**Title:** The “Neutral Theory” of Niche Dimensionality

**Introduction:**

In terrestrial systems, coexistence among plant species is governed by competition for a shared set of limiting resources (Tilman 1982). For stable coexistence to occur, niche theory states that trade-offs must exist between factors that affect plant growth to prevent competitive exclusion (Hutchinson 1957). As a result, it is theorized that greater *dimensionality*, or the number of limiting factors in a system, may confer more opportunities for these trade-offs to develop.

Different Dimensions of Trade-Offs and their environmental relationships

The number and types of trade-offs present in plant systems have been the subject of considerable exploration. Correlated patterns of variation in plant characteristics and abundance suggest several key axes on which niche differentiation occurs; plants are theorized to exhibit trade-offs between competition and colonization (Tilman 1994, Pacala and Rees 1998), herbivore defense and growth (Mattson and Herms 1992), or contrasts between leaf longevity and photosynthetic rate (Wright et al. 2004). Capture of these trade-off dimensions signals what factors produce ecological variation among species, evolutionary constraints in form or function, and mechanisms of plant coexistence.

Trade-offs as a lens to understand biodiversity loss / nutrient enrichment

As human actions have continued to alter many limiting factors in plant systems, the identification of key trade-offs has been used to understand resulting shifts in community structure. Among the most pervasive human-derived stressors is the increased availability of soil nutrients, such as nitrogen and phosphorous, that are known to reduce community richness and species relative abundances (Bobbink et al. 1998, Elser et al. 2007). In many cases, these effects are attributed to variation across a single axis of environmental resource availability, where nutrient enrichment causes a shift in competition for belowground resources to competition for light (Tilman 1984, Dybzinski and Tilman 2007, Hautier et al. 2009). However, plants are also known to be limited by (and compete for) multiple belowground resources (CITATIONS). As a result, biodiversity loss may also stem from trade-offs in the use and acquisition of individual soil nutrients, where fertilization causes a loss of *niche dimensionality* by collapsing a source of variation on which trade-offs operate (Harpole and Tilman 2007, Harpole et al. 2016).

What each trade-offs predicts about compositional response to nutrient enrichment – one vs. multiple axes of change.

While both trade-off mechanisms explain declines in species richness after fertilization, they contrast in predictions of community change across multiple nutrient enrichment treatments. (DeMalach and Kadmon 2017, Harpole et al. 2017). Under a one-dimensional trade-off mediated by light competition, the addition of any limiting belowground resource will shift species abundances across a single axis – treatment effects are directionally equivalent. Multidimensional trade-offs, however, predict that fertilization effects are dependent on resource identity, leading to directionally dissimilar shifts in composition across multiple nutrient enrichment treatments.

Multiple trade-offs are likely to manifest simultaneously, yet their strength will vary depending on plant growth strategies in a given environment. How do we detect these? Emphasize the dimension of variation here.

In natural systems, the trade-offs structuring species abundances are often complex, composed of multiple interacting drivers (Kuang and Chesson 2010). Rather than identifying which mechanism best explains observed responses, comparing the directional similarity among community responses to multiple fertilization treatments – the *dimensionality* of response – may be used to evaluate the relative contribution of potential trade-offs.

Why community outcomes may be single- or multi-dimensional

Constraints on plant physiology, functional traits, and environmental characteristics indicate that community response dimensionality may vary with local context. Globally, plant functional trait distributions suggests that a one-dimensional trade-off is likely to predominate; correlated variation among functional traits -- plant specific leaf area, leaf nutrient content, and plant size – coupled with relative consistence in tissues stoichiometry (Ågren 2008) imply general specialization to low and high resource conditions (Wright et al. 2004, Díaz et al. 2016). However, this contrasts with observed multi-dimensionality of root physiology and local variation in tissue stoichiometry that may generate trade-offs in the use of different belowground resources.

Critically, the importance of competition for belowground resources will depend on system-specific factors that structure plant communities (Passarge et al. 2006, Brauer et al. 2012, Hautier et al. 2018). Higher average fertility and less environmental heterogeneity may encourage development of multidimensional trade-offs, while plant strategies in more stressful or variable environments are more likely to be constrained along a fewer number of niche axes (Dwyer et al. 2015). Similarly, greater taxonomic or functional diversity may produce community outcomes that vary more strongly with fertilizer identity (Suding et al. 2005).

What we do in this study

To date, there exist few global-scale syntheses of the trade-off mechanisms that govern plant responses to fertilization. This may be due, in part, to the use of traditional analytical methods that focus on the magnitude of community response to treatment. While these approaches detect sensitivity to variation along different niche axes, a focus on the direction of change may better capture trade-offs among them. Using data from the Nutrient Network, a globally distributed experiment manipulating the availability of belowground resources, we quantify variation in the trajectories of change across multiple fertilization treatments. In a geometric approach, we compare observed directions of change to a “neutral” expectation (*sensu* Hubbell 2001) where species exhibit proportionally identical responses to the enrichment of multiple soil nutrients. Deviations from this neutral model thus form a metric of response dimensionality that may be used to infer the contributions of different trade-off mechanisms.

What we predict

By quantifying the variation among response trajectories, we aim to assess global and site-specific variation in the drivers of resource competition in grassland systems. We hypothesize that community responses to fertilization will be less varied (more one-dimensional) in spatially or temporally heterogeneous systems and those of lower productivity, where specialization on individual soil nutrients is unlikely to form an important axis of niche differentiation. In contrast, we expect multi-dimensional tradeoffs in belowground resource use to be more important in systems where diversity is maintained by local coexistence mechanisms in taxonomically diverse, resource-rich environments.

**Methods**

*Study Site*

For this study, we examined 49 study sites that are part of the Nutrient Network, a cooperative, globally distributed experiment. Nutrient Network study sites are constructed in a randomized block design, typically composed of 3 blocks divided into 10 5m x 5m plots, totaling 30 plots in each site. In addition to control plots, each block contains a full factorial combination of nitrogen (N), phosphorous (P), and potassium with other micronutrients (Kµ) fertilization treatments, in addition to fencing treatments crossed with +NPKµ enrichment. All nutrient enrichment treatments were applied at a rate of 10 g N/P/K m-2 year-1, with micronutrients only supplied during the first treatment year at a rate of 100g / m-2 to avoid toxicity.

For our analysis, experimental results were filtered to control plots and those receiving single nutrient addition treatments (+N, +P, or +Kµ) without fencing, resulting in 12 – 20 plots per site. Treatment plots each received 10g / m2 yr-1 of broadcast fertilizer. Because sites were initialized at different years and observed for different durations, we filtered our dataset to focus on sites with a sufficient number of treatment years to have confidence in observed community responses. All sites used in this analysis were observed for at least 5 years, including a pre-treatment year (Min = 5, Mean = 9.36, max = 13). A full list of sites and their characteristics is presented in Appendix 1.

*Response Measurements*

In each 5m x 5m plot, a 1m x 1m subplot was designated for community observation. Observers evaluated community composition annually, visually estimating areal cover of all species to the nearest 1 percent. To evaluate relationships between plant life history strategy and fertilization response, species were divided into four functional groups: graminoids (order *Poales*), legumes (family *Fabaceae*), woody species, and forbs. At each site, plants were also characterized by local longevity (annual / biennial / perennial) and provenance (native / introduced).

In most sites, photosynthetically active radiation (PAR) was measured using a ceptometer placed above the grassland “canopy” and at the soil surface. Light interception was estimated as the fraction of available PAR above the canopy relative to available PAR on the soil surface.

In a separate subplot, aboveground biomass was collected yearly in two 1m x 10cm strips of vegetation, air dried at 60º C for 48h, and weighed. In the first year of study, 250g of soil was collected to estimate pre-treatment soil nutrient availability. Soil was analyzed for total %C and %N using dry combustion gas chromatography (COSTECH ESC 4010 Element Analyzer) at the University of Nebraska. Assessment of elemental soil phosphorous, potassium, soil pH, and soil texture were performed at A&L Analytical Laboratory in Memphis, TN. For more detail, please visit <http://www.nutnet.org/exp_protocol>.

*Estimation of Treatment Response*

Given that species abundances often form lognormal distributions in natural communities, raw species abundances were log­2-transformed prior to model fitting (Anderson et al. 2006). Transformation yielded stronger adherence to model assumptions while still providing a natural scale for model responses, where a coefficient value of 1 corresponds to a doubling in abundance per unit change of a given covariate.

To estimate species responses to fertilization treatment, we fit multiple linear regression models to community composition data from each site:



Where **Y** is an *[n x s]* matrix of abundances of all *s* species present within a site, **X** is an [*n x p*] matrix of covariates, **B** is a [*p x s*] matrix of coefficients, and **E** is an [*n x s*] matrix of residuals. For sites containing three nutrient treatments, *i* plots, and *j* years, the coefficient matrix consists of the following terms:



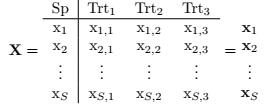
Where community abundance is estimated as a function of the quantity of fertilizer added in observation (expressed as the number of years of treatment), interannual variation in site-level species abundance (encoded as a factor variable), and plot-level variation in species abundance (encoded as a factor variable). Plot and year terms in this model formula act to de-trend species abundances, providing estimates of responses to nutrient enrichment while accounting for other sources of spatial and temporal variation in community composition.

Significance of model terms was evaluated using permutation-based ANOVA. We ordered model terms in a Type I ANOVA to account for the spatial and temporal variation in community composition before testing for effects of fertilization treatment.

*Response Dimensionality*

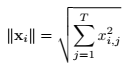
While multivariate linear modelling approaches may be used to estimate the rate of community change in response to treatment, their output does not provide a quantification of similarity among directions of change. To evaluate correlations among different trajectories of community response – the similarity among the responses of individual species that contribute to overall community response – we derive a geometric approach based on work of Cardinale et al. (2018).

In the context of this study, we evaluate trajectories of community change based on experimental manipulations of three limiting nutrients -- N, P, and Kµ. While the following description presents details for this three-dimensional case, our approach may extend to any *n*-dimensional set of treatments. First, we define **X** as a matrix describing the treatment responses (columns) of all *S* species observed in a community (rows). The response of each species to all three treatments are described in row vectors, **x­i**:



In this study, **X** was composed of the three vectors of estimated nutrient response coefficients computed in multiple regression model, **B.**

We captured to total magnitude of compositional change in response to treatments using the Euclidean (L­2) norm of column (treatment response) vectors, defined as:



Where *T* indexes over each of the three treatments in this study.

To standardize magnitudes of change across treatments, column vectors were standardized through dividing by L2 norm, such that . After standardization, community responses to treatment are equal in magnitude, allowing for comparison between directions of change.

To compare potential trade-offs among different axes of environmental change, bivariate relationships may be used to illustrate correlated patterns of change between pairs of treatments (Figure 1a). To evaluate these bivariate relationships, we fit Semi Major Axis (SMA) regressions to each pairwise combination of treatments, which account for uncertainty in both X and Y variables not captured in Ordinary Least Squares (OLS) regression.

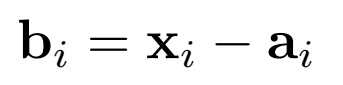
However, bivariate relationships do not provide an aggregate measure of similarity among variables in 3 or more dimensions. Instead, correlation among responses can be evaluated through projection onto a new coordinate basis. Conceptually, our approach is similar to dimensionality reduction through Principal Component Analysis (PCA). Rather than defining the first Principle Component through eigenvalue decomposition, axes are pre-specified under a null hypothesis. We define this null model as a “neutral” expectation where the effects of nutrient enrichment are one-dimensional, trajectories of community change will be directionally consistent. While the total magnitude of effect may vary, our null model assumes that species exhibit proportionally equal responses to multiple nutrient enrichment treatments.

First, we define a vector of 1’s, ***y***, to form a test of our “neutral” null hypothesis. Under this neutral expectation, proportionally equal responses to treatment will be perfectly captured by variation along this 1:1:1 vector (Figure 1b).

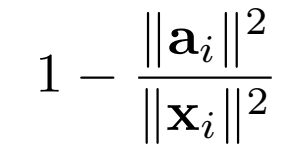
To evaluate the degree to which this null hypothesis captures the responses of species *i*, we define a vector, ***a***, as the projection of observed responses onto the 1:1:1 vector, ***y***:



The orthogonal compliment of the projection, ***b***, defines the elements of ***x*** not captured by projection onto ***y:***

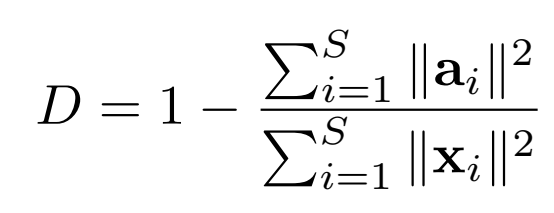


The fraction of variance in species response that is captured by this projection is thus defined as the ratio of squared norms (sums of squares) of ***a*** and ***x***:



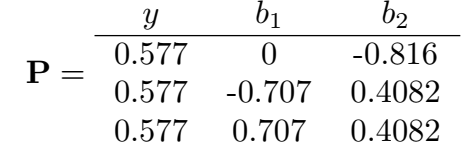
Under our null hypothesis, the set of responses observed for species *i,* ***x­I***, will be of equal magnitude to the projection, ***ai****,****.*** The proportional magnitude of these vectors thus serves as a measure of response dimensionality for a given species, *i*.

Extending this method to all *S* observed species gives an aggregate measure of community dimensionality, bounded between 0 and 1:



Where dimensionality (*D)* is equal to one minus the ratio of summed magnitudes of change when projected on ***y***over their observed magnitudes.When trajectories of community change are directionally identical (low dimensional), response vectors will be perfectly captured by this projection (*D = 0*). Orthogonal responses (high dimensional), where community responses to treatment are uncorrelated, will be poorly captured by this projection (*D = 1*).

When possible, elements of the rejection, ***b***, may be used to visualize deviations from this 1:1:1 line (Figure 1c). In this study, we project this remaining component to two other dimensions orthogonal to ***y***, constituting a change of basis. Thus, the overall projection onto ***y*** and residual coordinates may be expressed as **XPT**, with projection matrix:



Where column vectors above are standardized to unit length.

*Structural Equation Modeling*

To capture variation in site-level community properties and abiotic characteristics, we generated a series of derived variables to supplement observations made during sampling. Climate characteristics were obtained from each site using BioClim, a publicly available dataset of global climate layers. Following prior analyses of the Nutrient Network dataset (Grace et al. 2016), we chose to represent climatic effects on plant growth through site mean temperature at the wettest quarter of year (BIO8) and site mean precipitation during the warmest quarter of the year (BIO18).

Community properties were generated from compositional data collected during pre-treatment sampling. Species turnover was estimated using the ratio of site-level species richness to mean plot-level species richness (. Pre-treatment community composition was also used to calculate the relative abundance of plant functional groups present within each site, defined as the mean proportion of total cover across all plots. Estimates of the total site species pool were calculated by the total number of unique species observed in the first 5 years of sampling, to account for varying durations of observation across sites.

From sites with complete data (*n* = 35), we used structural equation modeling (SEM) to evaluate hypothesized links between environmental characteristics, community properties, and the dimensionality of community response to fertilization. In our initial model, we specified pathways capturing site resource limitation and community characteristics. We incorporated pathways between composite variables describing soil nutrient availability and climatic conditions on response dimensionality, also mediated through intermediate connections between community biomass and light availability. These same variables were also combined in pathways to estimate effects mediated by species turnover and the abundance of community functional groups. After fitting this initial model, we evaluated model fit and pruned non-significant pathways to reduce model complexity.

*Statistical Software*

All statistical analyses were performed in R version 4.0.2. Multivariate linear model fitting was conducted using RRPP (Collyer and Adams 2018). Semi-Major Axis (SMA) regression was performed using “smatr”. Linear mixed effects modeling was conducted using “lme4” and “lmerTest” packages. SEM analyses were conducted using “lavaan”.

**Results**

*Community Responses to Nutrient Enrichment*

*Focus purely on magnitude here – which treatments seem to be the most impactful?*

Of the 49 sites included in analysis, 37 showed significant (P < 0.05) community responses to nutrient addition treatments (Figure 2a). While a majority of sites exhibited significant effects of N enrichment, many sites showed strong community responses to multiple treatments. Consistent with this observation, community rate of change per year of treatment was greatest in response to N enrichment; once accounting for site-level variation in average effect, estimated mean magnitude of community change (in net Euclidean distance per year) was significantly greater following N fertilization than either P or Kµ (*T*96 = 3.10, P < 0.01).

*Correlation Among Community Trajectories*

*How correlated are community responses to different nutrients, globally? Do we see consistent patterns between different resources?*

After standardizing overall community trajectories to unit length within each site, semi major axis (SMA) regression was used to evaluate correlations among responses to treatments at the species level. Pairwise comparisons between nutrient addition treatments (N-P, N-Kµ, P-Kµ) revealed positively correlated responses among all treatments, generally (Figure 3, Table 1). However, these relationships varied as a function of plant functional group. Small intercept terms and slope coefficients equal to one indicate that *Forb*, *Graminoid* and *Woody* species exhibited relatively equal responses across all treatment comparisons. In contrast, SMA regression fits to *Legume* species yielded slope coefficients and intercept terms that suggest stronger responses to P and Kµ treatments than would otherwise be predicted by response to N.

Repeated SMA regression with respect to plant dominance or longevity showed no consistent deviations from general positive correlation in response coefficients (Appendix 2).

*Response Dimensionality*

*Global patterns in variation – how do these reflect the pairwise patterns seen before?*

Decomposition of estimated species responses across these three dimensions of nutrient enrichment demonstrated strong evidence for our null hypothesis as a dominant pattern in our data (Figure 4a). Projection of responses onto the ***y*** vector (assuming proportionally equal responses to treatment) captured 60.68% of the total observed variance across all species; overall species response dimensionality, *D*, was equal to 0.29. This proportion is nearly identical to the fraction of variance captured by the first component in Principal Component Analysis (PCA) of our data, 60.77%. Given that PCA attempts to transform data into a new coordinate basis that maximizes the fraction of variance present in the first component, projection onto the ***y*** vector under our null hypothesis effectively captures a strong pattern inherent in the data.

Consistent with observations made in pairwise comparisons of treatment responses, plant functional groups exhibited consistent patterns of deviation from the null hypothesis (Figure 4b, Table 2). While mean coordinates of plant functional groups did not differ significantly on either ***y*** or ***b1*** dimensions, the mean coordinate position of *Legume* species on the second rejection dimension, ***b2***, was significantly larger than the means of all other functional groups. Given the loadings specified in our projection, ***P***, larger average coordinate values in this second rejection dimension are correlated with proportionally more positive responses to P or Kµ treatments than N enrichment.

*Site Variation in Response Dimensionality*

*Under what circumstances do nutrient treatments have variable vs. one-dimensional impacts on community composition*

To evaluate the environmental and community determinants of response dimensionality, we subdivided data to calculate *D* for all species observed within each site, yielding estimates of *D* that ranged between 0.08 and 0.73 (Mean = 0.39).

Consistent with our hypotheses, SEM analysis identified significant relationships between soil resource availability, climatic characteristics, and response dimensionality (Figure 5). While increasing precipitation and lower growing season temperatures produced a positive, direct effect on response dimensionality, the effects of resource availability were primarily mediated through changes in average biomass and canopy light interception – experiments performed in more productive environments characterized by stronger competition for available light were significantly correlated with greater variation in trajectories of community change across our three fertilization treatments.

Site species richness, soil resources, and climate also had effects on response dimensionality through changes in pre-treatment spatial turnover in species diversity (Figure 5). Greater species turnover, implying non-local mechanisms of species coexistence, and pre-treatment abundance of legumes combined to have negative effects on the dimensionality of community response to treatment.

**Discussion**

**Broad overview – resource competition between plants is complex, given limitation by multiple nutrients. Nevertheless, many approaches focus on quantifying the strength of core patterns over many sites. While this is useful, a focus on dominant patterns is likely to miss on other important drivers.**

An increasing body of evidence indicates that the productivity, diversity, and composition of plant communities is controlled by the abundance of multiple limiting factors, including water, light, and soil nutrients (Fay et al. 2015). While multiple niche dimensions may give rise to multi-dimensional trade-offs in these systems, the realized trade-offs will depend on how strongly these limiting resources structure communities in each system. In the context of nutrient enrichment, the importance of a one-dimensional tradeoff in light competition vs. multi-dimensional tradeoffs for belowground nutrients will depend on whether species are better differentiated by their ability to compete for light or specialize on certain resource types, respectively.

We found that plants respond to variation across multiple axes of environmental change. Generally, community responses to N were strongest, though this is likely a function of the features of our dataset

Across sites, we found that fertilization treatments differed in their average effect on community composition (Figure 1). Consistent with studies of nutrient limitation in terrestrial plant communities and Nutrient Network data, sites exhibited more sensitivity to N enrichment than either P or K treatments. While this finding suggests that variation in N availability acts as more important niche dimension, this may also be a function of our dataset; the Nutrient Network’s focus on grassland ecosystems with disproportionate representation in temperate North America and Europe may skew these results. Nutrient demands are known to vary as a function of dominant ecotype, climatic characteristics, and edaphic properties.

When focused on the direction of change, we found that communities tended to respond in a similar fashion to different nutrient treatments, on average. Despite variation in magnitude of change, species often respond to fertilization in similar direction. Physiological reasons why this might be so.

*Global scale patterns*

The overall dominance of a one-dimensional community response to nutrient enrichment supports the hypothesis of a shift from competition for belowground resources to competition for light (Figure 4a). This result may not be surprising, given the preponderance of evidence linking fertilization to increased light limitation, compositional change, and biodiversity loss (Hautier et al. 2009, Borer et al. 2014, DeMalach et al. 2017). The relative importance of this one-dimensional trade-off mechanism is further supported by observed variation in plant functional traits. Species performance under nutrient enrichment is linked to plant growth rate, leaf nutrient content, stature, and root:shoot investment ; correlations among these characteristics at a global scale suggest that the relationship between plant functional strategy and soil resource availability is generally low dimensional.

However, we also observed distinct differentiation among species with different functional groups.

*Variation between species*

Despite the large proportion of response variation captured by our neutral model, consistent deviations from this one-dimensional relationship at the site- and species scale indicate that other trade-off mechanisms act as important drivers of community structure.

The observed segregation of the *Legume* functional type relative to other groups (Figure 4b, Table 3) is likely due to the unique nutrient demands of nitrogen fixation (McKey 1994). In general, the enzymatic costs of nitrogen fixation present much larger requirements for phosphorous, potassium, sulfates, and other micronutrients relative to other plants. Consistent with this demand, we found that legumes exhibited more positive responses to P and Kµ fertilization than N – though it is important to note that these responses were positively correlated with one another, on average. Variation in plant stoichiometry and resource use associated with this functional strategy appears to act as an additional trade-off mechanism accompanying a more general relationship related to light competition.

While functional group divisions serve as important distinctions between species in the Nutrient Network dataset, they are relatively coarse labels that average over variation in traits and stoichiometry. In addition to exploration of the aboveground trait spectrum and its relationship with fertilization, more concerted efforts to relate belowground nutrient trade-offs to root physiology and architecture are likely to prove insightful; root traits are thought to be more multi-dimensional than their aboveground counterparts (Kramer-Walter et al. 2016) and may play important roles in the acquisition of specific soil resources (Minden and Olde Venterink 2019).

And found that variation in the direction of change was related to features that capture the fertility of each site and mechanisms of species coexistence. Suggests that trade-offs in belowground resource use matter more in systems where local resource competition is likely important – higher fertility environments, which are more stable. In nutrient-poor environments, competition may be more driven by nutrient acquisition, rather than competition – storage effects, etc.

*Variation between sites*

Just as site-level covariates are known to control the magnitude of fertilization effect on community biomass and diversity (Suding et al. 2005), we found evidence that variation among a suite of characteristics related to pre-treatment resource limitation and compositional turnover constrained the dimensionality of community response (Figure 5). In this study, sites that exhibited greater pre-treatment fertility, productivity, and lower pre-treatment spatial turnover were correlated with more response variation between treatments – suggesting a stronger role of multi-dimensional tradeoffs in these systems.

The development of plant functional strategies is theorized to be constrained by the average resource supply in a system and the sources of environmental variation that give rise to niche differentiation (Westoby and Wright 2006, Kraft et al. 2015). In less stressful environments, plant traits are observed to be more varied, theorized to be the result of physiological constraints that limit the number of potential functional strategies.

Species coexistence in grassland environments, which often exhibit high disturbance and climatic stress, is known to depend on spatial and temporal storage effects in many circumstances (Chesson et al. 2004, Adler et al. 2006). Under conditions where growing season precipitation strongly controls plant growth and fitness, viable functional strategies are primarily distributed along a single axis related to relative growth rate and stress tolerance (Angert et al. 2009). While these adaptations promote climatic niche differentiation, physiological constraints likely prevent the emergence of trade-offs in belowground resource use that lead to varied trajectories in response to multiple nutrient enrichment.

*How are systems changing? We’re primarily focused on the total magnitude of biodiversity loss, which often increases as a function of the number of resources that are added. But under multiple nutrient enrichment treatments, both direction and magnitude combine to control biodiversity loss – which species are lost? Can effects be predicted by a single dimension of change, or must each be considered individually?*

*Global change*

Because many terrestrial systems are subject to multiple, interacting global change factors, an understanding of the mechanisms that drive community responses are critical to prediction and management. In many cases, the effects of nutrient fertilization, warming, and altered water availability act synergistically, leading to additive or super-additive effects on biodiversity and composition (Harpole et al. 2016, Komatsu et al. 2019). However, a focus on the magnitude of these effects may fail to capture ecological trade-offs that dictate the way in which communities respond to these changes – under simultaneous enrichment of multiple nutrients, sites governed more strongly by multivariate trade-offs are likely to experience biodiversity loss in a fashion more consistent with the niche dimensionality hypothesis (Harpole and Tilman 2007), as opposed to a one-dimensional gradient of change.

+ Similarity across multiple dimensions of ecological change? Nutrients are just one.

+ Some additional notes on limitations

+ Conclusion?

**References**

Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. Proceedings of the National Academy of Sciences of the United States of America 103:12793–12798.

Ågren, G. I. 2008. Stoichiometry and Nutrition of Plant Growth in Natural Communities. Annual Review of Ecology, Evolution, and Systematics 39:153–170.

Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. Proceedings of the National Academy of Sciences of the United States of America 106:11641–11645.

Bobbink, R., M. Hornung, J. G. M. Roelofs, M. Hornungt, and J. G. M. Roelofst. 1998. The Effects of Air-Borne Nitrogen Pollutants on Species Diversity in Natural and Semi- Natural European Vegetation The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Source: Journal of Ecology Journal of Ecology Journal of Ecology 86:717–738.

Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. a Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. a Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. a Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O’Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. a Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–20.

Brauer, V. S., M. Stomp, and J. Huisman. 2012. The nutrient-load hypothesis: Patterns of resource limitation and community structure driven by competition for nutrients and light. American Naturalist 179:721–740.

Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

DeMalach, N., and R. Kadmon. 2017. Light competition explains diversity decline better than niche dimensionality. Functional Ecology 31:1834–1838.

DeMalach, N., E. Zaady, and R. Kadmon. 2017. Light asymmetry explains the effect of nutrient enrichment on grassland diversity. Ecology Letters 20:60–69.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. Nature 529:167–171.

Dwyer, J. M., R. J. Hobbs, C. E. Wainwright, and M. M. Mayfield. 2015. Climate moderates release from nutrient limitation in natural annual plant communities. Global Ecology and Biogeography 24:549–561.

Dybzinski, R., and D. Tilman. 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. American Naturalist 170:305–318.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135–1142.

Fay, P. A., S. M. Prober, W. S. Harpole, J. M. H. Knops, J. D. Bakker, E. T. Borer, E. M. Lind, A. S. MacDougall, E. W. Seabloom, P. D. Wragg, P. B. Adler, D. M. Blumenthal, Y. M. Buckley, C. Chu, E. E. Cleland, S. L. Collins, K. F. Davies, G. Du, X. Feng, J. Firn, D. S. Gruner, N. Hagenah, Y. Hautier, R. W. Heckman, V. L. Jin, K. P. Kirkman, J. Klein, L. M. Ladwig, Q. Li, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, J. W. Morgan, A. C. Risch, M. Schütz, C. J. Stevens, D. A. Wedin, and L. H. Yang. 2015. Grassland productivity limited by multiple nutrients. Nature Plants 1:1–5.

Grace, J. B., T. M. Anderson, E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, Y. Hautier, H. Hillebrand, E. M. Lind, M. Pärtel, J. D. Bakker, Y. M. Buckley, M. J. Crawley, E. I. Damschen, K. F. Davies, P. A. Fay, J. Firn, D. S. Gruner, A. Hector, J. M. H. Knops, A. S. MacDougall, B. A. Melbourne, J. W. Morgan, J. L. Orrock, S. M. Prober, and M. D. Smith. 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature 529:390–393.

Güsewell, S. 2004. N:P ratios in terrestrial plants: Variation and functional significance. New Phytologist 164:243–266.

Harpole, W. S., L. L. Sullivan, E. M. Lind, J. Firn, P. B. Adler, E. T. Borer, J. Chase, P. A. Fay, Y. Hautier, H. Hillebrand, A. S. MacDougall, E. W. Seabloom, J. D. Bakker, M. W. Cadotte, E. J. Chaneton, C. Chu, N. Hagenah, K. Kirkman, K. J. La Pierre, J. L. Moore, J. W. Morgan, S. M. Prober, A. C. Risch, M. Schuetz, and C. J. Stevens. 2017. Out of the shadows: multiple nutrient limitations drive relationships among biomass, light and plant diversity. Functional Ecology 31:1839–1846.

Harpole, W. S., L. L. Sullivan, E. M. Lind, J. Firn, P. B. Adler, E. T. Borer, J. Chase, P. A. Fay, Y. Hautier, H. Hillebrand, A. S. MacDougall, E. W. Seabloom, R. Williams, J. D. Bakker, M. W. Cadotte, E. J. Chaneton, C. Chu, E. E. Cleland, C. D’Antonio, K. F. Davies, D. S. Gruner, N. Hagenah, K. Kirkman, J. M. H. Knops, K. J. La Pierre, R. L. McCulley, J. L. Moore, J. W. Morgan, S. M. Prober, A. C. Risch, M. Schuetz, C. J. Stevens, and P. D. Wragg. 2016. Addition of multiple limiting resources reduces grassland diversity. Nature 537:93–96.

Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. Nature 446:791–793.

Hautier, Y., P. a Niklaus, and A. Hector. 2009. Competition for light causes plant biodiversity loss after eutrophication. Science (New York, N.Y.) 324:636–638.

Hautier, Y., E. Vojtech, and A. Hector. 2018. The importance of competition for light depends on productivity and disturbance. Ecology and Evolution 8:10655–10661.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Hutchinson, G. 1957. Concluding remarks. Cold Spring Harbor Symposia on ….

Komatsu, K. J., M. L. Avolio, N. P. Lemoine, F. Isbell, E. Grman, G. R. Houseman, S. E. Koerner, D. S. Johnson, K. R. Wilcox, J. M. Alatalo, J. P. Anderson, R. Aerts, S. G. Baer, A. H. Baldwin, J. Bates, C. Beierkuhnlein, R. T. Belote, J. Blair, J. M. G. Bloor, P. J. Bohlen, E. W. Bork, E. H. Boughton, W. D. Bowman, A. J. Britton, J. F. Cahill, E. Chaneton, N. R. Chiariello, J. Cheng, S. L. Collins, J. H. C. Cornelissen, G. Du, A. Eskelinen, J. Firn, B. Foster, L. Gough, K. Gross, L. M. Hallet, X. Han, H. Harmens, M. J. Hovenden, A. Jagerbrand, A. Jentsch, C. Kern, K. Klanderud, A. K. Knapp, J. Kreyling, W. Li, Y. Luo, R. L. McCulley, J. R. McLaren, J. P. Megonigal, J. W. Morgan, V. Onipchenko, S. C. Pennings, J. S. Prevéy, J. N. Price, P. B. Reich, C. H. Robinson, F. L. Russell, O. E. Sala, E. W. Seabloom, M. D. Smith, N. A. Soudzilovskaia, L. Souza, K. Suding, K. B. Suttle, T. Svejcar, D. Tilmand, P. Tognetti, R. Turkington, S. White, Z. Xu, L. Yahdjian, Q. Yu, P. Zhang, and Y. Zhang. 2019. Global change effects on plant communities are magnified by time and the number of global change factors imposed. Proceedings of the National Academy of Sciences of the United States of America 116:17867–17873.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the United States of America 112:797–802.

Kramer-Walter, K. R., P. J. Bellingham, T. R. Millar, R. D. Smissen, S. J. Richardson, and D. C. Laughlin. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. Journal of Ecology 104:1299–1310.

Kuang, J. J., and P. Chesson. 2010. Interacting coexistence mechanisms in annual plant communities: Frequency-dependent predation and the storage effect. Theoretical Population Biology 77:56–70.

Mattson, D. A., and W. J. Herms. 1992. The Dilemma of Plants: To Grow or Defend. The Quarterly Review of Biology 67:283–335.

McKey, D. 1994. Legumes and nitrogen: The evolutionary ecology of a nitrogen-demanding lifestyle. Advances in Legume Systematics 5: The Nitrogen Factor 5:211–228.

Minden, V., and H. Olde Venterink. 2019. Plant traits and species interactions along gradients of N, P and K availabilities. Functional Ecology 33:1611–1626.

Pacala, S. W., and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. The American naturalist 152:729–737.

Passarge, J., S. Hol, M. Escher, and J. Huisman. 2006. Competition for nutrients and light: Stable coexistence, alternative stable states, or competitive exclusion? Ecological Monographs 76:57–72.

Rajaniemi, T. K. 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. Journal of Ecology 90:316–324.

Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America 102:4387–4392.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press.

Tilman, D. 1994. Competition and Biodiversity in Spatially Structured Habitats. Ecology 75:2–16.

Tilman, G. D. 1984. Plant Dominance Along an Experimental Nutrient Gradient. Ecology 65:1445–1453.

Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21:261–268.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornellssen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, Ü. Niinemets, J. Oleksyn, H. Osada, H. Poorter, P. Pool, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.