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# A decade of insights into grassland ecosystem responses to global environmental change

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**Earth's biodiversity and carbon uptake by plants, or primary productivity, are intricately interlinked, underlie many essential ecosystem processes, and depend on the interplay among environmental factors, many of which are being changed by human activities. While ecological theory generalizes across taxa and environments, most empirical tests of factors controlling diversity and productivity have been observational, single-site experiments, or meta-analyses, limiting our understanding of variation among site-level responses and tests of general mechanisms. A synthesis of results from ten years of a globally distributed, coordinated experiment, the Nutrient Network (NutNet), demonstrates that species diversity promotes ecosystem productivity and stability, and that nutrient supply and herbivory control diversity via changes in composition, including invasions of non-native species and extinction of native species. Distributed experimental networks are a powerful tool for tests and integration of multiple theories and for generating multivariate predictions about the effects of global changes on future ecosystems.**

The variety of life forms on Earth, 'biodiversity', and the conversion of sunlight energy and carbon into plant biomass, 'productivity', are two of the most fundamental properties of ecosystems and are changing globally[1,2] in response to ongoing changes in many factors[3,4], including nutrient pollution, species invasions, temperature, precipitation, and the distribution and density of domestic and wild grazers[5–7]. Ecosystem- and human-health both depend on biodiversity and productivity[8,9], highlighting the pressing need to understand how changing environments will influence ecological communities. The rich theoretical lineage of ecology provides generalizable, mechanistic hypotheses that guide empirical inquiry into the effects of a changing environment on biodiversity and primary productivity. A mechanistic understanding of this relationship has relevance for understanding how species interactions shape functional processes in communities, which in turn can predict the conditions under which species will buffer or exacerbate global environmental change. Historically, empirical tests of the hypotheses generated by theory have taken the form of observations at various scales[10–12], experiments at single sites[13,14], and meta-analyses that seek generality by quantitatively synthesizing the results of single-site experiments[15,16].

Meta-analysis, in particular, has provided a powerful tool to synthesize decades of empirical work in community ecology to generate insights into the drivers of—and linkages between—diversity and productivity. For example, meta-analyses spanning ecosystems and spatial scales have revealed little evidence for a single relationship between the existence (and shape) of the association between environmental productivity and species diversity in natural ecosystems[17,18], providing important evidence in a long-standing debate. Other long-standing paradigms hypothesized control of productivity and diversity by factors such as nutrients or herbivory. Meta-analysis overturned one prevailing 'bottom-up' paradigm, that nitrogen (N) limited productivity on land and in the ocean, whereas phosphorus (P) predominantly limited productivity in freshwater, by demonstrating strong similarities among ecosystems, with widespread evidence for co-limitation of primary production by both nitrogen and phosphorus across ecosystems[16,19]. Meta-analysis was also effective in tackling long-standing paradigms about the degree to which productivity and diversity were controlled by consumers from the 'top-down', demonstrating that across terrestrial and aquatic systems producer biomass and diversity are regulated by both consumers and nutrients, and that nutrient supply rates can mediate the effects of consumers[15,20–22]. However, in spite of the analytical strengths of this approach, meta-analyses rely on comparisons among data generated with differing goals and methodologies and are limited to the taxa and ecosystems that have been studied, all of which can leave substantial ambiguity in interpretation of results.

A decade ago, in response to both the insights and limitations of meta-analysis, the Nutrient Network (NutNet, www.nutnet.org), a distributed, coordinated experiment was designed to generate a new type of empirical data to directly inform fundamental questions about biodiversity and productivity[23] (Fig. 1). By using standardized methods to supply nutrients and fence out large herbivores[23] at nearly 80 sites (with observational data spanning >100 sites; Fig. 2) ranging from arctic, high alpine, and desert grasslands to tropical savannah and salt marshes, NutNet has created a unique capacity to test the generality of ecological theories about the relationships between diversity and productivity under widely varying biotic and abiotic conditions. With many sites within and among global ecoregions, these data have shed light on the biotic and abiotic conditions under which impacts of these experimental treatments are either mediated or exacerbated. Further, by adopting an integrative approach to the possible mechanisms that might control ecological communities, the NutNet study measures a large number of system

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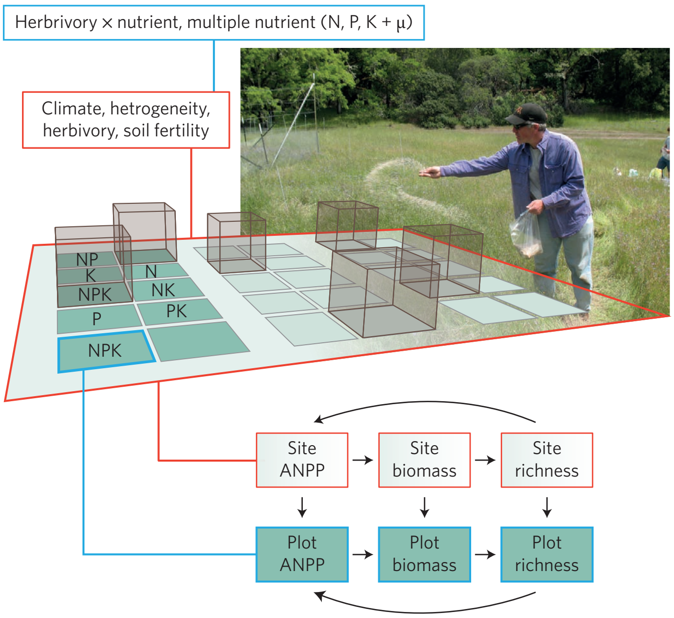


**Figure 1 | The NutNet collaborative experiment tests the interactive factors and feedbacks determining grassland biodiversity and productivity.** NutNet experimental treatments (green) are replicated at sites spanning a wide range of Earth's climate, soils, and biota (orange). Measurements at the plot and site scale (flowchart at the bottom) are used to test the generality of ecological theory. μ, micronutrients. Photo of E.W.S. by E.T.B.

properties, thereby maximizing the suite of questions that can be addressed and supporting fair tests of competing hypotheses about underlying mechanisms. Because of rapid advances in this field, the current intensive international work on policies for biodiversity[24], and the increasingly clear importance of distributed experimental networks for addressing questions at relevant scales, we synthesize a decade of the conceptual advances stemming from NutNet's distributed experimental approach. In the following sections of this Review, we lay out the scientific context that gave rise to this distributed experiment, then focus on advances in three areas motivated by theory and meta-analyses: productivity–diversity relationships; the ecological role of multiple nutrients; and the interactions between nutrient supply and herbivory.

## Developing a new tool for global ecology

Observational studies, single-site experiments and meta-analysis are foundational approaches for empirical ecology that can produce novel insights. However, each also lacks temporal, spatial or methodological generality, obscuring the ecological mechanisms that will determine ecosystem responses to new environments or novel, 'non-analogue' future conditions[25]. For example, observational data reflect natural conditions, often describing patterns across relevant gradients, but cannot unambiguously assign causation. Single-site experiments can assign causation but strong inference is restricted to local conditions[26]. Long-term studies within single sites expand insights into responses across a wider range of climatic conditions occurring at a site[27], but inference remains limited to local conditions (for example, soils) and species combinations.

Inference from meta-analysis has been particularly important for examining the effects of changes to consumers and ecosystem nutrient supply. This approach, imported into ecology from the social sciences in the 1990s[28], makes quantitative comparisons among the results of many individual studies to test theories and seek generality that transcends sites and species[29]. However, meta-analysis relies on comparison among data generated with differing goals and methodologies, thus it is limited by a variety of factors, especially methodological inconsistencies among original studies leading to heterogeneous data, such that analyses must be based on unitless response metrics and coarse community metrics (for example, aggregate biomass or number of species) and variable spatial, temporal, and taxonomic scales of resolution in the original studies[29,30]. In addition, some ecosystems and taxa are underrepresented in the literature; for example, terrestrial studies comprised only 7–9% of studies in cross-ecosystem meta-analyses of experimental consumer and fertilization manipulations[15,22] and 14% of the studies in a cross-ecosystem meta-analysis of fertilization studies[19]. Of the studies manipulating both fertilization and consumers in terrestrial systems, consumer manipulations are heavily dominated by studies of invertebrates (for example, 83% of the studies in ref. [15]). Thus, while meta-analytical syntheses have advanced our understanding of the role of environmental productivity, nutrients and consumers in controlling biodiversity and ecosystem functioning, they also have highlighted key data and knowledge gaps[30].

NutNet was conceived as a collaborative experimental approach to quantify site-scale responses to nutrient and consumer manipulations. By following the same treatments and data collection protocols at all sites over a decade, the aggregate dataset was designed to combine the strengths of meta-analysis, short- and long-term observational studies and single-site experiments[23]. The major goal of this hypothesis-based, question-driven initiative was to test the hypotheses arising from competing ecological theories and thereby gain empirical insights into the generality of diversity and productivity responses to changing environments, spanning a wide array of environmental conditions. Factorial experiments manipulating vertebrate herbivores and multiple nutrients in grasslands were the chosen approach for several reasons. First, grasslands span much of Earth's latitudes, elevations and precipitation, but are dominated by a single plant family (Poaceae), making manipulations and responses directly comparable. The grassland biome is highly sensitive to climatic change, particularly on geological time frames[31], shifting to desert or forest with long-term changes in regional temperature or precipitation. Grasslands have been heavily impacted by humans; more than two-thirds have been converted to human-dominated uses (primarily agriculture)[32,33], and a large proportion of the noxious weeds in many countries are grasses invading grasslands[34]. Finally, in spite of clear links between human impacts and ecological theory of biodiversity and productivity, grasslands, and the large vertebrate herbivores that roam them on nearly every continent, are substantially underrepresented in experimental manipulations of nutrients and grazers[15,19,22,35]. Data generated by this project have been used to address a wide variety of questions; here we review and synthesize the results from this project that have shed light on how globally changing nutrients and consumers will influence ecological communities.

## Relationship of productivity with diversity

A plethora of hypotheses about the mechanistic relationship between productivity and diversity have been proposed and hotly debated (reviewed in ref. [36] and the supplement to ref. [11]). However, experimental and observational studies have led to different conclusions about the mechanisms connecting productivity and species diversity[10,11,26,37–42]. For example, experimentally increased productivity in response to fertilization often reduces diversity[22,39], whereas experimentally increased species diversity often leads to increased productivity[37,38,43,44]. In unmanipulated ecosystems, in contrast, meta-analyses have found weak and inconsistent evidence for productivity as a determinant of diversity, while also detecting weaker relationships between diversity and productivity compared to the relationships between abiotic factors and both diversity and productivity[17,18,45]. Synthetic studies have commonly bemoaned the lack of appropriate data, especially data collected using consistent methods, to concurrently assess the relative importance of the

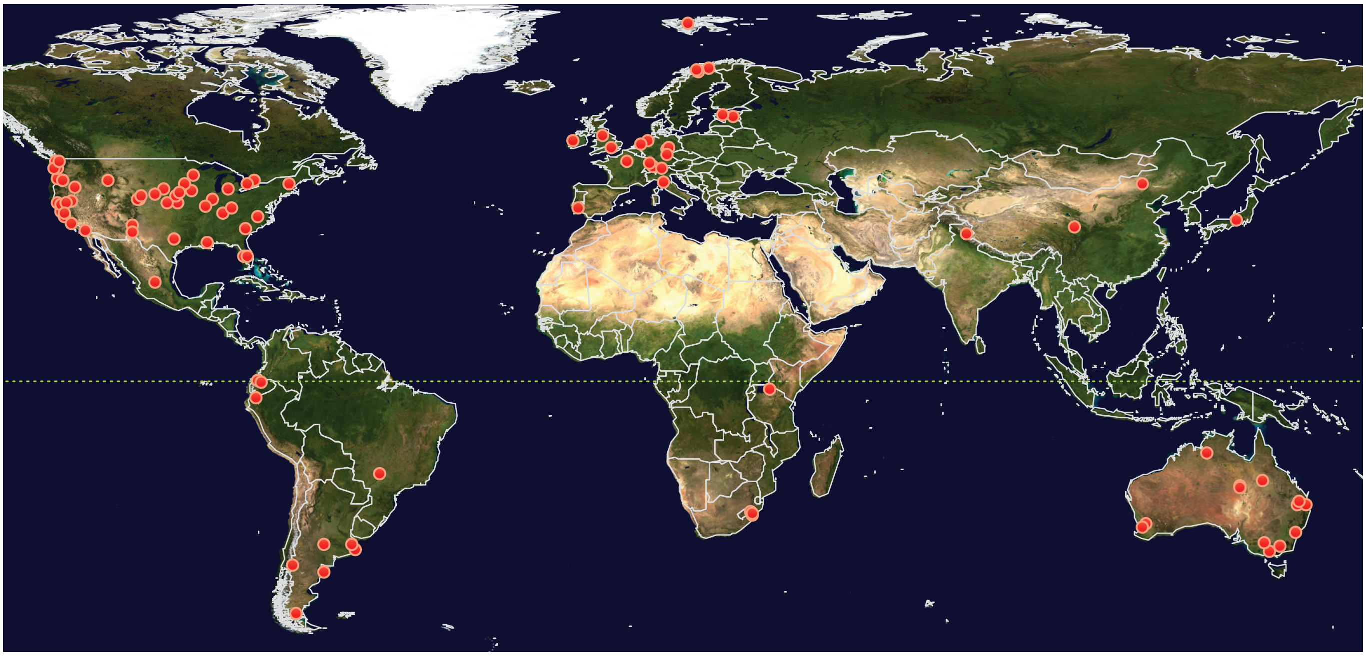

**Figure 2 | The spatial and environmental range of the >100 sites participating in the NutNet project.** NutNet sites (map made in R v. 3.1.1) overlain on a satellite image of Earth. Satellite image credit: NASA Goddard Space Flight Center Image by Reto Stöckli (land surface, shallow water, clouds). Enhancements by Robert Simmon (ocean colour, compositing, 3D globes, animation). Data and technical support: MODIS Land Group; MODIS Science Data Support Team; MODIS Atmosphere Group; MODIS Ocean Group Additional data: USGS EROS Data Center (topography); USGS Terrestrial Remote Sensing Flagstaff Field Center (Antarctica); Defense Meteorological Satellite Program (city lights).

many hypothesized mechanisms linking diversity and productivity in natural systems[30,46,47].

NutNet's methodologically consistent data collection across a wide range of environmental conditions (Figs 1,2) has shown that productivity, alone, explains very little of the variation in plant diversity within and among natural grasslands[12], consistent with earlier meta-analyses[17,18]. A sampling effort launched in response to Adler *et al.*[12] by Fraser *et al.*[10] also employed a distributed, collaborative model to collect data on diversity across productivity gradients, and found a similarly weak bivariate relationship between these two factors, with productivity explaining approximately 1% of the overall variation in richness in both studies[10,48]. Importantly, both papers ended by recognizing the significant limitations of these bivariate results for predicting species diversity[10–12,48], and each concluded that a more predictive understanding would come from evaluation of multiple competing hypotheses about the multivariate controls on species richness[10,12].

Because NutNet measurements include a broad range of covarying and possible controlling factors (for example, climate and soil nutrients) characterizing each site and plot, these data support a unique integration and concurrent testing of multiple competing hypotheses. Using data from more than a thousand plots collected from sites spanning five continents, NutNet data significantly advance our understanding of productivity–diversity relationships by demonstrating that variation in environmental factors (for example, climate, soil fertility, herbivory and light) can explain 60% (site) to 65% (regional) of the variation in species richness[11], whereas productivity alone can explain up to a maximum of 10% of this variation (and often far less)[10–12,48]. Further, concurrently examining many competing mechanisms clarifies that productivity also increases with increasing plant species richness, and both local competition and regional climate are important for predicting productivity. Thus, NutNet data provide a more comprehensive, mechanistic understanding of the relationships between productivity and diversity than was previously possible[11,46,49].

**Regulation of diversity and composition: species invasions.** Plant productivity and diversity relationships are also relevant for understanding compositional changes such as biological invasions. Hypotheses about the forces leading to species invasions generally seek to explain invasions via differences between invaded and uninvaded sites (that is, environmental filtering) or trait differences between invaders and the invaded community[50,51]. Empirical tests of the causes of species invasions have generated variable support for each of these classes of drivers, resulting in a context-dependent perception of invasion that often defies generalization across species or environments[50]. By employing data on the same species spanning many sites in their native and exotic ranges, information on both presence and proportional cover of exotics in each plot, and responses to identical experimental treatments in different regional contexts, NutNet data integrate and clarify many single-factor invasion hypotheses, supporting a multivariate perspective on invasion.

NutNet data demonstrate that traits underpinning the differing sensitivity of native and invading species to interacting global changes can lead to invasion, and these differences probably have evolutionary origins. In particular, NutNet data demonstrate that invaders can tolerate and even thrive with environmental change, especially nitrogen addition, whereas native species decline or are driven to local extinction[52]. However, nutrients and climate can interact, causing non-native species to increase more strongly with eutrophication at warmer and wetter sites[53], thus the underlying local conditions generate a range of observed invasion outcomes among regions and sites within a region[53]. Regional variation in levels of human disturbance, especially settlement and cultivation, is also strongly associated with plot-level richness and dominance by exotic species[54,55], further supporting the importance for invasion of differing sensitivity of native and exotic species to global change. NutNet data provide some evidence for evolutionary underpinnings of this difference: shared traits determine patterns of exotic species among sites, whereas natives are sorted by evolutionary differentiation[56]. However, at the scale of individual species, those that are successful in managed grasslands of Europe also tend to be successful in grasslands managed the same way elsewhere in the world, even in very different climates, suggesting that invasion success derives from the simultaneous 'invasion' of both species and land-management technologies[57]. Taken together, these results arising from identical experimental methods demonstrate that invasion outcomes vary among regions, are often tightly coupled with human activities, and the differing importance of evolutionary and ecological forces for natives versus non-natives leads to the divergent environmental responses of these groups.

## Interactive effects of multiple nutrients

Human activities are radically changing global nutrient cycles[58]: humans have doubled the cycling of nitrogen relative to natural rates and tripled that of phosphorus, and our impact on carbon cycling is a dominant contributor to global climate change[59]. However, the ways in which changes to multiple nutrients interact and the ways that changes in nutrient availability impact diversity loss and ecosystem carbon balance is mainly understood through a few related paradigms. One of the most general theoretical paradigms is that local species diversity can be maintained by spatial variability in the relative availability of resources[60,61], suggesting that high rates of input by one element may reduce diversity by reducing environmental heterogeneity. In contrast to the direct effects of resource limitation on diversity, increased plant biomass resulting from elevated nutrient supply can reduce diversity by increasing the intensity of aboveground competition for light, causing extinction of the poorest competitors[11,18,62]. In spite of many documented exceptions, nitrogen is canonically identified as the primary limiting resource for productivity—and strongly related to diversity loss—in terrestrial grasslands[63]. However, both diversity and productivity of plants are affected by a range of shared or unique causal factors[11,46], and identifying and quantifying the strength of these factors is necessary for mechanistic predictions of the impacts of environmental changes such as nutrient pollution on fixation and storage of carbon by plants[11].

**Multiple nutrient limitation of grassland biomass production.** Meta-analyses undertaken a decade ago supported the emerging paradigm that producer community biomass production is co-limited by multiple nutrients[19]. Although meta-analyses have demonstrated that N and P co-limitation is common in marine, freshwater and terrestrial ecosystems[16,19,64], our understanding of the roles of other limiting nutrients remains limited because the vast majority of studies manipulate only N or P (refs [64,65]), offering little information about the roles of elements such as K, Mg, S, Mo and Fe in natural systems, in spite of their known critical biochemical roles[64].

One primary goal in the establishment of NutNet was to address the degree and generality of grassland productivity limitation by more than two nutrients (that is, N and P). The NutNet fertilization experiment, a factorial combination of N, P and potassium (K) with micronutrients[23], is the first global-scale assessment of the relative importance of nutrients other than N and P in natural systems (Fig. 1). NutNet data have revealed surprising variation in the effect of nutrients on productivity in the world's grasslands[66]. For example, nutrient addition increased biomass production at 74% of the sites but, surprisingly, did not increase production at 26% of the sites. In addition, some form of nutrient co-limitation occurred at 69% of the sites, and limitation or co-limitation including K and micronutrients occurred at more than 50% of the sites[66]. This experiment has clearly demonstrated that nutrient co-limitation of grassland productivity is common and widespread. Given ongoing changes in regional nutrient supply to grasslands, these results highlight the need to further understand the conditions under which different elements play key roles in nutrient co-limitation.

NutNet data have further clarified the ways in which nutrients control many ecosystem properties in the world's grasslands, ultimately controlling primary productivity. Observational data from across NutNet show that variation in the balance of nutrients can alter diversity and species evenness, controlling ecosystem productivity[67], consistent with results of NutNet experimental nutrient addition[11,68]. Variation in plant composition is a strong predictor of soil microbial composition[69], suggesting the strong potential for feedbacks between plant compositional change and ecosystem function. Further, nutrient addition increases the synchrony of species in diverse grasslands, reducing the stabilizing effect of diversity on grassland primary production[70], consistent with experimentally planted diversity experiments[43]. Because NutNet has several sites within and among global regions, these data further demonstrate that the drivers of vegetation productivity can differ predictably among regions[66,71–73]. For example, NutNet data have discerned a pervasive signal of increased primary production in the world's grasslands in response to regionally elevated rates of anthropogenic N deposition[72], but in a region of low N deposition, precipitation is a stronger determinant of grassland productivity[71].

**Multiple nutrient limitation of grassland diversity.** Theory suggests that diversity may be maintained by trade-offs among species for below- and aboveground resources[74] or via trade-offs among species for ratios of essential elemental nutrients[75], with the potential for high-dimensional trade-offs to allow many more species than limiting resources[76]. If coexistence is mediated via below- versus aboveground competition, then fertilization, resulting in increased biomass, will cause decreased light availability, thus causing diversity loss via a shift from belowground competition to more intense aboveground competition[11]. If coexistence is mediated through competition for multiple resources, and if species have the appropriate trade-offs in terms of their requirements for different resources, then increased resource supply rates should reduce diversity by reducing niche dimensionality[74].

Analysis of NutNet data has demonstrated that light limitation in fertilized or more productive plots reduces plot scale plant diversity[11,68,77,78]. These data also support the niche dimensionality hypothesis, because diversity declines with the number of nutrients, even after controlling for the effect of nutrients on biomass and light[68]. Addition of different nutrients (for example, N, P or K) led to local communities with differing plant[68] and soil microbial[79] compositions, with nutrient-induced turnover in grassland plant composition frequently leading to greater loss of native species and increased dominance by exotic species[52,53]. Taken together, these results are consistent with resource competition theory[74] and high-dimensional trade-offs between species for multiple limiting resources including light, extending our understanding of species losses and gains in response to elevated resource supply.

NutNet's multiple nutrient experimental work provides added insights into the shared drivers and feedbacks between productivity and diversity in unmanipulated ecosystems[10–12,48], because multiple resources interact to determine ecosystem production, species diversity and composition[52,66,68]. A key synthetic finding from NutNet is that multiple factors concurrently contribute to species coexistence and diversity, and bivariate explanations of biodiversity are generally inadequate for effective predictions; spurious relationships between productivity and diversity can be found when the interrelated factors determining these responses are ignored because the factors that control diversity may also be the factors that limit production[11,46,49]. Observational and experimental evidence from NutNet provides consistent and strong support for the importance of multiple interacting factors in determining biodiversity and ecosystem productivity, pushing the field to move from simple paradigms of nutrient limitation to paradigms that embrace meaningful complexity and dimensionality.

## Interactive effects of herbivory and nutrients

Because altered herbivore communities and increasing rates of nutrient deposition may jointly determine future plant diversity and productivity in many of Earth's ecosystems, the conditions under which plant diversity is most limited by nutrients or herbivores has been hotly debated for decades[22,80,81]. Meta-analyses of hundreds of experiments have demonstrated that autotroph biomass and diversity are regulated by a combination of both top-down and bottom-up processes in nearly all situations[15,20,22]. Most studies find that consumer effects on biomass remain constant across nutrient supply gradients[15,20], but consumer effects also increase with plant tissue nutrient concentrations[82]. In contrast, top-down and bottom-up effects on autotroph diversity are mediated by nutrient supply and community structure[22]. While these extensive syntheses have informed our understanding of responses across ecosystem types, factorial experiments examining key habitats and organisms (for example, vertebrates in grasslands) are lacking[15], as are data to support a more extensive evaluation of the biological and abiotic contingencies of these responses.

By filling this data gap, NutNet data have demonstrated that nutrient addition decreases diversity[68,77], often by causing local extinctions of native species[52]. However, in both fertilized and unfertilized grassland plots, vertebrate herbivores can maintain plant diversity where grazing increases ground-level light[77] by benefitting native flowering plants[52]. Further, although a trade-off between competition for belowground resources and defence against herbivory characterizes the mechanistic basis for diversity maintenance in some cases[83], across NutNet (Fig. 2), species tend to increase in response to both nutrient availability and protection from vertebrate herbivory (fencing), suggesting that a growth–defence trade-off, not a competition–defence trade-off, dominates in herbaceous plant systems[84]. Thus, across a wide range of climatic conditions and species identities, species that increase in abundance with elevated nutrients are relatively more susceptible to vertebrate herbivory[84]. These results suggest that retention of resources, or herbivory defence, is another major niche axis determining which species will be lost under elevated nutrient conditions. When nutrients become less limiting[66,68,77], competition for light increases, spurring increased mean community height[78] and local extinction of small-statured native forbs[52]. Taken together, these results provide a more mechanistic understanding of patterns of species persistence and local extinction in the world's grasslands, suggesting that diversity, invasion and composition can be predicted based upon the independent and joint effects of nutrients and herbivores on plant acquisition of ground-level light[85].

## Future prospects

A decade of question-driven collaboration across NutNet has led to a variety of novel insights that, in turn, point to future directions for the field. For example, NutNet work has revealed that several proposed mechanisms act concurrently to determine species diversity in unmanipulated ecosystems[11]. Species diversity concurrently promotes and maintains productivity, although this effect is often not apparent in observational data. As global environments change, native plant diversity will likely decline with increasing numbers of added nutrients[68], and where nutrient addition or herbivore exclusion reduce ground-level light, plant diversity will decline[77]; these effects on diversity are predicted to play out via compositional shifts, including extinction of native species and invasions by human-adapted species[52,84]. Further, NutNet data have demonstrated that the inadvertent addition of atmospheric nitrogen by human activities is currently a dominant driver of global grassland productivity[72]. These results suggest areas in which new single-site studies and meta-analysis of existing data also could make important contributions to filling knowledge gaps. For example, while distributed experiments can assess the generality of factors controlling biodiversity and productivity across sites, site-specific studies can use this information as a starting point for assessing the relative importance of factors that generate and maintain diversity in local communities. The frequent importance of multiple interacting factors for predicting responses to NutNet experimental treatments additionally suggests that future work should focus on simultaneous effects of multiple factors rather than performing independent tests of single factors. In addition, while NutNet has demonstrated that relatively high rates of nutrient supply predictably reduce diversity and increase productivity[66,68,77], new experiments will be needed to test for the conditions under which communities or ecosystems experience non-linear responses across gradients of single nutrients and changing ratios of nutrient supply.

As the timescale of NutNet's large-scale and increasingly long-term dataset grows, so does the capacity of the dataset to quantify factors determining trajectories of ecosystem change. Unexpected outcomes, such as time lags, tipping points, cumulative effects or responses that change direction with time, can overturn paradigms, and long-term experimental data, particularly when replicated across sites with different characteristics, maximize the probability of capturing these events[27,86,87]. For example, the temporal turnover of species or feedbacks from dead biomass or soil microbial communities to composition or productivity in response to altered herbivory or nutrient enrichment may operate on decadal timescales[88]. Climate also is changing directionally over multi-decadal time scales[59], and this experiment promises to generate important insights into regional differences in grassland responses to interactions between nutrient enrichment and changing climate, a predictive capacity that will be necessary for future decisions about food, energy, and transportation[89]. However, the long-term, spatially replicated ecological data necessary for understanding the effects of these phenomena are exceedingly rare. Thus, the expanding temporal scale of this experiment will open up new classes of questions about the generality of biodiversity and productivity responses across globally relevant ecological gradients while also clarifying the role of context-dependence in these responses. A decade of NutNet research has demonstrated that a multi-continental, distributed, experimental approach, if designed well, can be a sustainable approach for generating high-quality, large-scale, long-term ecological datasets.

Finally, this globally extensive experimental study demonstrates that simultaneous testing of multiple hypotheses significantly advances our understanding of the causes and consequences of biodiversity and primary productivity. By testing *a priori*, theoretically grounded hypotheses across globally extensive biotic and abiotic gradients using identical treatments and broadly focused sampling of system attributes, the distributed experimental approach of NutNet allows testing and integration of 'competing' hypotheses. Thus, NutNet provides a proof of concept for the distributed experimental approach as a powerful empirical tool for generating predictions about conditions under which communities and ecosystems will respond most strongly to concurrent global changes. While the multi-continental, distributed, experimental approach is not a silver bullet for empirical ecology, a decade of this global scientific collaboration demonstrates that it is an approach complementary to single-site studies and meta-analysis for generating new empirical insights that can serve as a model to address a diversity of questions in ecology.

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## Author contributions

E.T.B. conceived and drafted the manuscript; J.B.G., W.S.H., A.S.M. and E.W.S. contributed to writing.

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## Competing interests

The authors declare no competing financial interests.