of peak biomass across NutNet, acting primarily by reducing the stabilizing force of interannual species asynchrony rather than via diversity loss [45,46]. Thus, while grassland diversity loss from elevated N is widespread, diversity loss is not likely to be the most common pathway by which N_{dep} will alter peak biomass and interannual variation.

Biomass, N, and climate

Aboveground biomass responsiveness to NutNet N addition is generally greatest at cooler, higher latitude sites, with weaker responses to the same N supply rate at warmer, low latitude sites [42], suggesting that, with rising temperatures, grassland aboveground biomass will be increasingly limited by factors other than N supply. NutNet studies examining drought effects have focused on N addition in combination with other elements; however, these results build on previous studies of N alone at single sites or in syntheses. Chronically elevated nutrients increase dominance by grasses, which exacerbated impacts on biomass of a widespread European drought [47]. Across sites, nutrient impacts during drought depend on site aridity and regional floras [48,49]. Across regions, elevated nutrients generally increase grassland sensitivity to precipitation variability [50] (Figure 1 and Table 1).

Consumers: grassland vertebrates, arthropods, and pathogens

N_{dep} may impact consumers through changes in plant quality and quantity, stoichiometric imbalances, and, for arthropods and pathogens, a cooler, moister microclimate resulting from increased aboveground biomass, decreased reproductive habitat, or reduced availability of host or prey species [51]. Increased insect herbivory in response to elevated foliar N concentrations has been reported in some locations [52], even inducing a population explosion in one documented case [53]. N_{dep} can alter nectar chemistry [54] and may reduce forb richness [18], inducing pollinator declines [55,56]. Although widespread butterfly population declines in Europe have been linked to N_{dep}-related increases in vegetation productivity and resulting changes in microclimates [57], most evidence demonstrating an impact of N_{dep} on arthropods comes from studies of individual herbivore species [52]. Pathogen infection prevalence can increase with N because N supply tends to favor faster growing, less-defended plant species [58]. N_{dep} can impact vertebrate consumers via reduced habitat quality and invertebrate food sources (e.g., northern flying squirrel, *Glaucomys sabrinus* [59] and red-backed shrike, *Lanius collurio* [60]), although extensive knowledge gaps remain about N impacts on higher trophic levels [4].

Plant quantity and quality changes with N

N addition in NutNet alters plant traits, generally increasing foliar N at the species level [26] and in aggregate biomass [61], likely improving foliage quality as a food source. N_{dep} [41] and experimental N supply [42] also tend to increase aboveground grassland biomass. From the perspective of plant pollinators, NutNet provides some evidence that elevated N can change flowering phenology, at least in some regional floras [62]. Finally, while there are no direct tests of the impact of N alone on plant defense in NutNet, an experiment performed at the same sites but with the addition of multiple elements, including N, uncovered evidence for increased investment in growth and reduced defense with elevated nutrients [63]. This is consistent with reduced defense in simulated N_{dep} studies [52] but extends the meta-analytical result by demonstrating the consistency of this response across sites and continents.

Consumption, infection, N, and climate

Invertebrate damage on plant foliage at nearly 30 NutNet sites increased in response to N addition, with greatest damage on grasses and nonleguminous forbs [64]. Pathogen damage on these same plants increased with N addition on grasses and legumes [64]. Arthropod and pathogen damage increase with site-level precipitation, but variation in damage with climate is independent of N supply. By contrast, when plants are protected from vertebrate herbivores, the supply of nutrients, including N, increases biomass N most strongly at low precipitation sites, but when vertebrate herbivores at dry sites can access fertilized plants, they consume the nutritious biomass, reducing aggregate biomass N content [61,65]. Nutrient supply also interacts with foliage chemistry and herbivory across this climate gradient. In particular, foliage at sites with low precipitation is relatively high in sodium, a critical element for consumers, and, under dry conditions, vertebrate herbivores tend to consume foliage of high-sodium plant species in fertilized plots [31] (Figure 1 and Table 1).

Consumer biomass and N

The NutNet experiment demonstrates that the N supply supports a greater mass of arthropods (i.e., secondary production) via compositional turnover to favor arthropod species with larger average body sizes [66]. Arthropod abundance also increases with N supply across these sites [66,67], particularly in response to greater mass of live and dead vegetation [66].

Consumers: soil microbial communities

While soil microbes have long been considered in the context of ecosystem processes and agriculture, the edaphic and climatic characteristics controlling microbial biomass and diversity across global gradients are only beginning to be uncovered [68,69]. N addition is known to impact soil microbial communities, often reducing biomass [70] and increasing dominance of bacteria over fungi [71]. Impacts of N via soil acidification may be especially important in controlling species composition [72]. N also has the potential to shift the relative abundance of functional groups, with loss of, for example, mycorrhizal fungal mutualists [73].

Soil communities, functional traits, N, and climate

NutNet data demonstrate that elevated N causes predictable responses in soil microbial composition, and that the magnitude of these changes tends to mirror the magnitude of plant community changes in response to N [74]. N addition tends to increase soil pathogenic fungi [75] and the abundance of archaea and fungal groups such as Ascomycota, whereas Glomeromycota, a group that dominates the arbuscular mycorrhizal fungi, consistently decline in abundance [74]. Across NutNet sites, N also reduces phosphorus-solubilizing bacteria [76]. These soil pathogens and mutualists do not vary with climate, but are, instead, constrained by plant composition and edaphic characteristics [75] which change with N supply (Figure 1 and Table 1).

Soil microbial biomass and N

Grassland microbial biomass and microbial biomass C:N chemistry were unchanged in response to NutNet's consistently increased N supply across a range of climatic and edaphic conditions [77–79]. Although N did not generally reduce soil pH, N supply reduced microbial genes associated with metabolism, reducing both microbial growth and respiration, particularly in surface soils [78,80].

Ecosystem pools and rates

N addition to ecosystems has considerable potential to alter processes, including cycling of N, carbon, and other nutrients. Recent focus has been on impacts of N_{dep} on carbon cycling [81], uncovering high among-study variability in the response of soil processes to N_{dep}. For example, a meta-analysis of the effect of N on litter decomposition showed that responses depended on N_{dep} or N addition rate and litter quality [82]. While soil respiration is commonly reduced by N addition [83], impacts on soil carbon stocks are variable [84]. Although some studies found relationships between N addition and N mineralization (N_{min}) (e.g., unimodal relationship in a tropical grassland) [85], the documented impacts on N cycling are variable in the literature, apparently due to dependence of microbially driven processes, such as mineralization and immobilization, on climate, management, and other factors (e.g., [86]).

Litter and decomposition, N, and climate

Although N increases live biomass in the NutNet experiment, elevated N supply has variable effects on litter across sites around the world [21]. Litter disappearance is poorly predicted by climate alone, instead varying most among continents, suggesting the combined importance of factors including vegetation, microbial communities, and climate [87]. N accelerates initial decomposition and biochemical transformation of standard substrates, particularly at cool sites, but not at warm sites [88]. Furthermore, similar to aboveground biomass, decomposition is co-limited by multiple nutrients, and precipitation jointly determines this rate. However, while N speeds decomposition in the initial years, it slows late-stage decomposition [109] (Figure 1 and Table 1).

Soil carbon, N, and climate

Among sites, NutNet N addition causes losses and gains of soil carbon, but identical treatments do not induce consistent responses after 2–3 years [89] or 10 years [90]. N effects on soil carbon likely occur where N supply reduces the soil organic carbon to N ratio and increases soil aggregation, reducing microbial respiration and increasing soil microbial carbon-use efficiency [78,80]. The availability of other elements likely has an important role in constraining N effects on changes in soil carbon [91]. When other elements are supplied along with N, changes in both soil carbon stocks [89] and microbial carbon-use efficiency [78] vary along a moisture gradient (precipitation and soil sand content) (Figure 1 and Table 1).

Soil nutrient cycling, N, and climate

Across NutNet, N_{min} in grassland soils is greatest at sites with high microbial biomass, soil organic C, and warm, wet, growing seasons [92], and elevated nutrients tend to reduce N_{min} only when vertebrate herbivores are excluded from plots. Particularly under elevated nutrients, the impact of herbivory on the soil N pool varies with climate [93]. While these studies received N in combination with other nutrients, they demonstrate that N cycling is controlled via multiple, interactive factors, including elevated N, under field conditions. Other work in NutNet demonstrates that elevated N alone increases P cycling by increasing bacterial phosphatase production [76] (Figure 1 and Table 1).

Concluding remarks

Given that regions around the world differ in climate, biota, and input rates of N and other elements, and changes in these factors differ among regions in both direction and pace, sorting apart the sources of variation in biotic responses to N_{dep} remains a difficult challenge. This is particularly true because most experiments are performed at single sites and characterize one or a limited suite of response variables, making it difficult to uncover site or regional contingencies. The NutNet experiment, adding an identical rate of N across locations and conditions, demonstrates that impacts of elevated N on plant species traits, plant biomass, and ecosystem rates (e.g., decomposition) are strongly contingent on local climatic conditions (Figure 1). The interplay of this multicontinent experiment with the existing literature on N_{dep} highlights emergent, synthetic perspectives and points to future research directions (see Outstanding questions).

Replication across time and space

Variation in N_{dep} and its effects across both time and space mean that empirical evidence for the rate, locations, and types of biotic impacts is heterogeneous. Many studies have documented N limitation of biomass, but this review highlights that, while N limitation is rapidly apparent at a small subset of sites [42], it becomes apparent in an increasing number of locations with longer, chronic inputs [21]. This review also highlights that N effects on plants, consumers, and ecosystem processes vary with soil mineralogy and micronutrient supply, underscoring the need for increased attention to the role of inputs of other elements (e.g., [94]) and local edaphic characteristics in controlling biotic responses to N_{dep}. Effects consistent across conditions raise additional questions. For example, while N_{dep} increases plant palatability and reduces defense across a range of site conditions, successful use of grazing in management will rely on understanding the condition dependence of response times [95], tipping points [96], and the role of local edaphic and climate conditions in recovery potential [97]. Results from NutNet and the many other studies reviewed here suggest that long-term, cross-continent experiments are needed to uncover N_{dep} impacts that may take years to emerge and may differ across conditions [98]. Finally, few experiments impose gradients of N addition [14], but these will provide key insights into the shape of biotic responses and risk of tipping points with increasing N_{dep}.

Climate and N_{dep}

While often studied in isolation, changing climate and N_{dep} rates can interact to impact many biotic responses (Figure 1 and Table 1). Precipitation mean and variation are particularly prominent in modifying the biotic responses reviewed here. For example, in response to NutNet's elevated N supply, control of grassland biomass and plant chemistry shifts from herbivores to nutrients with increasing precipitation [61,65], whereas precipitation variability determines whether native or non-native plants decline [29]. Together with scant, but compelling, evidence in the literature about the impacts of N_{dep} on consumers, this review also demonstrates the importance of climate in mediating N impacts with potentially far-reaching, but mostly unknown, implications spanning trophic levels. The results reviewed here emphasize the need to understand the dependence of biotic responses to N_{dep} on climate to avoid unexpected outcomes under future climatic conditions.

Acknowledgments

This work would not have been possible without the Nutrient Network collaborators and experiment, funded at the site scale by individual researchers and supported by grants to E.T.B. and others from the US National Science Foundation (NSF-DEB-1042132 and NSF-DEB-1831944).

Declaration of interests

None declared by authors.

Outstanding questions

Where will N limitation shift to nutrient co-limitation of biomass in the future? Co-limitation is far more common than thought previously. It remains unclear where that will change in the future, with rising CO_2 possibly offsetting increasing N_{dep} in some regions.

Under what conditions are N_{dep} impacts on grassland consumers greatest? Identifying species, regions, and conditions where N_{dep} will spread through above- and belowground grassland foodwebs and feed back to impact plant biomass and soils is an open question.

How will concurrently changing climate and N_{dep} impact grassland soil carbon storage? Grasslands store ~20% of the world's soil carbon, yet this review highlights large, mostly unexplained, variation in the soil carbon response to N addition. Uncovering how climatic, biotic, and edaphic factors interact with N_{dep} to control soil organic carbon stocks remains a key challenge.

How can we best translate knowledge into habitat management to mitigate N_{dep} impacts? N_{dep} is impacting protected habitats in many areas of moderate and high deposition. Yet limited research exists into the efficacy of offsetting elevated N via vegetation removal or increasing habitat resistance via other management approaches.

Which existing knowledge is generalizable to understudied regions? Regional policies rely on biotic response data to inform critical load values, yet the existence of data on responses to N_{dep} varies among continents, with a near absence in several global regions. Supporting and engaging with scientists in these regions is a critical need for informing policy development.

Which habitats will recover from the impacts of N_{dep}? Results are mixed on the potential for recovery from N_{dep} but suggest that recovery will be slow, and alternative states are possible, requiring active management for a return to previous conditions.

Resources

[i]https://nutnet.org/

References

1. Wolfe, A.H. and Patz, J.A. (2002) Reactive nitrogen and human health: acute and long-term implications. *AMBIO* 31, 120–125
2. Bobbink, R. *et al.* (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* 20, 30–59
3. Elser, J.J. *et al.* (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142
4. Stevens, C.J. *et al.* (2018) Atmospheric nitrogen deposition in terrestrial ecosystems: Its impact on plant communities and consequences across trophic levels. *Funct. Ecol.* 32, 1757–1769
5. Schlesinger, W.H. (2009) On the fate of anthropogenic nitrogen. *Proc. Natl. Acad. Sci. U. S. A.* 106, 203–208
6. Ackerman, D. *et al.* (2019) Global estimates of inorganic nitrogen deposition across four decades. *Glob. Biogeochem. Cycles* 33, 100–107
7. Galloway, J.N. *et al.* (2008) Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science* 320, 889–892
8. Clark, C.M. *et al.* (2019) Potential vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur in the United States. *Nat. Plants* 5, 697–705
9. Li, Y. *et al.* (2016) Increasing importance of deposition of reduced nitrogen in the United States. *Proc. Natl. Acad. Sci. U. S. A.* 113, 5874–5879
10. de Gouw, J.A. *et al.* (2014) Reduced emissions of CO2, NOx, and SO2 from U.S. power plants owing to switch from coal to natural gas with combined cycle technology. Earth's. *Future* 2, 75–82
11. Aksoyoglu, S. *et al.* (2020) Role of ammonia in European air quality with changing land and ship emissions between 1990 and 2030. *Atmos. Chem. Phys.* 20, 15665–15680
12. Zhang, Y. *et al.* (2018) Long-term trends in total inorganic nitrogen and sulfur deposition in the US from 1990 to 2010. *Atmos. Chem. Phys.* 18, 9091–9106
13. Greaver, T.L. *et al.* (2016) Key ecological responses to nitrogen are altered by climate change. *Nat. Clim. Chang.* 6, 836–843
14. Midolo, G. *et al.* (2019) Impacts of nitrogen addition on plant species richness and abundance: a global meta-analysis. *Glob. Ecol. Biogeogr.* 28, 398–413
15. Galloway, J.N. *et al.* (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry* 70, 153–226
16. Wilkins, K. *et al.* (2016) Vegetation community change points suggest that critical loads of nutrient nitrogen may be too high. *Atmos. Environ.* 146, 324–331
17. Simkin, S.M. *et al.* (2016) Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proc. Natl. Acad. Sci. U. S. A.* 113, 4086–4091
18. Stevens, C.J. *et al.* (2010) Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Funct. Ecol.* 24, 478–484
19. Hautier, Y. *et al.* (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324, 636–638
20. Basto, S. *et al.* (2015) Long-term nitrogen deposition depletes grassland seed banks. *Nat. Commun.* 6, 6185
21. Seabloom, E.W. *et al.* (2021) Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. *Ecology* 102, e03218
22. Harpole, W.S. *et al.* (2016) Addition of multiple limiting resources reduces grassland diversity. *Nature* 537, 93–96
23. Chadwick, O.A. *et al.* (1999) Changing sources of nutrients during four million years of ecosystem development. *Nature* 397, 491–497
24. Borer, E.T. *et al.* (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508, 517–520
25. Chapin, F.S.I. (1980) The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11, 233–260
26. Firn, J. *et al.* (2019) Leaf nutrients, not specific leaf area, are consistent indicators of elevated nutrient inputs. *Nat. Ecol. Evol.* 3, 400–406
27. Broadbent, A.A.D. *et al.* (2020) Dominant native and non-native graminoids differ in key leaf traits irrespective of nutrient availability. *Glob. Ecol. Biogeogr.* 29, 1126–1138
28. Seabloom, E.W. *et al.* (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nat. Commun.* 6, 7710
29. Flores-Moreno, H. *et al.* (2016) Climate modifies response of non-native and native species richness to nutrient enrichment. *Philos. Trans. R. Soc. B Biol. Sci.* 371, 20150273
30. Tognetti, P.M. *et al.* (2021) Negative effects of nitrogen override positive effects of phosphorus on grassland legumes worldwide. *Proc. Natl. Acad. Sci. U. S. Am.* 118, e2023718118
31. Borer, E.T. *et al.* (2019) More salt, please: global patterns, responses and impacts of foliar sodium in grasslands. *Ecol. Lett.* 22, 1136–1144
32. LeBauer, D.S. and Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89, 371–379
33. Crowley, K.F. *et al.* (2012) Do nutrient limitation patterns shift from nitrogen toward phosphorus with increasing nitrogen deposition across the northeastern United States? *Ecosystems* 15, 940–957
34. Kaspari, M. (2021) The invisible hand of the periodic table: how micronutrients shape ecology. *Annu. Rev. Ecol. Evol. Syst.* 52, 199–219
35. Braun, S. *et al.* (2020) Foliar nutrient concentrations of European beech in Switzerland: relations with nitrogen deposition, ozone, climate and soil chemistry. *Front. Forests Global Change* Published online March 31, 2020. https://doi.org/10.3389/ffgc.2020.00033
36. Rao, L.E. and Allen, E.B. (2010) Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. *Oecologia* 162, 1035–1046
37. Grace, J.B. *et al.* (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* 529, 390–393
38. Isbell, F. *et al.* (2013) Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc. Natl. Acad. Sci. U. S. A.* 110, 11911–11916
39. Zhang, Y. *et al.* (2016) Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Glob. Chang. Biol.* 22, 1445–1455
40. Li, W. *et al.* (2015) The effects of simulated nitrogen deposition on plant root traits: a meta-analysis. *Soil Biol. Biochem.* 82, 112–118
41. Stevens, C.J. *et al.* (2015) Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. *Ecology* 96, 1459–1465
42. Fay, P.A. *et al.* (2015) Grassland productivity limited by multiple nutrients. *Nat. Plants* 1, 15080
43. Radujković, D. *et al.* (2021) Soil properties as key predictors of global grassland production: have we overlooked micronutrients? *Ecol. Lett.* 24, 2713–2725
44. Cleland, E.E. *et al.* (2019) Belowground biomass response to nutrient enrichment depends on light limitation across globally distributed grasslands. *Ecosystems* 22, 1466–1477
45. Hautier, Y. *et al.* (2014) Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508, 521–525
46. Carroll, O. *et al.* (2021) Nutrient identity modifies the destabilising effects of eutrophication in grasslands. *Ecol. Lett.* 25, 754–765
47. Van Sundert, K. *et al.* (2021) Fertilized graminoids intensify negative drought effects on grassland productivity. *Glob. Chang. Biol.* 27, 2441–2457

48. Bharath, S. *et al.* (2020) Nutrient addition increases grassland sensitivity to droughts. *Ecology* 101, e02981
49. La Pierre, K.J. *et al.* (2016) Drivers of variation in aboveground net primary productivity and plant community composition differ across a broad precipitation gradient. *Ecosystems* 19, 521–533
50. Bharath, S. *et al.* (2021) Multiple resource limitations explain biomass-precipitation relationships in grasslands. *bioRxiv* Published online March 10, 2021. https://doi.org/10.1101/2021.03.09.434527
51. Nijssen, M.E. *et al.* (2017) Pathways for the effects of increased nitrogen deposition on fauna. *Biol. Conserv.* 212, 423–431
52. Throop, H.L. and Lerdau, M.T. (2004) Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems* 7, 109–133
53. Bobbink, R. *et al.* (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86, 717–738
54. Ceulemans, T. *et al.* (2017) The role of above-ground competition and nitrogen vs. phosphorus enrichment in seedling survival of common European plant species of semi-natural grasslands. *PLoS ONE* 12, e0174380
55. Baude, M. *et al.* (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* 530, 85–88
56. David, T.I. *et al.* (2019) Understanding how changing soil nitrogen affects plant–pollinator interactions. *Arthropod Plant Interact.* 13, 671–684
57. Wallis de Vries, M.F. and Van Swaay, C.A.M. (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Glob. Chang. Biol.* 12, 1620–1626
58. Cappelli, S.L. *et al.* (2020) Sick plants in grassland communities: a growth-defense trade-off is the main driver of fungal pathogen abundance. *Ecol. Lett.* 23, 1349–1359
59. Clark, C.M. *et al.* (2017) Nitrogen-induced terrestrial eutrophication: cascading effects and impacts on ecosystem services. *Ecosphere* 8, e01877
60. Dise, N.B. *et al.* (2011) Nitrogen as a threat to European terrestrial biodiversity. In *The European Nitrogen Assessment: Sources, Effects and Policy Perspectives* (Sutton, M.A. *et al.*, eds), pp. 463–494, Cambridge University Press
61. Anderson, T.M. *et al.* (2018) Herbivory and eutrophication mediate grassland plant nutrient responses across a global climatic gradient. *Ecology* 99, 822–831
62. Biederman, L. *et al.* (2017) Nutrient addition shifts plant community composition towards earlier flowering species in some prairie ecoregions in the U.S. Central Plains. *PLoS ONE* 12, e0178440
63. Lind, E.M. *et al.* (2013) Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. *Ecol. Lett.* 16, 513–521
64. Ebeling, A. *et al.* (2022) Nutrient enrichment increases invertebrate herbivory and pathogen damage in grasslands. *J. Ecol.* 110, 327–339
65. Borer, E.T. *et al.* (2020) Nutrients cause grassland biomass to outpace herbivory. *Nat. Commun.* 11, 6036
66. Lind, E.M. *et al.* (2017) Increased grassland arthropod production with mammalian herbivory and eutrophication: a test of mediation pathways. *Ecology* 98, 3022–3033
67. La Pierre, K.J. and Smith, M.D. (2016) Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems. *Oecologia* 180, 485–497
68. Bastida, F. *et al.* (2021) Soil microbial diversity–biomass relationships are driven by soil carbon content across global biomes. *ISME J.* 15, 2081–2091
69. Thaler, D.S. (2021) Is global microbial biodiversity increasing, decreasing, or staying the same? *Front. Ecol. Evol.* Published online April 19, 2021. https://doi.org/10.3389/fevo.2021.565649
70. Farrer, E.C. *et al.* (2013) Nitrogen deposition, plant carbon allocation, and soil microbes: changing interactions due to enrichment. *Am. J. Bot.* 100, 1458–1470
71. Zhang, T.A. *et al.* (2018) Global negative effects of nitrogen deposition on soil microbes. *ISME J.* 12, 1817–1825
72. Rousk, J. *et al.* (2011) Fungal and bacterial growth responses to N fertilization and pH in the 150-year 'Park Grass' UK grassland experiment. *FEMS Microbiol. Ecol.* 76, 89–99
73. Van Geel, M. *et al.* (2020) Diversity and community structure of ericoid mycorrhizal fungi in European bogs and heathlands across a gradient of nitrogen deposition. *New Phytol.* 228, 1640–1651
74. Leff, J.W. *et al.* (2015) Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proc. Natl. Acad. Sci. U. S. A.* 112, 10967–10972
75. Lekberg, Y. *et al.* (2021) Nitrogen and phosphorus fertilization consistently favor pathogenic over mutualistic fungi in grassland soils. *Nat. Commun.* 12, 3484
76. Widdig, M. *et al.* (2019) Nitrogen and phosphorus additions alter the abundance of phosphorus-solubilizing bacteria and phosphatase activity in grassland soils. *Front. Environ. Sci.* Published online November 26, 2019. https://doi.org/10.3389/fenvs.2019.00185
77. Schleuss, P.M. *et al.* (2021) Microbial substrate stoichiometry governs nutrient effects on nitrogen cycling in grassland soils. *Soil Biol. Biochem.* 155, 108168
78. Widdig, M. *et al.* (2020) Microbial carbon use efficiency in grassland soils subjected to nitrogen and phosphorus additions. *Soil Biol. Biochem.* 146, 107815
79. Risch, A.C. *et al.* (2020) Global impacts of fertilization and herbivore removal on soil net nitrogen mineralization are modulated by local climate and soil properties. *Glob. Chang. Biol.* 26, 7173–7185
80. Riggs, C.E. *et al.* (2015) Nitrogen addition changes grassland soil organic matter decomposition. *Biogeochemistry* 125, 203–219
81. Song, J. *et al.* (2019) A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nat. Ecol. Evol.* 3, 1309–1320
82. Knorr, M. *et al.* (2005) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology* 86, 3252–3257
83. Janssens, I.A. *et al.* (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.* 3, 315–322
84. Neff, J.C. *et al.* (2002) Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* 419, 915–917
85. Verma, P. and Sagar, R. (2020) Effect of nitrogen (N) deposition on soil-N processes: a holistic approach. *Sci. Rep.* 10, 10470
86. Giese, M. *et al.* (2011) Nitrogen availability in a grazed semi-arid grassland is dominated by seasonal rainfall. *Plant Soil* 340, 157–167
87. O'Halloran, L.R. *et al.* (2013) Regional contingencies in the relationship between aboveground biomass and litter in the world's grasslands. *PLoS One* 8, e54988
88. Ochoa-Hueso, R. *et al.* (2020) Microbial processing of plant remains is co-limited by multiple nutrients in global grasslands. *Glob. Chang. Biol.* 26, 4572–4582
89. Crowther, T.W. *et al.* (2019) Sensitivity of global soil carbon stocks to combined nutrient enrichment. *Ecol. Lett.* 22, 936–945
90. Keller, A. *et al.* (2021) Soil carbon stocks in temperate grasslands differ strongly across sites but are insensitive to decade-long fertilization. *Glob. Chang. Biol.* 28, 1659–1677
91. Zhao, Q. *et al.* (2020) Strong mineralogic control of soil organic matter composition in response to nutrient addition across diverse grassland sites. *Sci. Total Environ.* 736, 137839
92. Risch, A.C. *et al.* (2019) Soil net nitrogen mineralisation across global grasslands. *Nat. Commun.* 10, 4981
93. Sitters, J. *et al.* (2020) Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Glob. Chang. Biol.* 26, 2060–2071
94. Vet, R. *et al.* (2014) A global assessment of precipitation chemistry and deposition of sulfur, nitrogen, sea salt, base cations, organic acids, acidity and pH, and phosphorus. *Atmos. Environ.* 93, 3–100
95. Stevens, C.J. (2016) How long do ecosystems take to recover from atmospheric nitrogen deposition? *Biol. Conserv.* 200, 160–167
96. Hastings, A. (2016) Timescales and the management of ecological systems. *Proc. Natl. Acad. Sci. U. S. A.* 113, 14568–14573
97. Suding, K.N. *et al.* (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53

98. Silvertown, J. *et al.* (2010) Environmental myopia: a diagnosis and a remedy. *Trends Ecol. Evol.* 25, 556–561
99. Borer, E.T. *et al.* (2014) Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* 5, 65–73
100. Jia, X. (2020) *The Effects of Different N Deposition Simulation Methods on Productivity and Biodiversity of Grassland*, Institute of Agricultural Resources and Regional Planning
101. Nilsson, J. and Grennfelt, P. (1988) *Critical loads for sulphur and nitrogen*, Nordic Council of Ministers
102. Bobbink, R. and Hettelingh, J., eds (2011) *Review and Revision of Empirical Critical Loads and Dose-Response Relationships: Proceedings of an Expert Workshop, Noordwijkerhout, 23–25 June 2010*, Rijksinstituut voor Volksgezondheid en Milieu RIVM B-WARE
103. Pardo, L.H. *et al.* (2011) Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecol. Appl.* 21, 3049–3082
104. Wen, Z. *et al.* (2020) Changes of nitrogen deposition in China from 1980 to 2018. *Environ. Int.* 144, 106022
105. Zhao, Y. *et al.* (2011) Will PM control undermine China's efforts to reduce soil acidification? *Environ. Pollut.* 159, 2726–2732
106. Liu, X. *et al.* (2011) Nitrogen deposition and its ecological impact in China: an overview. *Environ. Pollut.* 159, 2251–2264
107. Sutton, M.A. *et al.* (2020) The Kampala Statement-for-Action on reactive nitrogen in Africa and globally. In *Just Enough Nitrogen* (Sutton, M.A. *et al.*, eds), pp. 583–594, Springer International Publishing
108. Cunha-Zeri, G. and Ometto, J. (2021) Nitrogen emissions in Latin America: a conceptual framework of drivers, impacts, and policy responses. *Environ. Dev.* 38, 100605
109. A Gill, et al., Nitrogen increases early-stage and slows late-stage decomposition in grasslands spanning continents, *J. Ecol.*, https://doi.org/10.1111/1365-2745.13878. (In press).