**Introduction**

In terrestrial systems, coexistence among plant species is governed by competition for a shared set of limiting resources. For stable coexistence to occur, niche theory states that trade-offs must exist between factors that affect plant growth to prevent competitive exclusion. 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 has been the subject of considerable exploration. Plants are known to exhibit competition-colonization trade-offs (Tilman 1994, Pacala and Rees 1998), trade-offs between herbivore defense and growth (Mattson and Herms 1992), or contrasts between leaf longevity and photosynthetic rate described the leaf economic spectrum (Wright et al. 2004). Depending on factors such as disturbance regime, herbivore abundance, or environmental stress, variation across these different niche axes present conditions where one competitor will be favored over others.

In response to global biodiversity loss, trade-offs have been used to understand changes in plant composition in diversity following human-derived increases in nutrient availability. In most cases, biodiversity loss driven by nutrient enrichment is attributed to a shift in competition for belowground resources to competition for light (Tilman 1984, Dybzinski and Tilman 2007, Hautier et al. 2009). This one-dimensional trade-off that physiological adaptations designed to increase nutrient uptake belowground come at the expense of investment into photosynthetic tissues that intercept available photosynthetic radiation. Increases in fertility through nutrient enrichment thus selects for species of larger stature with proportionally greater investment to aboveground vs. belowground components.

This one-dimensional trade-off suggests that effects on community depend on changes in total resource availability, irrespective of which belowground resource is enriched. However, many systems are known to be limited by more than one belowground resource, that implies the presence of multivariate tradeoffs that depend on nutrient identity (Fay et al. 2015, Harpole et al. 2016). In this perspective, plant species exhibit nutrient-specific niches that impart specialization on different belowground resources. Under these multi-dimensional trade-offs, biodiversity loss is interpreted through a loss of *niche dimensionality*, where nutrient addition removes limitation of that resource, “collapsing” a source of variation on which trade-offs operate (Harpole and Tilman 2007, Harpole et al. 2016).

Central to the distinction between these two perspectives are an emphasis on resource supply vs. resource stoichiometry as core determinants of species abundances in plant communities (DeMalach and Kadmon 2017, Harpole et al. 2017). When communities are subject to enrichment of different belowground resources, a one-dimensional focus on light competition suggests that changes in species abundances will be directionally consistent, varying only in magnitude based on shifts in total resource supply generated by fertilization. In contrast, multi-dimensional trade-offs in belowground resource use imply uncorrelated trajectories of community change across different types of nutrient enrichment; shifts in resource stoichiometry act on niche differentiation between interacting species, that vary in their ability to utilize specific belowground resources.

In natural communities subject to enrichment by multiple resources, trade-offs governed by investment to belowground vs. aboveground tissues and multi-dimensional tradeoffs for soil resources are likely to operate simultaneously. However, the strength of each mechanism is likely to be constrained by plant physiology, environmental characteristics, and community properties of locally interacting species (Passarge et al. 2006, Hautier et al. 2018).

Broadly speaking, stoichiometric analyses of plant tissue chemistry suggest that demand for belowground resources may scale proportionally with plant growth rate (Knecht and Göransson 2004, Ågren 2008). This evidence supporting a generally one-dimensional niche axis between low and high fertility environments is further compounded by physiological constraints on root architecture (Chapin 1980). Physiological adaptations designed to increase the uptake of one mineral nutrient are likely to operate similarly for others; large, deep root systems composed of fine roots generally exhibit greater absorptive capacity than less expansive ones.

These broad patterns are subject to further sub-specialization, however. Plants are known to exhibit variation in tissue stoichiometry, resource use plasticity, and present adaptations that increase the uptake and use of specific resource types (Güsewell 2004, Ågren 2008). Specialized root structures may increase rates of phosphorous extraction from recalcitrant soil types, while in many species, microbial symbionts are known to reduce plant dependence on available soil nitrogen and other micronutrients (Suding et al. 2005, Lambers et al. 2008).

In turn, the development of these nutrient-specific tradeoffs will depend other mechanisms of species coexistence in a given context. The availability of different belowground resources presents one subset of the total niche space on which species are distributed; coexistence in many environments is also predicated on trade-offs in water use and storage, herbivore defense, or tolerance of disturbance. Adaptations that produce niche differentiation on these axes may constrain development of others; greater plant investment into root tissues to provide drought tolerance, for example, may necessarily decrease competitive ability under high resource conditions.

Finally, resource competition theory emphasizes that successful species can reduce resources to lower concentrations than their competitors – as such, variation in trajectories of community change following multiple resource enrichment will depend on characteristics of interacting species prior to fertilization. Greater taxonomic or functional diversity, for example, may be correlated with greater niche differentiation across belowground resources, leading to effects that differ in direction.

To understand the importance of belowground resource supply and stoichiometry to plant coexistence, we use data from the Nutrient Network, a globally distributed experiment manipulating the available of individual soil resources. Rather than comparing the relative fit of models assuming one-dimensional or multi-dimensional trade-offs in belowground resource acquisition, we synthesize these perspectives to capture how these mechanisms interact to control community composition.

To capture variation in community change following fertilization of different belowground resources, we constructed a null model based on a “neutral” assumption (*sensu* Hubbell 2001) that species respond only to changes in nutrient supply, rather than stoichiometry. Under a neutral expectation, communities will exhibit consistent trajectories across treatments, forming a one-dimensional axis of change. The degree of deviation from this null model thus forms a measure of *response dimensionality* – variation among trajectories of change following different treatments – that may be used to infer the trade-offs governing species coexistence.

Across sites, a one-dimensional trade-off governed by light competition will act as a strong determinant of species responses to nutrient enrichment, yielding a high relative fit of our null model. However, we hypothesize that this null model will better capture community responses under in spatially or temporally heterogeneous systems, and those of lower productivity, where specialization on individual resource types 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*

The 50 study sites 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 supplied during the first treatment year.

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. 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.

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 massed. 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 for *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:



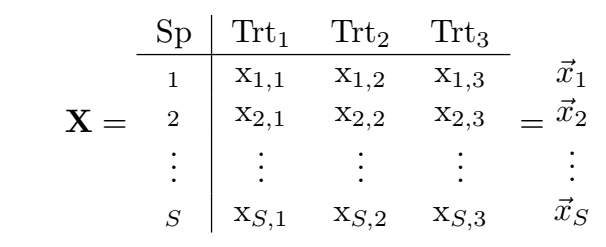
Where community abundance is estimated as a function of the quantity of fertilizer added in observation (expressed as the number of years of treatment), interannual variation in site-level species abundance (encoded as a factor variable), and plot-level variation in species abundance (encoded as a factor 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 were evaluated using residual permutation procedures using permutation-based ANOVA. All model fitting conducted using RRPP (Collyer and Adams 2018).

*Response Dimensionality*

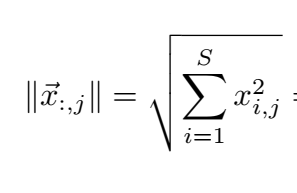
To evaluate the similarities between multiple trajectories of community change, we derive a geometric approach based on work of Cardinale et al. (2018). Under a “neutral” expectation where the effects of nutrient enrichment depend solely on changes in total resource supply, rather than stoichiometric ratios, trajectories of community change will be directionally consistent – species exhibit proportionally equal responses to multiple nutrient enrichment treatments, once accounting for the overall magnitude of community response.

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, may extend to any *n*-dimensional set of treatments. First, we define **X** as a vector describing a species response to three distinct treatments, recorded for all *S* species:

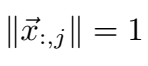


In this study, **X** was composed of the three vectors of estimated nutrient response coefficients computed in multiple regression model, **B.**

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



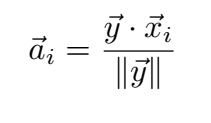
Where *S* is the number of observed species within a site.

To standardize magnitudes of change across treatments, column vectors were standardized through dividing by L2 norm, such that 

For each possible pair of treatments, bivariate relationships between sets of treatment responses may be used to illustrate correlations among trajectories of change (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. To assess the *dimensionality* of community response, 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).

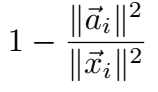
To evaluate the degree to which this null hypothesis captures species responses, we defined a vector, ***a***, as the projection of observed responses onto the 1:1:1 vector, ***y***:



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

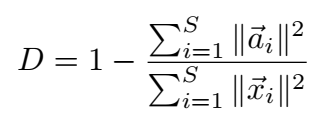


The fraction of variance in species response that is captured by this projection is thus defined as the ratio of squared norms (sums of squares) of ***a*** and ***x***:



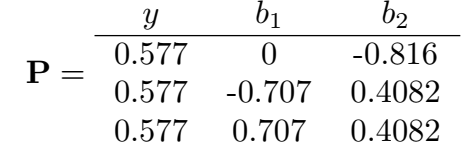
Under our null hypothesis, the set of responses observed for species *i,* ***x­I***, will be of equal magnitude to the projection, ***ai****,****.*** The proportional magnitude of these vectors thus serves as a measure of response dimensionality for a given species.

Extending this method to all 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 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 vectors are standardized to unit length.

Conceptually, this geometric approach is similar to dimensionality reduction through principal components analysis (PCA). Rather than defining the first principle component through eigenvalue decomposition, axes are pre-specified under a null hypothesis.

*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 hypothesizes 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 describing soil and climatic conditions were also combined in pathways with estimates to the site species pool 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. 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 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*

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 X).

*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.

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*

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**

**CORE POINT**

Both mechanisms have a role to play; their strength will depend on how the niche space is occupied.

* **Mechanisms of coexistence**
  + Evidence for simultaneous mechanisms of change
  + Trade-offs will be bounded by the dimensionality of limiting resources; high dimensional niche spaces may also give rise to high dimensional trade-offs.
* The development of these trade-offs will be constrained by relevant sources of niche variation
* Comment on the number of sites exhibiting multiple resource limitation
* Both resource supply and resource stoichiometry act simultaneously to govern species abundances;
* Reflect on patterns;
  + 1:1:1 relationship forms a dominant pattern, as was expected by our null model
  + Trade-offs related to plant functional strategy
    - FAB-ACES paper? Read to get ideas
* The importance of these two mechanisms to overall community functioning will depend on
* Site heterogeneity
  + While site characteristics are known to predict sensitivity to nutrient enrichment, these may also direct community response
  + Site-level patterns of evolutionary characteristics are important;
    - Low dimensional responses at desert grassland sites, for example.
  + **Mechanisms of coexistence critical to understanding response to global change factors**
* Plasticity in species response
* First global analysis of dimensionality of community response

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