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

**Abstract:** To be added

**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 the factors that control 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.

The number and types of trade-offs present in plant systems have been the subject of considerable scientific exploration. Correlated patterns of variation in plant functional 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). In empirical settings, the 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.

As human actions have continued to alter many limiting factors in plant systems, the identification of key trade-offs has been used to understand the resulting shifts in community structure (Grime 2006). 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 evenness (Vitousek et al. 1997, Bobbink et al. 2010). 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, Clark et al. 2018). However, plants are also known to be limited by (and compete for) multiple belowground resources, even in high productivity contexts (Wilson and Tilman 1991, Fay et al. 2015, Harpole et al. 2016). 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* through the collapse of source of variation on which trade-offs operate (Harpole and Tilman 2007, Harpole et al. 2016).

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 across multiple nutrient treatments. Multidimensional trade-offs, however, predict that fertilization effects depend on resource identity, leading to directionally dissimilar shifts in composition that vary as a function of the specific soil nutrient added.

Experimental approaches to understanding nutrient-driven biodiversity loss often focus on identifying which mechanism best explain observed patterns. However, in natural systems, the trade-offs structuring species abundances are complex, composed of multiple interacting drivers (Leibold et al. 2004, Kraft et al. 2015). Because trade-offs governed by light competition and belowground resource use are likely to act simultaneously, comparing the directional similarity among community responses to different nutrient enrichment treatments – community *response dimensionality* – may better evaluate the relative contribution of different mechanisms.

Constraints on plant physiology, functional traits, and environmental characteristics indicate that the relative contributions of different trade-off mechanisms (and thus, 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 consistency in tissue stoichiometry imply general specialization to low and high resource conditions (Wright et al. 2004, Ågren 2008, 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 (Güsewell 2004, Kramer-Walter et al. 2016).

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).

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 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.

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, productive environments.

**Methods**

*Study Sites*

For this study, we examined 49 study sites that are part of the Nutrient Network, a cooperative, globally distributed experiment (Borer et al. 2014) . Nutrient Network study sites are constructed in a randomized block design, typically composed of 3 blocks divided into 5m x 5m plots. In each block, we selected four plots to be used in experimental analysis: control plots with no supplemental nutrient enrichment and plots subject to fertilization of either nitrogen (N), phosphorous (P), or potassium with other micronutrients (Kµ), yielding 12 – 20 plots per site.

All nutrient enrichment treatments were applied at a rate of 10 g N/P/K m-2 year-1 as time-release urea, triple-super-phosphate, and potassium sulfate, respectively. A micronutrient mix (17% Fe, 12% S , 6% Ca, 3% Mg, 2.5% Mn, 1% Zn, 1% Cu, 0.1% B, and 0.05% Mo) supplied as part of the Kµ treatment occurred only during the first treatment year at a rate of 100g m-2 to avoid accumulation toxicity.

Because sites were initialized at different years and observed for different durations, we filtered our dataset to focus on sites with at least 5 years of treatment, a sufficient number of treatment years to have confidence in observed community responses. All sites used in this analysis also included 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. Cover for each species was estimated independently, yielding total cover values that often exceeded 100% in vertically stratified communities. We focused our analysis on species with well-characterized responses to nutrient enrichment by excluding taxa that were not observed in each treatment, or not present in at least 33% of all community observations within a site.

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:



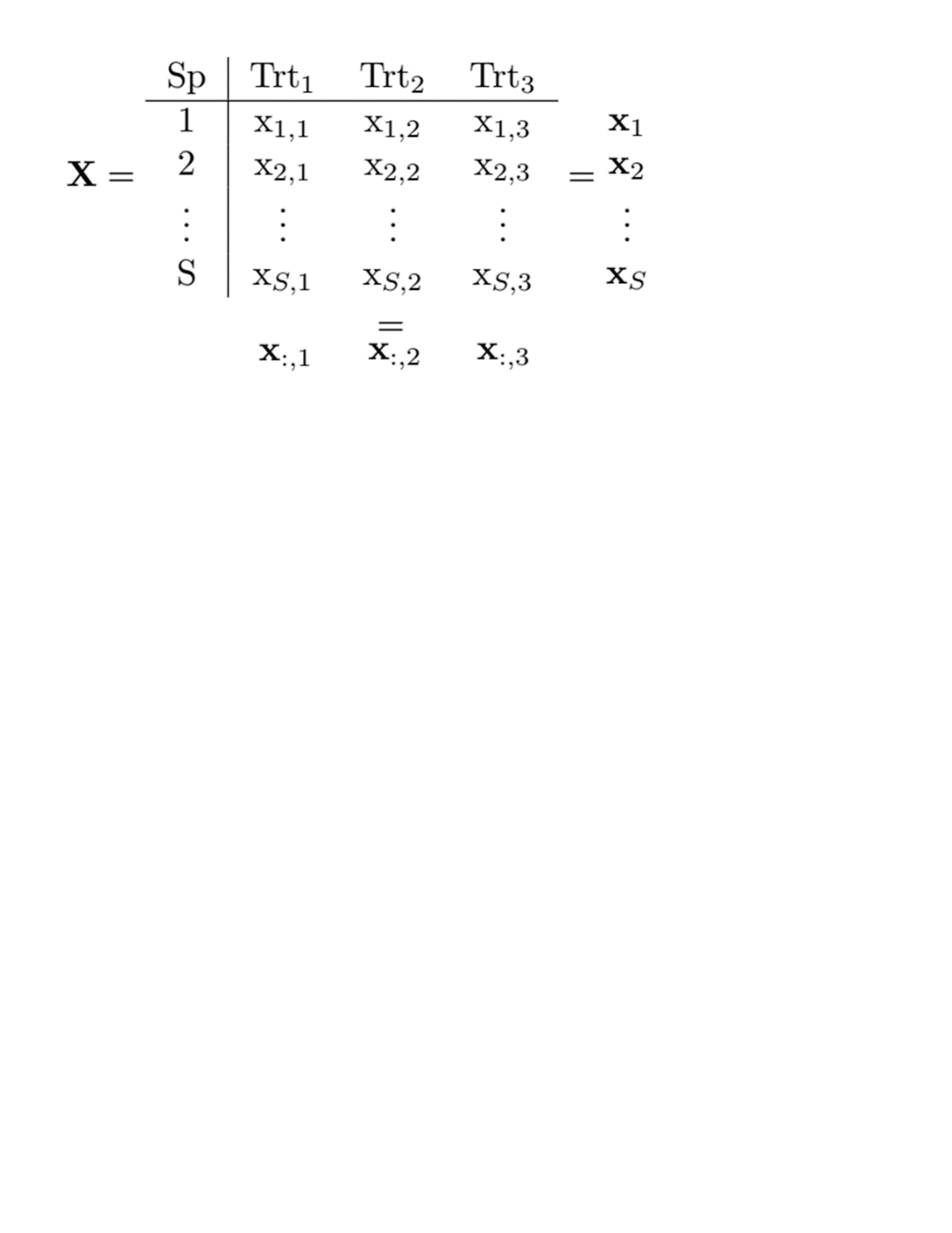
where community abundance is estimated as a function of the quantity of fertilizer added in observation (expressed as the number of years of treatment), interannual variation in site-level species abundance (encoded as a factor variable), and plot-level variation in species abundance (encoded as a factor 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*

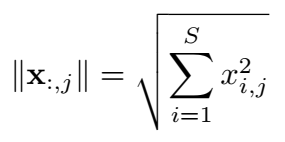
While multivariate linear modelling approaches may be used to estimate the rate of community change in response to treatment, their output does not provide a quantification of similarity among directions of change. To evaluate correlations among different trajectories of community response – proportional consistency across 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). For simplicity in notation, we define each row vector consisting of the *i*thspecies responses to different treatments as **xi**; column vectors describing the response of all species within the *j*th community to a given treatment as **x:,j**.



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 *i* iterates over the *S* species present within each community.

To control for differences in 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 length, 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.

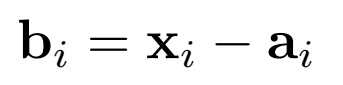
However, bivariate relationships do not provide an aggregate measure of similarity among variables in 3 or more dimensions. Instead, correlation among responses can be evaluated through projection onto a new coordinate basis. Conceptually, our approach is similar to dimensionality reduction through Principal 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, resulting in trajectories of community change that are directionally equivalent. 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 an estimate of species responses under 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).

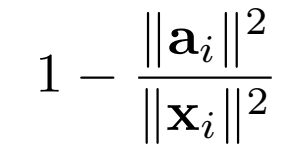
To evaluate the degree to which this null hypothesis captures the responses of species *i*, we define a vector, ***a***, as the projection of observed responses onto the 1:1:1 vector, ***y***:



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

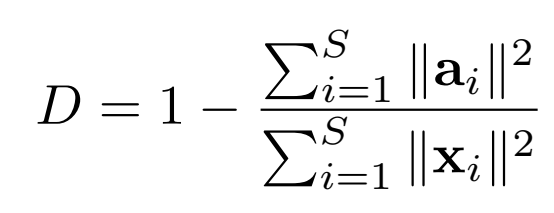


The fraction of variance in species response that is captured by this projection is thus defined as the ratio of squared norms (sums of squares) of ***a*** and ***x***:



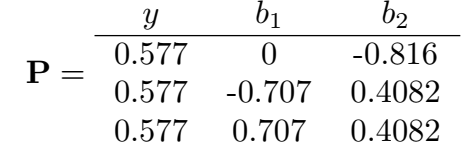
Under our null hypothesis, the set of responses observed for species *i,* ***x­I***, will be of equal magnitude to the projection, ***ai****,****.*** The proportional magnitude of these vectors thus serves as a measure of response dimensionality for a given species, *i*.

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 rejection 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*

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 (30) exhibited significant effects of N enrichment, significant impacts of P (20) and K (17 sites) addition were also common. Accordingly, 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 (F2,96 = 4.8, P < 0.05; Appendix 2).

*Correlation Among Community Trajectories*

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 nearly equal to 1 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: positive intercept terms and slope coefficients greater than 1 produced when comparing responses to N and P treatments, for example, demonstrate the legumes exhibit more positive responses to P enrichment than N, which skew more strongly to P as total response magnitude increases (Figure 3, Table 1).

Repeated SMA regression with respect to plant dominance or longevity showed no consistent deviations from general positive correlation in response coefficients (Appendix 3).

*Global Scale Response Dimensionality*

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.

In line 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*

To evaluate the environmental and community determinants of response dimensionality, we subdivided data to calculate community response dimensionality, *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**

In terrestrial plant communities, trade-offs among multiple niche axes are theorized to govern the coexistence of diverse, interacting species. Despite the complexity of these ecological processes, prior evaluations of fertilization-driven change in community composition have focused primarily on the magnitude of treatment effect, rather than direction of change. In this study, we expand upon magnitude-focused approaches to compare the trajectories of community response to multiple nutrient addition treatments. Using data from a globally replicated experiment in grassland systems, we find support for the simultaneous contribution of two mechanisms – a shift from belowground to aboveground resource limitation and multi-dimensional belowground tradeoffs – that vary in their relative importance across sites.

*Magnitude of fertilization effect*

Consistent with other studies of nutrient limitation in grassland systems, including those using data from the Nutrient Network experiment, we found that nitrogen enrichment produced greater average effects on composition than either phosphorous or potassium and micronutrient fertilization (Crawley et al. 2005, Fay et al. 2015, Harpole et al. 2016, Soons et al. 2017). Given constraints on nitrogen fixation in many terrestrial systems (Vitousek and Howarth 1991), these results are unsurprising and suggest that nitrogen availability may often act as a dominant niche axis of belowground resource availability. However, these findings may also be skewed by the disproportionate representation of Nutrient Network sites in temperate North America and Europe (Appendix 1). In arid environments and those composed of more weathered soils, plant demands for phosphorous and other micronutrients may exceed those of nitrogen (Handreck 1997, Vitousek et al. 2010); experimental sites in Australia, for example, often exhibited the strongest community responses to phosphorous enrichment, on average .

*Global patterns*

After controlling for differences in the total magnitude of compositional change, characterization of all species responses to multiple fertilization treatments found support for a strongly one-dimensional pattern of variation (Figure 4a). The dominance of a single axis of variation implies the presence of a general trade-off between plant performance in low or high nutrient conditions, likely driven by asymmetric competition for light. This result supports other findings that identify light limitation as a primary mechanism of fertilization-driven compositional change.

Support for this finding is further enhanced by studies that identify core patterns of variation in plant form and function that reflect a one-dimensional tradeoff. Global plant functional trait distributions identify a small number of axes that capture a substantial proportion of overall trait variance (Wright et al. 2004, Díaz et al. 2016). Differentiation among species along the leaf economic spectrum and ratios of aboveground:belowground tissue investment suggest that plants have evolved suites of characteristics that facilitate the general acquisition of belowground resources or compete for light (Grime et al. 1997, Reich et al. 1997, Westoby et al. 2002). Broadly speaking, the development of multi-dimensional trade-offs for belowground resources may be constrained by physiology and tissue stoichiometry. Adaptations such as high specific root length that increase soil nitrogen uptake rates, for example, often increase absorptive capacity for many belowground resources (Chapin 1980).

*Plant Functional Variation*

However, consistent deviations from our neutral model across species and sites indicate that plant responses to fertilization are not uniformly predicted by a single trade-off axis. Instead, we find evidence that plant functional strategies and the context of interspecific interaction constrain the development of multidimensional trade-offs.

While light competition intensity is known to increase as a function of soil fertility, plant interactions along resource gradients indicate that belowground competition continues to operate at higher levels of productivity (Wilson and Tilman 1991). Belowground nutrient availability and distributions are complex; variable chemical forms and diffusion rates may allow for nutrient-specific tradeoffs to emerge through changes in root morphology and microbial symbioses. In this study, we found that species in the *Legume* functional group responded more strongly to enrichment of phosphorous or potassium and micronutrients (Figure 3b, Table 3), consistent with other findings. This is likely due to the enzymatic costs of nitrogen fixation, which result in steeper requirements for phosphorous, potassium, sulfate, and other micronutrients relative to other plant functional types (McKey 1994). However, it is important to note that responses to all nutrients were generally positively correlated across nitrogen-fixing species – nutrient-specific resource demands appear to act as additional dimensions of variation, but still operate on a broadly one-dimensional distribution of responses across treatments.

While functional group classifications capture important differences in life history strategy, they are relatively coarse distinctions that average over other traits known to control plant response to nutrient enrichment. More concerted efforts to relate trade-offs in belowground resource use to features such as tissue stoichiometry, clonality, and root physiology are likely to prove insightful. Root traits, in particular, 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).

*Site-specific constraints*

Just as initial site productivity, soil fertility, and species pools control the susceptibility of plant communities to nutrient enrichment (Clark et al. 2007), we found that a similar suite of characteristics constrained trajectories of community response to multiple fertilizers. Relationships between response dimensionality, climatic resource availability, light availability, and species turnover suggest that responses to fertilization are directionally more varied in more productive, lower-stress environments. Given that many of these drivers have been found to act on fertilization sensitivity in a similar fashion, it appears that trade-offs in belowground resource use are more likely to emerge in systems where soil nutrient availability forms an important axis of niche differentiation.

Lower dimensionality of community response in stressful environments may be the result of functional constraints that limit the development of belowground tradeoffs. While variation across many dimensions of plant performance may produce a range of functional strategies, the increased cost of adopting extreme trait values is likely to limit the number of trade-offs that operate in stressful environments (Westoby and Wright 2006, Dwyer and Laughlin 2017). In these systems, increased covariance among multiple traits reduces plant functional variation across a smaller number of dimensions.

In grasslands, disturbance and climatic stress frequently act as strong habitat filters. Variation in these environmental characteristics, along with other density-dependent mechanisms, are known to act as important mechanisms of species coexistence (Chesson 2000, 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). In response to nutrient enrichment, differentiation along an axis of general resource availability may limit the strength of belowground tradeoffs that characterize nutrient-specific community trajectories.

*Global change*

Terrestrial plant ecosystems are often subject to multiple, interacting global change factors including warming average temperatures, altered climatic regimes, and nutrient enrichment (Franklin et al. 2016). While prior syntheses of global change effects have often focused on the overall magnitude response, we emphasize that the direction of this change forms an important complement to these approaches that may better capture potential mechanisms driving community dynamics. The identification of potential trade-off axes is particularly important in predicting plant community responses to simultaneous sets of stressors, which often have additive or super-additive effects when applied in tandem (Zavaleta et al. 2003, Harpole et al. 2016, Komatsu et al. 2019). Comparison of response trajectories among single and composite sets of stressors is likely required to identify important axes of plant functional variation – e.g. the relative contribution of light competition and multidimensional belowground tradeoffs to overall community response. Together, these two perspectives are needed to better predict the consequences of future changes in ecosystem function.

*Limitations*

Our study presents a general characterization of the community response trajectories to multiple nutrient enrichment. While able to assess key axes of variation, these patterns do not provide a direct mechanistic link to trade-offs governed by light limitation or belowground resource use. The effects of nutrient enrichment on plant community are often mediated by a series of direct and indirect pathways; the core trade-offs we focus on in this study represent the most likely mechanisms of plant response to community change, but may also be mediated by effects on herbivore abundance, soil acidification, and many others. However, our results may also be viewed as somewhat conservative, given that one treatment (potassium and micronutrients) manipulated many soil resource dimensions at once. Future work would benefit from consideration of a greater number of treatment types, such as water availability, in varied contexts to better evaluate the trade-off mechanisms governing plant community structure.

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