Grassland productivity limited by multiple nutrients

Philip A. Fay *et al*.*

Terrestrial ecosystem productivity is widely accepted to be nutrient limited[1]. Although nitrogen (N) is deemed a key determinant of aboveground net primary production (ANPP)[2,3], the prevalence of co-limitation by N and phosphorus (P) is increasingly recognized[4–8]. However, the extent to which terrestrial productivity is co-limited by nutrients other than N and P has remained unclear. Here, we report results from a standardized factorial nutrient addition experiment, in which we added N, P and potassium (K) combined with a selection of micronutrients ($K_{+\mu}$), alone or in concert, to 42 grassland sites spanning five continents, and monitored ANPP. Nutrient availability limited productivity at 31 of the 42 grassland sites. And pairwise combinations of N, P, and $K_{+\mu}$ co-limited ANPP at 29 of the sites. Nitrogen limitation peaked in cool, high latitude sites. Our findings highlight the importance of less studied nutrients, such as K and micronutrients, for grassland productivity, and point to significant variations in the type and degree of nutrient limitation. We suggest that multiple-nutrient constraints must be considered when assessing the ecosystem-scale consequences of nutrient enrichment.

Terrestrial ecosystem productivity is widely accepted to be nutrient limited[1], and many studies have focused on limitation by a single nutrient, nitrogen[2,3]. In grasslands, and in other systems, the role of additional nutrients is increasingly recognized. A recent meta-analysis of 1400 N and P fertilization studies[4] showed the limitation of terrestrial productivity by both N and P. Furthermore, these nutrients were often synergistically co-limiting, where together they limited productivity more than the sum of their individual limitations. This meta-analysis is the most comprehensive assessment of ecosystem nutrient limitation to date. However, the global extent and magnitude of multiple limitation by nutrients other than N and P remains poorly understood in natural systems[4,5,9], including grasslands[3,10], a critically endangered biome that accounts for approximately one-third of Earth's terrestrial net primary production[11]. More importantly, multiple-nutrient limitation has not been experimentally tested in grasslands on a global scale using a standardized experimental approach. The potential for synergistic co-limitation of grasslands by multiple nutrients, or conversely, failing to account for the absence of single- or multiple-nutrient limitation, means we may misestimate the magnitude and extent of nutrient limitation of terrestrial net primary productivity.

Humans now produce more reactive N than is produced from all natural terrestrial sources, primarily as fertilizers, industrial products, and through fossil fuel combustion[12,13]. Anthropogenic increases in atmospheric N will result in further terrestrial N deposition, altering ecosystem function[13–17] and potentially increasing limitation by other nutrients, such as P, K, or trace elements[16]. K occurs in high concentrations in plant tissues[18] and its uptake is correlated with that of other nutrients[19,20]. Our understanding of limitation by nutrients other than N in grasslands lags that of agro-ecosystems, where the importance of P, K and micronutrients is better understood[20].

Here we report the frequency, magnitude and global extent of nutrient limitation of grassland ANPP by N, P and K combined with micronutrients ($K_{+\mu}$) at 42 grassland sites in the Nutrient Network (NutNet; Supplementary Information and Borer *et al.*[21]). All sites conducted the same standardized N-P-$K_{+\mu}$ addition experiment, the definitive test for nutrient limitation. This approach overcomes major constraints of previous meta-analyses[4], that is, differing nutrient addition rates and methodologies and the rarity of factorial nutrient treatments in the underlying studies[5].

Sites were located on five continents (Supplementary Fig. 1) and spanned a 23-fold range in ANPP (Supplementary Fig. 2a), over 25° in absolute latitude (actual latitudes 54°N to 37°S), nearly 3,500 m in elevation, and wide ranges in mean annual precipitation (260–1,900 mm), mean annual temperature (0.3–22°C; Supplementary Fig. 1), soil texture, and pretreatment soil N, P and K pools (Supplementary Table 1). The sites included both native and previously cultivated grassland, and some sites were managed with burning, grazing or other practices. Thus, we were able to evaluate single and multiple-nutrient limitation of ANPP at global, continental and site spatial extents, as influenced by management, climate and soils.

N, P and $K_{+\mu}$ were factorially applied annually to replicated 5 m^2 plots at the beginning of each site's growing season at rates commonly used in grassland fertilization experiments[22,23]. The $K_{+\mu}$ treatment included a micronutrient mix in the first treatment year only, to avoid micronutrient toxicity. Nutrient limitation of ANPP was quantified by harvesting current year standing crop biomass for 3 to 5 years, and computing the log response ratio (LRR), the natural logarithm of the ratio of treatment plot to control plot ANPP, a metric commonly used in meta-analyses[24].

Multiple-nutrient limitation of ANPP often occurs in the form of co-limitation[5]. Co-limitation is synergistic when the response to multiple nutrients is greater than the sum of the responses to each nutrient added individually, additive if the multiple-nutrient response equals the sum of the individual nutrient responses, and sub-additive if less than the sum of the single-nutrient responses[5]. Across all sites and years, the combined addition of N and P increased ANPP by an average of 40% over controls (LRR = 0.34), compared to increases of only 18% (LRR = 0.16) for N individually and 9% for P individually (LRR = 0.09; $P = 0.03$, Fig. 1a and Supplementary Fig. 3). This provides clear evidence for globally-averaged synergistic co-limitation of ANPP by N and P in these grasslands. Synergistic co-limitation by N and P across sites and years emerged from frequent occurrence of NP co-limitation at the site level. Some form of NP co-limitation averaging 67% (LRR = 0.51) occurred at 60% of the sites, including sites on all five continents, with synergistic NP co-limitation at 13 sites and sub-additive co-limitation at 12 sites (Supplementary Table 3). Globally averaged synergistic co-limitation of grassland ANPP by N and P contradicts the long-held perception that N is the

*A full list of authors and their affiliations appears at the end of the paper.
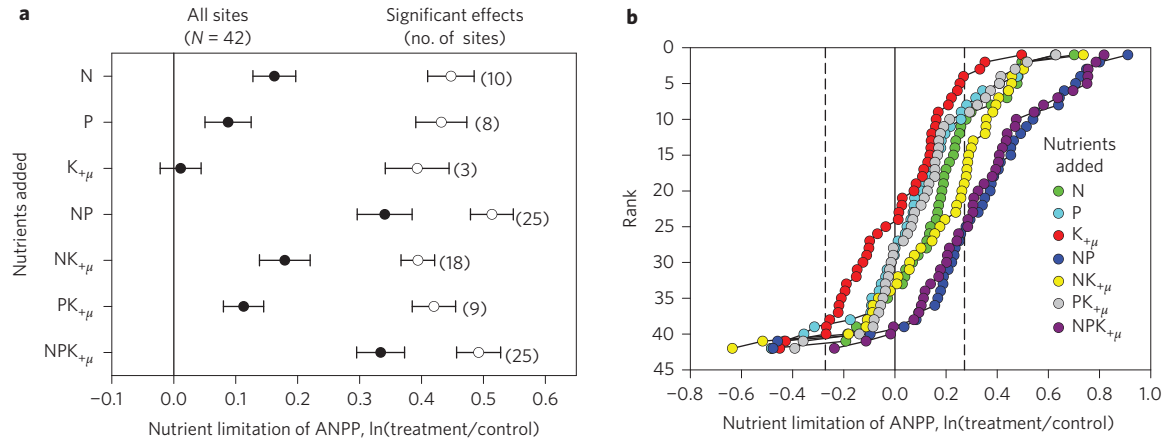
NATURE PLANTS | VOL 1 | JULY 2015 | www.nature.com/natureplants

1

Figure 1 | Nutrient limitation of ANPP (LRRs, ln(treatment/control)) by N, P and K plus year 1 micronutrients ($K_{+\mu}$). a, Mean ± s.e.m. over all years available at each site. Means for all sites are closed symbols. Means of sites where individual nutrient treatments had significant positive effects (defined in **b**) are open symbols. **b**, Site nutrient limitation of ANPP ranked by the magnitude of limitation, averaged over all available years. Vertical dashed lines mark the effect sizes approximating a 0.05 significance level for negative and positive nutrient effects on ANPP. Note that the sites rank in a different order in each nutrient treatment.

predominant nutrient limiting grassland productivity[3,10] and highlights a critical role for P.

There was no globally averaged single- or multiple-nutrient limitation involving $K_{+\mu}$ ($P > 0.32$, Supplementary Table 2). However, this did not preclude frequent site-level single- and multiple-nutrient $K_{+\mu}$ limitation of grassland ANPP. ANPP was limited at three sites by $K_{+\mu}$ alone and co-limited by $NK_{+\mu}$ at 18 sites, both averaging 48% (LRR = 0.39; Fig. 1a and Supplementary Table 3). Additionally, ANPP was co-limited by $PK_{+\mu}$ at nine sites by an average of 52% (LRR = 0.42), approaching the magnitude of ANPP limitation at sites where N (57%) or P (54%) individually limited ANPP (Fig. 1a). Site-level $NK_{+\mu}$ and $PK_{+\mu}$ co-limitation occurred in synergistic, additive and sub-additive forms, and in total, single- or multiple-nutrient limitation involving $K_{+\mu}$ occurred at 21 sites again occurring on all five continents (Supplementary Table 3). This finding represents the broadest assessment to date of potential $K_{+\mu}$ limitation of grassland ANPP, and suggests that

single- and multiple-nutrient K limitation, potentially augmented by micronutrient addition during year 1, occurs more frequently than previously recognized[20,25].

Although single- and multiple-nutrient limitation of ANPP was widespread, there were nonetheless 13 sites that showed no evidence of multiple-nutrient limitation, and 12 of the 13 showed no evidence of single-nutrient limitation (Supplementary Table 3). The presence and magnitude of nutrient limitation may depend on site climate, soil development or fertility[26,27]. For these reasons, greater site-level limitation of ANPP by one nutrient may correlate with greater limitation by one or more additional nutrients. Indeed, site-level individual nutrient limitation of ANPP increased with limitation by other individual nutrients (R^2 0.08–0.15; Fig. 2a,b,d), and ANPP limitation by nutrient pairs increased with that of a third individual nutrient (R^2 0.07–0.21; Fig. 2c,e,f). These correlations suggest that site-level attributes may predict the magnitude of single- and multiple-nutrient limitation of ANPP.
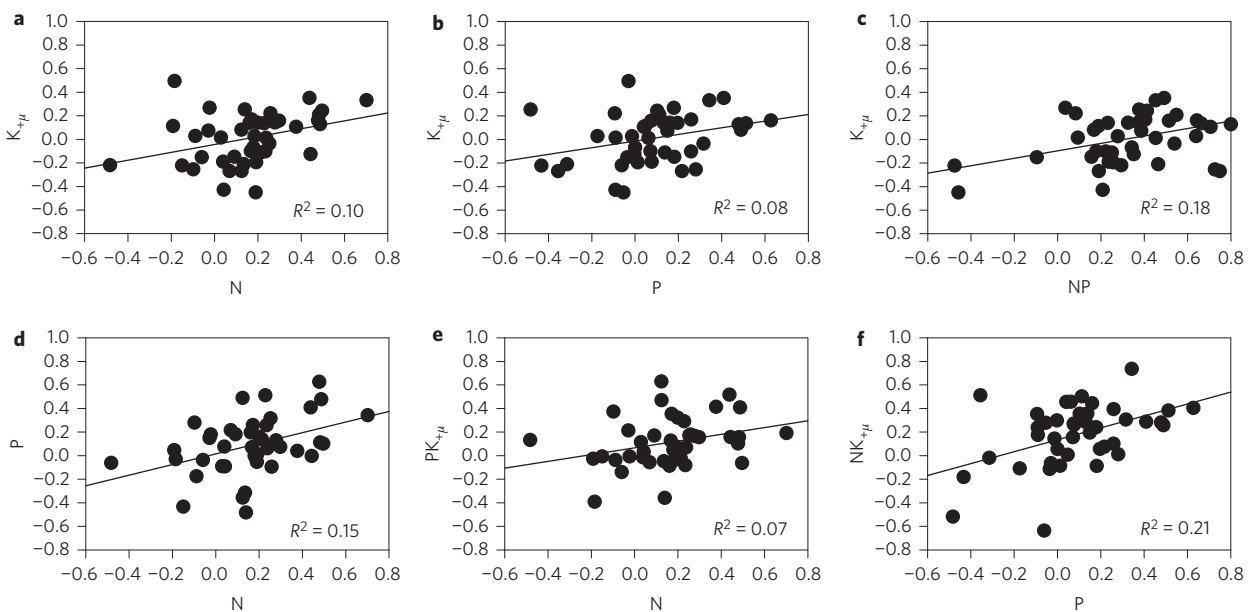

Figure 2 | Correlations of nutrient limitation of ANPP (LRRs, ln(treatment/control)) among single and paired nutrients. a,b,d, Correlations among single nutrients. **c,e,f**, Correlations of nutrient pairs with the third nutrient. R^2 denotes coefficients of determination from linear regression ($0.002 \leq P \leq 0.05$).
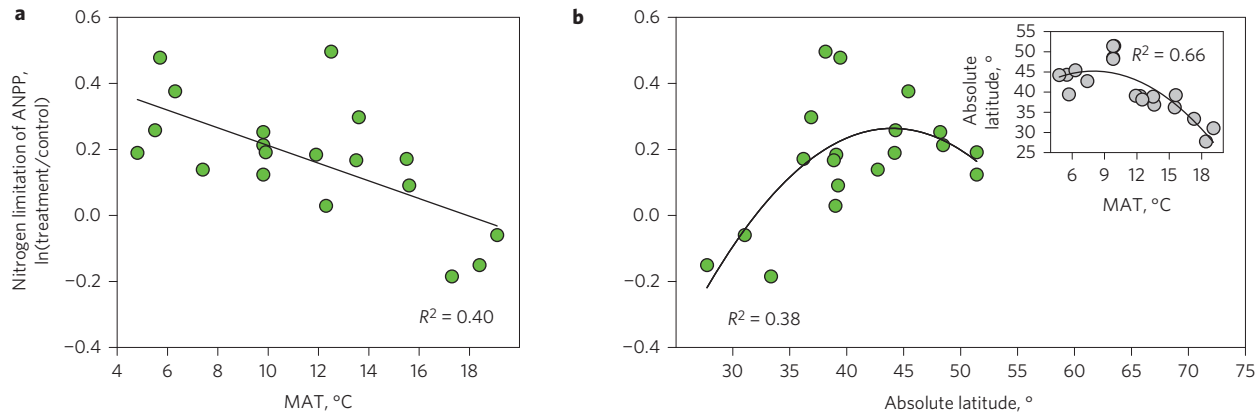
Figure 3 | Predictors of N limitation of ANPP (LRRs, ln(treatment/control)). a, Site MAT. **b**, Site latitude, in degrees away from the equator, and (inset) MAT relationship with site latitude. N limitation values are means of five continuous years of nutrient treatment from 19 sites.

Sites differed in various potential qualitative and quantitative predictors of the presence and magnitude of nutrient limitation of ANPP (Supplementary Table 1). We found no evidence that nutrient limitation differed among the qualitative predictors continent, history of management with burning, grazing, previous cultivation, and predominant soil texture (Supplementary Fig. 4 and Supplementary Table 4). Quantitative predictors were examined at the 19 longest-running sites, where estimates of site mean nutrient limitation should best correspond to site mean climate and soil attributes. N limitation increased with decreasing site mean annual temperature (MAT; $R^2 = 0.40$, $P = 0.002$, Fig. 3a) and peaked at temperate latitude sites (~45°; $R^2 = 0.38$, $P = 0.009$, Fig. 3b) with lower MAT ($R^2 = 0.66$, $P < 0.0001$, Fig. 3b inset). Limitation of ANPP by other single- or multiple-nutrient combinations was not correlated with soil texture fractions, pretreatment soil nutrient contents, soil pH or climate variables ($P > 0.05$, data not shown). These findings suggest that N limitation predominated at cooler temperate latitudes, as others have predicted[26], and validate the power of these experiments to detect spatial trends in ecosystem nutrient limitation.

The magnitude of single- or multiple-nutrient limitation of grassland ANPP may increase through time (Supplementary Fig. 2b). To isolate the temporal signal of nutrient addition effects on ANPP, we calculated new ANPP response ratios using the pretreatment year (that is, year 0) ANPP for each treatment plot rather than the control plot, to control for plot-to-plot spatial variation in ANPP. For 37 sites with no missing ANPP data in years 1–3, the ANPP response to nutrient addition increased through time in all treatments, and ANPP increased each year more in treatments containing N ($P < 0.005$, Fig. 4 and Supplementary Table 2) compared to the P, $K_{+\mu}$ and $PK_{+\mu}$ treatments. Thus, the larger global-averaged increase in ANPP with N than P or $K_{+\mu}$ (Fig. 1a) can be explained partly by both smaller and later manifestation of P and $K_{+\mu}$ effects. The full extent of nutrient limitation of grassland ANPP, particularly for nutrients other than N, may require additional years to emerge.

Multiple-nutrient limitation of ANPP in these grasslands was spatially and temporally varied, often included K and micronutrients, but sometimes none of the nutrients we considered. Thus, while N was an important limiting nutrient in many grasslands, P and $K_{+\mu}$ were also limiting in many instances, both alone and in combination with each other and with N. These estimates for globally averaged nutrient limitation in these grasslands are conservative because nutrient limitation increased in successive treatment years. The magnitude of nutrient limitation may require revision upward if the increases continue in future years.

Multiple-nutrient limitation in grasslands, especially synergistic co-limitation, makes the consequences of anthropogenic nutrient inputs in these and other systems more difficult to predict. For example, nutrient co-limitation may actually restrict the impacts of single-nutrient inputs such as N deposition[17], but ecosystems may respond more rapidly than expected to subsequent inputs of the co-limiting nutrient. Considering only one of the co-limiting nutrients would risk reaching erroneous conclusions about the consequences of future inputs for biodiversity or the provision of ecosystem goods and services[14,15,28,29]. It is imperative to consider multiple-nutrient constraints on primary productivity in grasslands and other ecosystems.
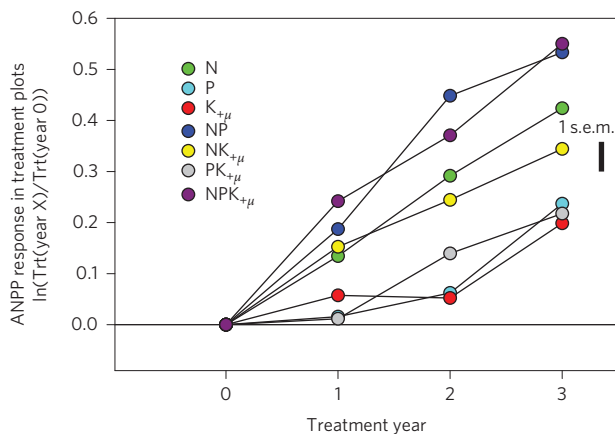

Figure 4 | ANPP responses to factorial N, P and K plus year 1 micronutrient ($K_{+\mu}$) treatments by year in 37 grasslands with three continuous years of ANPP data. Data represent the mean LRR of ANPP in the treatment year to ANPP in the pretreatment year in the same plot, which controls for plot-to-plot variation.

Methods

Study system. The rationale, goals and experimental protocols used at grasslands in the Nutrient Network (NutNet) are described in Borer *et al.*[21], and are summarized here. This study used aboveground net primary productivity (ANPP) data from a standardized nutrient addition experiment conducted at 42 NutNet sites in eight countries (Australia, Canada, China, Switzerland, Tanzania, UK, USA, South Africa) on five continents (Australia ($N = 4$), Africa ($N = 4$), Europe ($N = 5$), Asia ($N = 1$), North America ($N = 28$); Supplementary Fig. 1 and Supplementary Table 1).

The grassland types included alpine/montane grasslands, shortgrass, mixed and tallgrass prairies, desert and semi-arid grasslands, old fields and pastures, savannah and shrub-steppe, and annual grasslands. Sites span wide ranges of mean annual precipitation (MAP; 252–1,898 mm per year), mean annual temperature (MAT; 0.3–22.1 °C; Supplementary Fig. 1), elevation (50–3,500 m), and absolute latitude (over 25°, actual latitudes 54° N to 37° S, Supplementary Table 1). Site climate data were

derived from the WorldClim database (version 1.4)[30]. Local investigators classified sites as to management practice (burned, grazed, other management) and native or anthropogenic (restored grassland and agricultural pasture) origin. Sites collected pretreatment soil nutrient content and texture data.

At each site, N, P and K were added in full factorial combination (eight treatments including control plots) to 5×5 m plots in a randomized complete blocks design with $N = 3$ for most sites (range 2–6). This experimental scale is well suited for the relatively short-statured herbaceous vegetation in grasslands. Micronutrients (6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo and 1% Zn) were added with K only in year 1 to avoid possible micronutrient toxicity. Nutrient additions began at most sites in 2008 ($N = 28$), and additional sites began in 2009 ($N = 9$), 2010 ($N = 3$) and 2011 ($N = 2$).

Sampling. Total ANPP (g m^{-2} yr^{-1}) was estimated annually from clip samples of current year peak aboveground biomass from two 0.1 m^2 quadrats per plot. Samples were dried to constant mass at 60 °C.

Statistical analyses. We tested for nutrient treatment effects on ANPP using linear mixed models in SAS/STAT v 9.2. First, we tested for variation among sites in nutrient main and interactive effects and their variation with treatment year (equation (1)):

$$\ln(\text{ANPP})_{ijkl} = \mu + nutrients_i + nutrients(\text{site})_{ij} + nutrients(\text{year})_{ik}$$
$$+ nutrients(\text{site} \times \text{year})_{ijk} + e_{ijkl} \qquad (1)$$

where *nutrients* refers to the eight factorial combinations of added N, P and K. Nutrient treatments (*i*) were nested within site (*j*), within year (*k*), and within site × year (*jk*). Year was not treated as a repeated effect because each site experienced each year differently, and thus both the year effects and the covariance among years were not the same at each site. There were 42 sites with 3 years of data, 33 sites with 4 years, and 22 sites with 5 years. Model (1) was tested using all available treatment years, and with only the first three treatment years to ascertain whether any nutrient × year interactions were caused by sites added later with fewer years of nutrient addition.

We tested whether ANPP responses to nutrient treatments varied with continent, management, dominant soil texture and origin by replacing the site term in equation 1 with each of the site classification and soil variables, one at a time. Europe and Asia were combined in tests of continent because of the single Asian site.

Calculation of nutrient effect sizes. Effect sizes of the nutrient treatments were calculated and graphed as natural-log response ratios (LRRs). LRRs were calculated in two ways. First, by comparing the ANPP of each treatment plot to the ANPP of the control plot in the same block (2), to isolate treatment effects; and second, by comparing treatment plot ANPP to that of its pretreatment (that is year 0) ANPP (3). This isolated the temporal signal of nutrient addition responses.

$$\text{LRR} = \ln\left(\frac{\text{ANPPtrt}}{\text{ANPPcontrol}}\right) \qquad (2)$$

$$\text{LRR} = \ln\left(\frac{\text{ANPPtrt(year X)}}{\text{ANPPtrt(year 0)}}\right) \qquad (3)$$

We estimated a critical threshold LRR (4) for categorizing the significance of site LRRs. An LRR was considered statistically significant if it exceeded a value corresponding to the critical Z-score (1.65) at $P = 0.05$, computed as:

$$\text{Threshold LRR} = \frac{1}{7}\frac{(\text{LRR}_N + \text{LRR}_P + \text{LRR}_K + \cdots + \text{LRR}_{NPK})}{\text{pooled s.d.}} \qquad (4)$$

Correlations of site variables with nutrient effects. We used linear regression analyses to test whether LRRs for each single nutrient and nutrient pair were predicted by site latitude (absolute value), elevation, mean annual precipitation (MAP), mean temperature annual (MAT), potential evapotranspiration (PET), soil fractions of sand, silt and clay, pretreatment soil N, P and K contents, and soil pH. We presented regressions only where $P < 0.05$, and fitted polynomial curves where indicated by evaluation of residuals.

References

1. Chapin, F. S., Matson, P. A. & Vitousek, P. M. *Principles of Terrestrial Ecosystem Ecology.* 2nd edn (Springer, New York, 2011).
2. Vitousek, P. & Howarth, R. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**, 87–115 (1991).
3. LeBauer, D. S. & Treseder, K. K. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**, 371–379 (2008).
4. Elser, J. J. *et al.* Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **10**, 1135–1142 (2007).
5. Harpole, W. S. *et al.* Nutrient co-limitation of primary producer communities. *Ecol. Lett.* **14**, 852–862 (2011).
6. Bracken, M. E. S. *et al.* Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions. *Oikos* **124**, 113–121 (2015).
7. Ågren, G. I., Wetterstedt, J. Å. & Billberger, M. F. K. Nutrient limitation on terrestrial plant growth – modeling the interaction between nitrogen and phosphorus. *New Phytol.* **194**, 953–960 (2012).
8. Carnicer, J. *et al.* Global biodiversity, stoichiometry and ecosystem function responses to human-induced C-N-P imbalances. *J. Plant Physiol.* **172**, 82–91 (2015).
9. Fisher, J. B., Badgley, G. & Blyth, E. Global nutrient limitation in terrestrial vegetation. *Glob. Biogeochem. Cycles* **26**, GB3007 (2012).
10. Hooper, D. U. & Johnson, L. C. Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. *Biogeochemistry* **46**, 247–293 (1999).
11. Hoekstra, J. M., Boucher, T. M., Ricketts, T. H. & Roberts, C. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* **8**, 23–29 (2005).
12. Galloway, J. N. *et al.* The nitrogen cascade. *BioScience* **53**, 341–356 (2003).
13. Rockstrom, J. *et al.* A safe operating space for humanity. *Nature* **461**, 472–475 (2009).
14. Stevens, C. J., Dise, N. B., Mountford, J. O. & Gowing, D. J. Impact of nitrogen deposition on the species richness of grasslands. *Science* **303**, 1876–1879 (2004).
15. Fenn, M. E. *et al.* Ecological effects of nitrogen deposition in the Western United States. *BioScience* **53**, 404–420 (2003).
16. Mahowald, N. *et al.* Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Glob. Biogeochem. Cycles* **22**, GB4026 (2008).
17. Phoenix, G. K. *et al.* Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Glob. Change Biol.* **18**, 1197–1215 (2012).
18. Øgaard, A. F., Krogstad, T. & Løes, A. K. Potassium uptake by grass from a clay and a silt soil in relation to soil tests. *Acta Agr. Scand. B-S P* **51**, 97–105 (2001).
19. Veresoglou, D. S. & Fitter, A. H. Spatial and temporal patterns of growth and nutrient uptake of five co-existing grasses. *J. Ecol.* **72**, 259–272 (1984).
20. Kayser, M. & Isselstein, J. Potassium cycling and losses in grassland systems: a review. *Grass Forage Sci.* **60**, 213–224 (2005).
21. Borer, E. T. *et al.* Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* **5**, 65–73 (2014).
22. Guevara, J. C., Stasi, C. R., Estevez, O. R. & Le Houerou, H. N. N and P fertilization on rangeland production in Midwest Argentina. *J. Range Manage.* **53**, 410–414 (2000).
23. Clark, C. M. & Tilman, D. Recovery of plant diversity following N cessation: effects of recruitment, litter, and elevated N cycling. *Ecology* **91**, 3620–3630 (2010).
24. Hedges, L. V., Gurevitch, J. & Curtis, P. S. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**, 1150–1156 (1999).
25. Olff, H. & Pegtel, D. Characterisation of the type and extent of nutrient limitation in grassland vegetation using a bioassay with intact sods. *Plant Soil* **163**, 217–224 (1994).
26. Walker, T. W. & Syers, J. K. The fate of phosphorus during pedogenesis. *Geoderma* **15**, 1–19 (1976).
27. Laliberte, E. *et al.* Experimental assessment of nutrient limitation along a 2-million-year dune chronosequence in the south-western Australia biodiversity hotspot. *J. Ecol.* **100**, 631–642 (2012).
28. Wedin, D. A. & Tilman, G. D. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* **274**, 1720–1723 (1996).
29. Jones, L. *et al.* A review and application of the evidence for nitrogen impacts on ecosystem services. *Ecosystem Services* **7**, 76–88 (2014).
30. Hijmans, R. J. *et al.* Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).

Author contributions

P.A.F. wrote the manuscript, drafted the figures, and led the data analysis; E.M.L. developed the database; S.M.P. and W.S.H. contributed to data analysis; S.M.P., W.S.H., J.M.H.K., J.D.B., E.T.B., A.S.M., E.W.S. and P.D.W. contributed conceptual development and data interpretation. All co-authors contributed data and manuscript editing. This work was generated using data from the Nutrient Network (http://www.nutnet.org) experiment.

Philip A. Fay[1]*, Suzanne M. Prober[2], W. Stanley Harpole[3,4,5,6], Johannes M. H. Knops[7], Jonathan D. Bakker[8], Elizabeth T. Borer[9], Eric M. Lind[9], Andrew S. MacDougall[10], Eric W. Seabloom[9], Peter D. Wragg[9], Peter B. Adler[11], Dana M. Blumenthal[12], Yvonne M. Buckley[13], Chengjin Chu[14], Elsa E. Cleland[15], Scott L. Collins[16], Kendi F. Davies[17], Guozhen Du[14], Xiaohui Feng[18], Jennifer Firn[19], Daniel S. Gruner[20], Nicole Hagenah[21], Yann Hautier[22], Robert W. Heckman[23], Virginia L. Jin[24], Kevin P. Kirkman[21], Julia Klein[25], Laura M. Ladwig[16], Qi Li[26], Rebecca L. McCulley[27], Brett A. Melbourne[17], Charles E. Mitchell[23], Joslin L. Moore[28], John W. Morgan[29], Anita C. Risch[30], Martin Schütz[30], Carly J. Stevens[31], David A. Wedin[32] and Louie H. Yang[33]

[1]USDA-ARS Grassland Soil and Water Research Lab, Temple, Texas 76502, USA. [2]CSIRO Land and Water Flagship, Private Bag 5, Wembley, Western Australia 6913, Australia. [3]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa 50011, USA. [4]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig D-04103, Germany. [5]Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Permoserstr. 15, Leipzig 04318, Germany. [6]Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, Halle (Saale) 06108, Germany. [7]School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588, USA. [8]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195, USA. [9]Department of Ecology, Evolution, and Behavior, University of MN, St. Paul, Minnesota 55108, USA. [10]Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada. [11]Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322, USA. [12]USDA-ARS Rangeland Resources Research Unit, Fort Collins, Colorado 80526, USA. [13]School of Natural Sciences, Zoology, Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland. [14]Research Station of Alpine Meadow and Wetland Ecosystems, Lanzhou University, Lanzhou 730000, China. [15]Ecology, Behavior & Evolution Section, University of California, La Jolla, San Diego, California 92093, USA. [16]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, New Mexico 88003, USA. [17]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309, USA. [18]Department of Plant Biology, University of Illinois, Urbana, Illinois 61801, USA. [19]School of Earth, Environment and Biological Sciences, Queensland University of Technology, Brisbane, Queensland 4001, Australia. [20]Department of Entomology, University of Maryland, College Park, Maryland 20742, USA. [21]School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg 3209, South Africa. [22]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, Utrecht, CH 3584, Netherlands. [23]Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599, USA. [24]USDA-ARS Agroecosystem Management Research Unit, Lincoln, Nebraska 68538, USA. [25]Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, Colorado 80523, USA. [26]Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China. [27]Department of Plant and Soil Sciences, University of Kentucky, Lexington, Kentucky 40546, USA. [28]School of Biological Sciences, Monash University, Victoria 3800, Australia. [29]Department of Botany, La Trobe University, Bundoora 3083, Victoria, Australia. [30]Swiss Federal Institute for Forest, Snow and Landscape Research, Community Ecology, Birmensdorf 8903, Switzerland. [31]Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK. [32]School of Natural Resources, University of Nebraska, Lincoln, Nebraska 68583, USA. [33]Department of Entomology and Nematology, University of California, Davis, California 95616, USA. *e-mail: philip.fay@ars.usda.gov