

Summer 7-28-2017

Nutrient additions alter semi-arid grassland response to fire

Alec A. Carrigy
University of New Mexico

Follow this and additional works at: https://digitalrepository.unm.edu/biol_etds



Part of the [Biology Commons](#)

Recommended Citation

Carrigy, Alec A.. "Nutrient additions alter semi-arid grassland response to fire." (2017). https://digitalrepository.unm.edu/biol_etds/270

This Thesis is brought to you for free and open access by the Electronic Theses and Dissertations at UNM Digital Repository. It has been accepted for inclusion in Biology ETDs by an authorized administrator of UNM Digital Repository. For more information, please contact disc@unm.edu.

Alec Carrigy

Candidate

Department of Biology

Department

This thesis is approved; and it is acceptable in quality and form for publication:

Approved by the Thesis Committee:

Scott Collins, Chairperson

Jennifer Rudgers

William Pockman

**NUTRIENT ADDITIONS ALTER SEMI-ARID GRASSLAND RESPONSE TO
FIRE**

BY

ALEC CARRIGY

BSc. Ecology, University of Alberta, 2016

THESIS

Submitted in Partial Fulfillment of the Requirements for the Degree of

**Master of Science
Biology**

The University of New Mexico
Albuquerque, New Mexico

December, 2017

ACKNOWLEDGEMENTS

I thank Dr. Scott Collins, my advisor and committee chair, for encouraging me to pursue my goals. His support and encouragement throughout my graduate career has been invaluable, and his guidance and style I hope to emulate throughout my career.

I thank my committee members, Dr. Jennifer Rudgers and Dr. William Pockman for their guidance and recommendations. Dr. Rudgers provided wonderful assistance in writing, analysis, and professional development.

Data for this project are from Dataset 231, which can be found at <http://sev.lternet.edu>. We would like to thank the members of the Collins and Rudgers/Whitney labs for helpful comments throughout, as well as the Sevilleta LTER Field Crew for data collection. This work was supported by grants from NSF to the University of New Mexico for Long-term Ecological Research.

I would also like to acknowledge my family, Colin, Jan, and Nick for their many years of support.

And finally, to Monica, who stayed up many late nights and took time to discuss results, edit my early drafts, and listen to my practice presentations. Your patience is unparalleled.

NUTRIENT ADDITIONS ALTER SEMI-ARID GRASSLAND RESPONSE TO FIRE

By

Alec Carrigy

BSc. Ecology, University of Alberta, 2016

M.S. Biology, University of New Mexico, 2017

ABSTRACT

Knowledge of how multiple global change drivers interact to affect community structure is critical for predicting future community states, especially when community structure drives ecosystem function. Disturbances such as fire and nutrient additions often shift communities away from their mean composition, but less is known about how disturbances affect spatial variation among local patches of the community over time (spatiotemporal dispersion). Dispersion may increase (local communities diverge in composition), stay the same, or decrease (communities converge) in response to disturbance. We compared patterns of spatiotemporal dispersion and temporal trajectories in community composition across three sites in a northern Chihuahuan Desert grassland with different disturbance histories: unburned, burned, or burned plus fertilized. To fertilize, nitrogen, phosphorus, and potassium were added in a fully factorial design following the protocol of Nutrient Network. Community change in all sites tracked inter-annual variation in yearly climate, but there was no directional, temporal trajectory in community composition following a natural fire in 2009. In contrast to patterns in mesic

grasslands, fertilization had no effect on plant productivity or species richness. However, burned-fertilized sites had the highest community dispersion, while dispersion was lowest at the unburned-unfertilized site. Nitrogen additions alone and nitrogen plus phosphorus both increased community dispersion, thereby magnifying spatiotemporal heterogeneity in community composition across the landscape, relative to unfertilized conditions. Our results highlight the importance of examining spatiotemporal variation in community responses to multiple global change drivers, in addition to understanding shifts in mean community composition.

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	viii
INTRODUCTION	1
METHODS	3
Study area.....	3
Nutrient experiment	4
Environmental and community variables	4
Analysis.....	5
Fire and nutrient effects on plant community dynamics.....	5
Dispersion among sites	6
Dispersion among nutrient treatments	7
Nutrient effects on univariate community metrics.....	7
RESULTS	7
Community dynamics under fire and nutrient additions.....	7
Dispersion among sites	8
Dispersion among nutrient treatments	9
DISCUSSION	10
Climate drives community dynamics across sites	10
Dispersion among sites	11
Conclusion	13
REFERENCES	14

LIST OF TABLES

Table 1. Description of study sites. A (+) symbol indicates the presence of the disturbance, (-) indicates its absence. Years in brackets indicate the year the site burned.	18
Table 2. Average abundance of each plant species and its cumulative contribution to community differences between sites, based on SIMPER analysis. Differences are across all years in spring and fall separately.....	19
Table 3. Average abundance of species contributing most to differences in community structure between 2011 vs. all other years, by season, based on similarity percentage (SIMPER) analysis.....	21
Table 4. Pairwise comparisons of multivariate dispersions using PERMDISP across sites in either the spring or fall.....	22
Table 5. Nutrient treatment effects on richness, evenness, and biomass in the burned + fertilized site (NutNet). Significant results are bolded, and marginally significant results are italicized.	23
Table 6. Homogeneity of multivariate dispersions test (PERMDISP) results for the effect of nutrient treatments on community dispersion at the Nutrient Network site. Significant p-values are bolded, and marginally significant p-values ($p < 0.10$) are italicized.	24

LIST OF FIGURES

- Figure 1. Non-metric multidimensional scaling (NMDS) of plant community composition for plots with different disturbance histories (unburned, burned, and burned + fertilized) in the spring (left) and fall (right). Each point corresponds to a site. The burned + fertilized site has a different composition than the other sites. Data from 2008 on were used to create this graph. Error bars are ± 1 SE. 25
- Figure 2. Non-metric multidimensional scaling (NMDS) of plant community composition in unburned and burned plots in the spring (left) and fall (right). Note that unburned sites include all of the years of mixed-grass unburned, plus the first year of nutrient network data. The burned sites include all of the mixed-grass burned, and after the first year of nutrient network data. Arrows show the trajectory of the community over time, from the 1st year post-burn (shown by 1 in the plot) to the 11th year post-burn. There is no definitive pattern of community trajectory following fire. 2011 is shown in green circles, a dry year with an unusual deep winter freeze. Error bars are ± 1 SE. 26
- Figure 3. Non-metric multidimensional scaling (NMDS) ordination of plant community composition for each site (mean of all quadrats) in the spring (left) and fall (right) across all sites separately (a) and mixed-grass sites combined (b). Years are separated by color. Hand-drawn ellipses surround sites for clarity, and are labelled by site. NutNet plots were significantly more dispersed than combined MG sites (MG + MGB) for both the spring and fall (p-values show differences in dispersion based on PERMDISP analysis). Error bars are ± 1 SE. 27
- Figure 4. Rank-abundance curves (RACs) for each site. The burned + fertilized site has a greater abundance of less dominant species. 28
- Figure 5. NMDS ordination showing differences in community composition across plots with and without N and P in both the spring (left) and fall (right). Communities with N and P added are more dispersed than plots with P alone in both spring and fall. Error bars are ± 1 SE. 29
- Figure 6. Rank-abundance curves for the NutNet site in plots with nitrogen and phosphorus (N x P), nitrogen only (N), phosphorus only (P), and neither nitrogen or phosphorus (Control) in spring (left) and fall (right). There is a similar number of species on both curves, but a greater abundance of rare species with N added. 30

INTRODUCTION

Predicting how communities will respond to multiple global change drivers is an important goal in ecology that has become even more pressing in the face of increasing environmental change (Sala et al. 2000, Smith et al. 2009). While most studies focus on the mean response of communities to changing environmental conditions, much less is known about the variability (dispersion) in community responses around the mean (Anderson 2006). This focus is important because variability has important implications for both biodiversity and community stability (Avolio et al. 2015, Wang and Loreau 2014, 2016).

Community responses to disturbance are often expressed as changes in total community abundance and species composition relative to an undisturbed state, and can be detected with a variety of multivariate techniques (McCune and Grace 2002). While community similarity is often used to examine the mean response (differences between group centroids in multivariate space), it can also be used to quantify dispersion of replicate communities around the mean (Anderson 2006). In theory, disturbances may cause a change in the mean with no change in dispersion; alternatively, the mean community composition could remain stable, but dispersion may increase (replicate communities diverge in composition) or decrease (replicate communities converge) (Avolio et al. 2015). By analyzing dispersion among local communities, we can quantify the strength of different environmental drivers through increases (divergence) or decreases (convergence) in dispersion.

Nutrient enrichment and fire are two disturbances that can alter community composition, and have the potential to affect community dispersion. For example, studies of mesic grasslands have shown nutrient additions may cause convergence (Inouye and Tilman 1995) or divergence (Houseman et al. 2008) of communities. However, these studies either added nitrogen alone or multiple nutrients together, which precludes the ability to detect interactive effects among different nutrients (Fay et al. 2015). Furthermore, single and interacting disturbances may also affect community dispersion. For example, fire may homogenize species composition and decrease dispersion by creating landscapes dominated by fire-tolerant species (Collins 1992, Pausas and Verdú 2008). Alternatively, fire could increase community dispersion by creating a mosaic of patch types, only some of which favor disturbance-tolerant species (Perry et al. 2011, Burkle et al. 2015). Together, multiple disturbances can create outcomes for dispersion that are not predictable from knowledge of the responses of communities to single disturbances alone (Houseman et al. 2008). Considerable uncertainty remains regarding which pattern (convergence, divergence) can be expected in different ecosystems, especially in semi-arid grasslands, where few studies of this type have been conducted. This information may be critical for understanding the responses of arid ecosystems to multiple global change drivers, as these systems cover ~45% of terrestrial land (Huang et al. 2016), and may be especially sensitive to changes in future climate (Diffenbaugh et al. 2008).

In this study, we compared patterns of spatiotemporal dispersion and temporal trajectories in community composition over 11 years of change in three sites in a northern Chihuahuan Desert grassland experiencing different disturbance histories: unburned,

burned, or burned plus fertilized. Specifically, we addressed the following questions: 1) How do long-term nutrient additions and fire affect plant community dynamics? 2) What are the individual and combined effects of nutrient additions and fire on plant community dispersion? 3) How do different nutrients individually and interactively affect plant community dispersion? Based on prior research, we predicted that 1) both burned sites will follow a circular trajectory post-fire and eventually return close to their initial composition (Steiner and Leibold 2004), but the interaction with nutrients will lead to the development of alternative stable states in burned + fertilized plots (Houseman et al. 2008) corresponding with different nutrient treatments, 2) nutrient additions will increase dispersion, whereas fire will reduce dispersion initially, and then increase dispersion as dominant grasses recover (Gosz and Gosz 1996), and 3) nutrient treatments will differ in their effects on dispersion, but nitrogen and phosphorus together will have the largest effect, because these nutrients often co-limit productivity in grasslands (Fay et al. 2015).

METHODS

Study area

Our study was conducted at three sites (~300 m apart) at the Sevilleta National Wildlife Refuge (SEV; 34°20'00" N, 106°43'00" W) in Socorro County, central New Mexico, USA (Table 1 for site summary). The vegetation is northern Chihuahuan Desert grassland and is considered a mixed grass site because it is co-dominated by the perennial grasses *Bouteloua eriopoda* (black grama) and *B. gracilis* (blue grama), along with scattered forbs and small shrubs (Mulhouse et al. 2017). The SEV has hot summers and cool

winters, with an average annual temperature of 13.9 C. The mean temperature in December is 2.4 C and is 25.3 C in July. About 250 mm of precipitation falls annually, 60% of which occurs within July-September during the summer monsoon (Notaro et al. 2010, Petrie et al. 2014).

In 2007, a nutrient addition experiment was established following protocols of the Nutrient Network (NutNet; see Borer et al. 2014) (abbreviated NutNet). In 2009 the site was entirely burned in a wildfire, providing the opportunity to test whether nutrient enrichment modifies plant community responses to fire. In addition, to investigate the trajectory of the plant community following fire, we compared plant community responses to those in two nearby sites that were established in 2004: one burned in a 2003 management fire, but has since been undisturbed and has never received fertilizer (mixed-grass burned; MGB), and the other has not been burned in recent history, with fire records dating back to 1989 (mixed-grass; MG).

Nutrient experiment

The nutrient experiment is a fully crossed, completely randomized design with eight treatment combinations, replicated five times each. Nutrients were added in a fully factorial design of nitrogen (N), phosphorus (P), or potassium plus other micronutrients (K), each added at a rate of 10 g m⁻² yr⁻¹. Nutrients were added annually in late June before the start of the summer monsoon. Treatments were randomly assigned to the forty 5 m x 5 m plots, with a 1 m buffer separating each plot.

Environmental and community variables

At all three sites, plant community composition, percentage cover of each species, and aboveground net primary production (NPP) were measured each year in permanently marked 1-m² subplots at each site. At NutNet, there was one 1-m² plot per replicate. At MG and MGB there were 40 1-m² permanent NPP plots. To calculate NPP, vascular plant living biomass was estimated for each species using a non-destructive volumetric method (Huenneke et al. 2001, Muldavin et al. 2008). Volume measurements of all individual plants were recorded in spring (April/May) and fall (September/October) each year in the permanently located 1-m² subplots. Biomass was calculated allometrically via linear regression models with intercepts forced through the origin; these were developed for each species from plants collected outside of the permanent sampling plots in each season and year (Muldavin et al. 2008). Ancillary measurements include daily precipitation and temperature. We used data from 2004-2014 in both of the mixed-grass sites, and from 2008-2014 at the NutNet site. Plant and environmental data are publicly available on the Sevilleta Long Term Ecological Research website, at <http://sev.lternet.edu>.

Analysis

Fire and nutrient effects on plant community dynamics

To determine how fire and nutrient additions affected plant community dynamics, we performed three separate analyses. To test whether nutrient additions amplified plant community response to fire, we ran a permutational analysis of variance (perMANOVA) with fire and nutrients as categorical variables (present/absent, equivalent to testing site), and quadrat as a random factor. To test whether there was a temporal effect of fire (e.g.

lag effects), we ran a second perMANOVA and included fire as a continuous variable (years since fire) and quadrat as a random factor. To assess whether variation among years was a strong driver of community shifts irrespective of fire, we ran a third perMANOVA, including year as a fixed factor and site (unburned, burned only, burned + fertilized) and quadrat as random factors, with quadrat nested within site. We analyzed spring and fall data separately due to large differences between seasons in precipitation, temperature, primary production, and species composition. For perMANOVA analyses, we used 9999 permutations of raw data, generating pseudo- F values. All multivariate analyses were performed using the *perMANOVA+* package for PRIMER (Primer-E Ltd V.6; United Kingdom). To visually assess the trajectory of community composition following fire, we used non-metric multidimensional scaling analysis (NMDS) with a Bray-Curtis distance metric and 9999 random restarts. To determine the relative contribution of plant species to differences in community composition between burn and unburned plots (burned + fertilized and burned vs. unburned only), similarity percentages (SIMPER) using Bray-Curtis dissimilarities were calculated.

Dispersion among sites

To test whether dispersion increased in nutrient enriched plots and decreased in burned plots, we used permutational analysis of multivariate dispersions (PERMDISP) to test for differences in group centroids and dispersions among sites across all years by season. Where significant results were found, we followed this initial test with pairwise comparisons between sites. To visually examine the response of dominant and rare species to nutrient enrichment, we used rank-abundance curves by season.

Dispersion among nutrient treatments

To determine differences in dispersion among nutrient treatments in the burned + fertilized (NutNet) site, we used PERMDISP to test for differences in group centroids and dispersions among nutrient treatments across all years by season. We tested pairwise comparisons where significant nutrient treatment interactions were present.

Nutrient effects on univariate community metrics

To test for nutrient effects on plant species richness, evenness, and total biomass, we constructed linear mixed-effects models using the *lme* function in the R package *nlme* (Pinheiro et al. 2017). We included fixed factors nitrogen, phosphorus, potassium, year, and all their interactions, as well as an additive season effect. In all models, we tested and then accounted for temporal autocorrelation using an autoregressive 1 variance-covariance matrix, and included quadrat as a random factor. All models were run in R (version 3.3.1).

RESULTS

Community dynamics under fire and nutrient additions

All sites differed in plant species composition, as shown by significant fertilizer by fire interactions in the spring (pseudo- $F = 15.14$, $p = 0.0001$) and fall (pseudo- $F = 16.46$, $p = 0.0001$). However, the greatest difference in composition was between the burned and fertilized plots and the other sites (Fig. 1). This divergence was mainly due to a lower abundance of the two dominant grasses, *B. eriopoda* and *B. gracilis*, at the

burned + fertilized site in the spring, and a greater abundance of *B. eriopoda* and a lower abundance of *B. gracilis* at this site in the fall (SIMPER, Table 2).

Plant community composition shifted strongly in successive years following fire, as there was a significant burn effect between every pair of years ($p < 0.001$ for all pairwise comparisons). However, there was no pattern to the trajectory of the communities post-fire (e.g. directional, circular), and instead, community shifts between successive years appeared stochastic (Fig. 2).

In years in which there were data for all three sites, all three followed a similar trajectory, tracking inter-annual variation, likely related to annual climate (Fig. 2). Pairwise comparisons of community composition between each pair of years were all non-significant ($p > 0.09$). However, we ran an individual test on 2011 vs. all other years, because this year received low total and monsoon precipitation and had a deep winter freeze. Year 2011 was different than all other years in the fall (pseudo- $F = 5.78$, $p = 0.008$), but not in the spring (pseudo- $F = 1.03$, $p = 0.402$). Based on SIMPER analysis, the difference between fall 2011 and all other years was due to a decline in the biomass of both *B. gracilis* and *B. eriopoda*, contributing to 56% of the cumulative difference between years (Table 3).

Dispersion among sites

Across the nutrient addition plots, spatiotemporal dispersion among local communities was 9% higher than across plots that lacked fertilization (burned only) and 18% higher than plots that were undisturbed (unburned, no fertilizer) (Fig. 3a). Among the three sites, the burned and fertilized community had the greatest spatiotemporal

dispersion in both spring and fall (Fig. 3a; see Table 4 for pairwise comparisons), and this difference remained when all the unfertilized sites were combined (spring: pseudo- $F = 25.90$, $p = 0.0001$; fall: pseudo- $F = 9.08$, $p = 0.001$; Fig. 3b).

Rank abundance curves for all species showed that burned + fertilized plots together contained more species than burned only or undisturbed plots, and these species were more evenly abundant in both the spring and fall (Fig. 4). The burned + fertilized plot had a greater abundance of rare species, mostly forbs, which were a nearly even mix of annual and perennial species (Fig. 4).

Nutrient treatments had no effect on species richness or evenness (Table 5). However, there were strong year and season effects on richness and biomass and year effects on evenness (Table 5), indicating sufficient statistical power to detect nutrient treatment effects, if they were present. Nitrogen (N), phosphorus (P), and potassium (K) together increased total biomass, as did N + P and N alone (Table 5).

Dispersion among nutrient treatments

N increased community dispersion when P was present, by 6% in the spring and 10% in the fall (Table 6; Fig. 5). Additions of P, K, PK, and NPK had no effect on community dispersion in either the spring or fall (Table 6). Rank abundance curves for the fall showed that plots with N and P had a higher abundance of subordinate species than P alone and control (Fig. 6). In the spring, N and P together and N alone had a greater abundance of rare species than P alone (Fig. 6). Species richness was similar in both the spring and fall (~30 species in the spring, and ~40 species in the fall). In the spring, subordinate species were more abundant in N+P plots than in controls (Fig. 6),

these species were mostly forbs, including a mix of annuals and perennials. In the fall, species that were subordinate, but not rare (in the middle of the rank abundance curve) were more abundant in N+P plots and were composed of a mix of grass and forbs, both annuals and perennials.

DISCUSSION

Fire and nutrient additions had little effect on mean plant community responses relative to annual climate, which is known to have strong effects on variability in this system (Collins et al. 2017), but these disturbances had a large effect on community spatiotemporal dispersion. These results are in contrast with well-established responses of mesic grassland communities to nutrient additions, namely increased productivity followed by decreases in plant diversity (Hautier et al. 2009, Borer et al. 2014). We included a wider range of nutrient combinations than previous dispersion studies, which allowed us to show that some nutrient combinations (N + P) increased local community divergence, but others did not. Overall, we demonstrated that community variation is an important metric that can reveal patterns of community dynamics that are not detectable when looking at mean responses alone.

Climate drives community dynamics across sites

There was a clear pattern of inter-annual divergence in community composition, as evidenced by a strong year effect on community structure. The strongest difference among years was the divergence in 2011, a dry year preceded by a hard winter freeze (-30 C). Precipitation is low and variable among years in semiarid systems, which could

lead to high variability in the temporal trajectories of communities. Precipitation has been previously shown to influence desert grassland recovery post-fire (Drewa and Havstad 2001, Scheintaub et al. 2009, Pastro et al. 2011) by speeding grass recovery through greater soil moisture (Drewa et al. 2006). That nutrients had no discernable effect on community structure post-fire is consistent with the idea that water limitation is stronger than nutrient limitation in semi-arid grasslands (Ladwig et al. 2012). Future studies could examine whether there is a tipping point across a precipitation gradient at which nutrient additions alter grassland recovery post-fire, as nutrients instead of water become the main limiting resource for growth.

Dispersion among sites

Contrary to our hypothesis, dispersion was higher in burned plots relative to unburned plots. Stochastic effects, such as dispersal and demography, may have played a prominent role (Chase 2007), because forbs were more abundant in burned and fertilized plots. This increased dispersion may have been caused by a decline in dominant grass abundance following fire, which may have decreased the impact of resource competition (Foster et al. 2004), and potentially allowed for more rare dispersal events by forbs. Because the fire was natural not experimental, it is also possible that plots within the burned sites were inherently more heterogeneous in resource availability to plants (e.g. light, water), leading to greater dispersion and possibly greater initial susceptibility to fire. Although we tried to minimize these heterogeneities by comparing closely-spaced sites, we cannot rule out this possibility.

Alternatively, fire may have increased spatial heterogeneity among plots within a site, which could lead to more divergent community compositions. For example, across

three alpine forests, Burkle et al. (2015) found that mixed-severity fires created more diverse habitat conditions through plant mortality, litter combustion, and canopy removal, which led to the highest species turnover among plots, while high-severity fires led to more homogeneous habitats through complete stand removal. Similarly, in an aquatic system, benthic mollusk communities adjacent to gas drilling platforms were more dispersed than communities far from platforms, due to greater environmental heterogeneity caused by fouling from the drilling platforms on the sea floor (Terlizzi et al. 2009).

Consistent with our hypothesis, nitrogen and phosphorus together had the greatest effect on plant community dispersion, although the mechanism is unclear. Similar to fire, nutrients could have created a greater dispersion because of spatial differences in the amount and type of nutrients among plots. A greater abundance and diversity of nutrients in the landscape may have increased the available niche space (MacArthur 1957), resulting in a greater evenness under fertilization. Nutrient additions could also allow for a greater influence of stochastic events: N and P have also been shown to increase spatial variability (mean difference in composition among plots) in tallgrass prairie (Koerner et al. 2016), caused by invasion of plots by species not in the original species pool, mostly annual forbs. In another study of 18 nitrogen addition experiments in grasslands, nitrogen increased dispersion by increasing spatial variation in alpha diversity and species turnover in space, independent of alpha diversity (Chalcraft et al. 2008).

A common response of mesic grasslands to nutrient additions is increased productivity, which leads to a decrease in diversity, due to increased growth by dominant species (Hautier et al. 2009, Borer et al. 2014). This could cause dispersion to decrease,

however, light is not a limiting resource in deserts, and nutrient limitation in desert systems is often contingent on soil moisture (Hall et al. 2011, Ladwig et al. 2012). Consistent with our alternative hypothesis that desert systems would not show diversity declines under fertilization, our nutrient additions had no effect on plant species richness or evenness, and spatiotemporal dispersion among local community patches increased. Fertilization increases species growth rates, and dispersion is often higher in more productive sites in both terrestrial and aquatic systems (Steiner and Leibold 2004, Soininen et al. 2005, Houseman et al. 2008, but see Chalcraft et al. 2008). That we did not find effects of K may be due to its limited effects on plant growth in grasslands, relative to N and P (Fay et al. 2015).

Conclusion

Our results showed that community dispersion is driven strongly by environmental conditions, which affect species occurrence among communities as well as abundance within communities. Building upon findings in mesic grasslands, we demonstrated that both fire and nutrient additions can drive divergence among local communities. These responses would not have been detectable by looking solely at mean community responses (e.g. group centroids). Community dispersion analysis is a powerful tool that can be used to detect complex patterns and underlying processes of community structure, not only in semi-arid grasslands, but in other systems globally.

REFERENCES

- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Borer, E. T., W. S. Harpole, P. B. Adler, E. M. Lind, J. L. Orrock, E. W. Seabloom, and M. D. Smith. 2014. Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution* 5:65–73.
- Burkle, L. A., J. A. Myers, and R. T. Belote. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. *Ecosphere* 6:1–14.
- Chalcraft, D. R., S. B. Cox, C. Clark, E. E. Cleland, K. N. Suding, E. Weiher, and D. Pennington. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology* 89:2165–2171.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104:17430–17434.
- Collins, S.L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology* 73: 2001-2006.
- Collins, S.L., L.M. Ladwig, M.D. Petrie, S.K. Jones, J.M. Mulhouse, J Thibault and W.T. Pockman. 2017. Press-pulse interactions: Effects of warming, N-deposition, altered winter precipitation and fire on desert grassland community structure and dynamics. *Global Change Biology* 23: 1095-1108.
- Diffenbaugh, N. S., F. Giorgi, and J. S. Pal. 2008. Climate change hotspots in the United States. *Geophysical Research Letters* 35:L16709.
- Drewa, P. B., and K. M. Havstad. 2001. Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands. *Journal of Arid Environments* 48:429–443.
- Drewa, P. B., D. P. C. Peters, and K. M. Havstad. 2006. Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert. *Oecologia* 150:29–39.
- 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* 1:15080.

- Foster, B. L., T. L. Dickson, C. A. Murphy, I. S. Karel, and V. H. Smith. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. *Journal of Ecology* 92:435–449.
- Gosz, R. J., and J. R. Gosz. 1996. Species interactions on the biome transition zone in New Mexico: response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) to fire and herbivory. *Journal of Arid Environments* 34:101–114.
- Hall, S. J., R. A. Sponseller, N. B. Grimm, D. Huber, J. P. Kaye, C. Clark, and S. L. Collins. 2011. Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. *Ecological Applications: A Publication of the Ecological Society of America* 21:640–660.
- Hautier, Y., P. A. Niklaus, and A. Hector. 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638.
- Houseman, G. R., G. G. Mittelbach, H. L. Reynolds, and K. L. Gross. 2008. Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology* 89:2172–2180.
- Huang, J., H. Yu, X. Guan, G. Wang, and R. Guo. 2016. Accelerated dryland expansion under climate change. *Nature Climate Change* 6:166–171.
- Huenneke, L. F., D. Clason, and E. Muldavin. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* 47:257–270.
- Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 years of nitrogen addition. *Ecology* 76:1872–1887.
- Koerner, S. E., M. L. Avolio, K. J. La Pierre, K. R. Wilcox, M. D. Smith, and S. L. Collins. 2016. Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *Journal of Ecology* 104:1478–1487.
- Ladwig, L. M., S. L. Collins, A. L. Swann, Y. Xia, M. F. Allen, and E. B. Allen. 2012. Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *Oecologia* 169:177–185.
- MacArthur, R.H. 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America* 43, 293-295.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- Muldavin, E. H., D. I. Moore, S. L. Collins, K. R. Wetherill, and D. C. Lightfoot. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123–132.

- Mulhouse, J. M., L. M. Hallett, and S. L. Collins. 2017. The influence of seasonal precipitation and grass competition on 20 years of forb dynamics in northern Chihuahuan Desert grassland. *Journal of Vegetation Science* 28:250–259.
- Notaro, M., Z. Liu, R. G. Gallimore, J. W. Williams, D. S. Gutzler, and S. Collins. 2010. Complex seasonal cycle of ecohydrology in the Southwest United States. *Journal of Geophysical Research: Biogeosciences* 115:G04034.
- Pastro, L. A., C. R. Dickman, and M. Letnic. 2011. Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecological Applications* 21:3238–3253.
- Pausas, J. G., and M. Verdú. 2008. Fire reduces morphospace occupation in plant communities. *Ecology* 89:2181–2186.
- Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262:703–717.
- Petrie, M. D., S. L. Collins, D. S. Gutzler, and D. M. Moore. 2014. Regional trends and local variability in monsoon precipitation in the northern Chihuahuan Desert, USA. *Journal of Arid Environments* 103:63–70.
- Pinheiro J, D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: Linear and nonlinear mixed effects models. R package version 3.1-131, <https://CRAN.R-project.org/package=nlme>.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Sala, O. E., F. S. Chapin, Iii, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Scheintaub, M. R., J. D. Derner, E. F. Kelly, and A. K. Knapp. 2009. Response of the shortgrass steppe plant community to fire. *Journal of Arid Environments* 73:1136–1143.
- Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279–3289.
- Soininen, J., P. Tallberg, and J. Horppila. 2005. Phytoplankton community assembly in a large boreal lake – deterministic pathways or chaotic fluctuations? *Freshwater Biology* 50:2076–2086.
- Steiner, C. F., and M. A. Leibold. 2004. Cyclic assembly trajectories and scale-dependent productivity–diversity relationships. *Ecology* 85:107–113.

Terlizzi, A., M. J. Anderson, S. Bevilacqua, S. Frascetti, M. Włodarska-Kowalczyk, and K. E. Ellingsen. 2009. Beta diversity and taxonomic sufficiency: Do higher-level taxa reflect heterogeneity in species composition? *Diversity and Distributions* 15:450–458.

Wang, S., and M. Loreau. 2014. Ecosystem stability in space: α , β and γ variability. *Ecology Letters* 17:891-901.

Wang, S., and M. Loreau. 2016. Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters* 19:510-518.

Table 1. Description of study sites. A (+) symbol indicates the presence of the disturbance, (-) indicates its absence. Years in brackets indicate the year the site burned.

Site	Nutrient Network (burned+fertilized)	Mixed-grass (burned only)	Mixed-grass (unburned)
Fire	+ (2009)	+ (2003)	-
Nutrient additions	+ / -	-	-
Abbreviation	N	MGB	MG
Year established	2008	2004	2004

Table 2. Average abundance of each plant species and its cumulative contribution to community differences between sites, based on SIMPER analysis. Differences are across all years in spring and fall separately.

Spring			
	Average abundance		Cumulative contribution (%)
	N	MG	
<i>Bouteloua eriopoda</i>	4.22	10.45	28.21
<i>Bouteloua gracilis</i>	0.14	5.91	48.19
<i>Gutierrezia sarothrae</i>	4.42	0.09	57.97
<i>Cryptantha crassisepala</i>	3.11	1.13	64.25
	N	MGB	
<i>Bouteloua gracilis</i>	0.14	24.56	37.64
<i>Bouteloua eriopoda</i>	4.22	27.24	68.86
	MG	MGB	
<i>Bouteloua gracilis</i>	5.91	24.56	40.76
<i>Bouteloua eriopoda</i>	10.45	27.24	78.54
Fall			
	Average abundance		Cumulative contribution (%)
	N	MG	
<i>Bouteloua eriopoda</i>	37.96	35.56	34.88
<i>Bouteloua gracilis</i>	1.06	18.06	53.37
<i>Machaeranthera pinnatifida</i>	5.80	0.00	58.82
<i>Sporobolus</i> spp.	2.07	4.05	62.89
	N	MGB	
<i>Bouteloua eriopoda</i>	37.96	27.24	35.38

Table 2 (cont.)

<i>Bouteloua gracilis</i>	1.06	24.56	60.79
	MG	MGB	
<i>Bouteloua eriopoda</i>	35.56	27.24	40.11
<i>Bouteloua gracilis</i>	18.06	24.56	71.37

Table 3. Average abundance of species contributing most to differences in community structure between 2011 vs. all other years, by season, based on similarity percentage (SIMPER) analysis.

	Average abundance		Cumulative contribution (%)
Fall			
Year	2011	Other years	
<i>Bouteloua eriopoda</i>	2.65	43.58	40.43
<i>Bouteloua gracilis</i>	0.64	10.14	55.94
<i>Machaeranthera pinnatifida</i>	0.49	3.77	61.28

Table 4. Pairwise comparisons of multivariate dispersions using PERMDISP across sites in either the spring or fall.

Spring			
	Mean \pm SE	<i>t</i>	<i>p</i>
N, MG	54.61 \pm 0.69	3.04	0.008
N, MGB	51.29 \pm 0.86	6.71	0.001
MG, MGB	46.35 \pm 1.03	3.58	0.002
Fall			
	Mean \pm SE	<i>t</i>	<i>p</i>
N, MG	62.18 \pm 0.51	5.39	0.001
N, MGB	57.30 \pm 0.80	14.44	0.001
MG, MGB	46.38 \pm 1.03	8.15	0.001

Table 5. Nutrient treatment effects on richness, evenness, and biomass in the burned + fertilized site (NutNet). Significant results are bolded, and marginally significant results are italicized.

	Richness			Evenness		Biomass	
	<i>df</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
N	1, 32	0.57	0.45	0.15	0.70	11.53	0.002
P	1, 32	0.42	0.52	1.97	0.17	0.70	0.41
K	1, 32	0.001	0.98	0.05	0.83	0.95	0.34
Year	5, 398	16.83	<0.0001	6.94	<0.0001	3.42	0.005
Season	1, 398	89.64	<0.0001	0.54	0.46	155.43	<0.0001
N*P	1, 32	0.29	0.59	0.04	0.84	4.00	0.05
N*K	1, 32	0.67	0.42	1.29	0.26	3.34	<i>0.08</i>
P*K	1, 32	0.26	0.62	0.75	0.39	0.14	0.71
N*Yr	5, 398	1.08	0.37	0.31	0.91	1.60	0.16
P*Yr	5, 398	1.58	0.17	0.82	0.54	0.28	0.93
K*Yr	5, 398	0.81	0.54	0.20	0.96	0.21	0.96
N*P*K	1, 32	0.87	0.36	0.62	0.44	5.09	0.03
N*P*Yr	5, 398	0.66	0.65	1.84	0.10	0.69	0.63
N*K*Yr	5, 398	0.65	0.66	0.35	0.88	0.99	0.43
P*K*Yr	5, 398	0.84	0.52	0.40	0.85	0.11	0.99
N*P*K*Yr	5, 398	0.21	0.96	0.95	0.45	1.10	0.36

Table 6. Homogeneity of multivariate dispersions test (PERMDISP) results for the effect of nutrient treatments on community dispersion at the Nutrient Network site. Significant p-values are bolded, and marginally significant p-values ($p < 0.10$) are italicized.

Treatment	Spring		Fall	
	<i>Pseudo-F</i>	<i>p</i>	<i>Pseudo-F</i>	<i>p</i>
N	8.00	0.01	9.98	0.01
P	0.67	0.47	2.66	0.17
K	0.16	0.74	2.53	0.17
NP	2.82	<i>0.07</i>	4.13	0.04
NK	2.51	0.12	<i>3.40</i>	<i>0.08</i>
PK	0.46	0.77	1.79	0.27
NPK	1.35	0.34	2.00	0.22

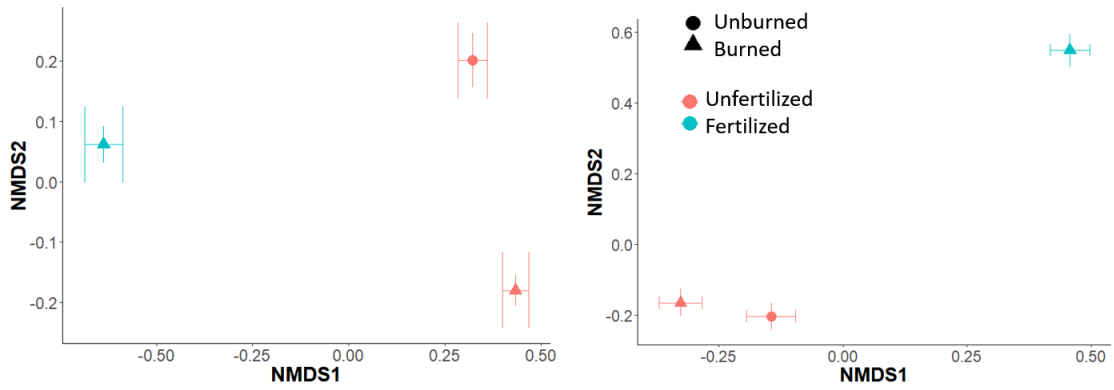


Figure 1. Non-metric multidimensional scaling (NMDS) of plant community composition for plots with different disturbance histories (unburned, burned, and burned + fertilized) in the spring (left) and fall (right). Each point corresponds to a site. The burned + fertilized site has a different composition than the other sites. Data from 2008 on were used to create this graph. Error bars are ± 1 SE.

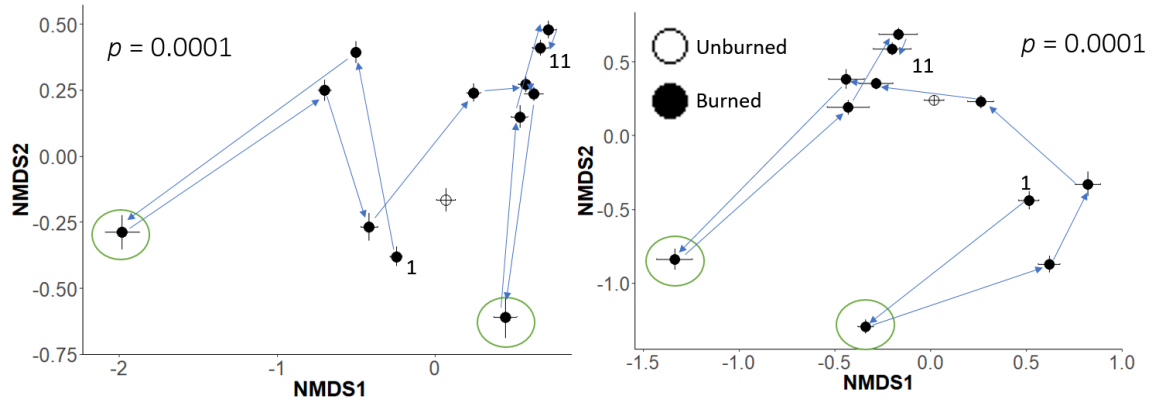


Figure 2. Non-metric multidimensional scaling (NMDS) of plant community composition in unburned and burned plots in the spring (left) and fall (right). Note that unburned sites include all of the years of mixed-grass unburned, plus the first year of nutrient network data. The burned sites include all of the mixed-grass burned, and after the first year of nutrient network data. Arrows show the trajectory of the community over time, from the 1st year post-burn (shown by 1 in the plot) to the 11th year post-burn. There is no definitive pattern of community trajectory following fire. 2011 is shown in green circles, a dry year with an unusual deep winter freeze. Error bars are ± 1 SE.

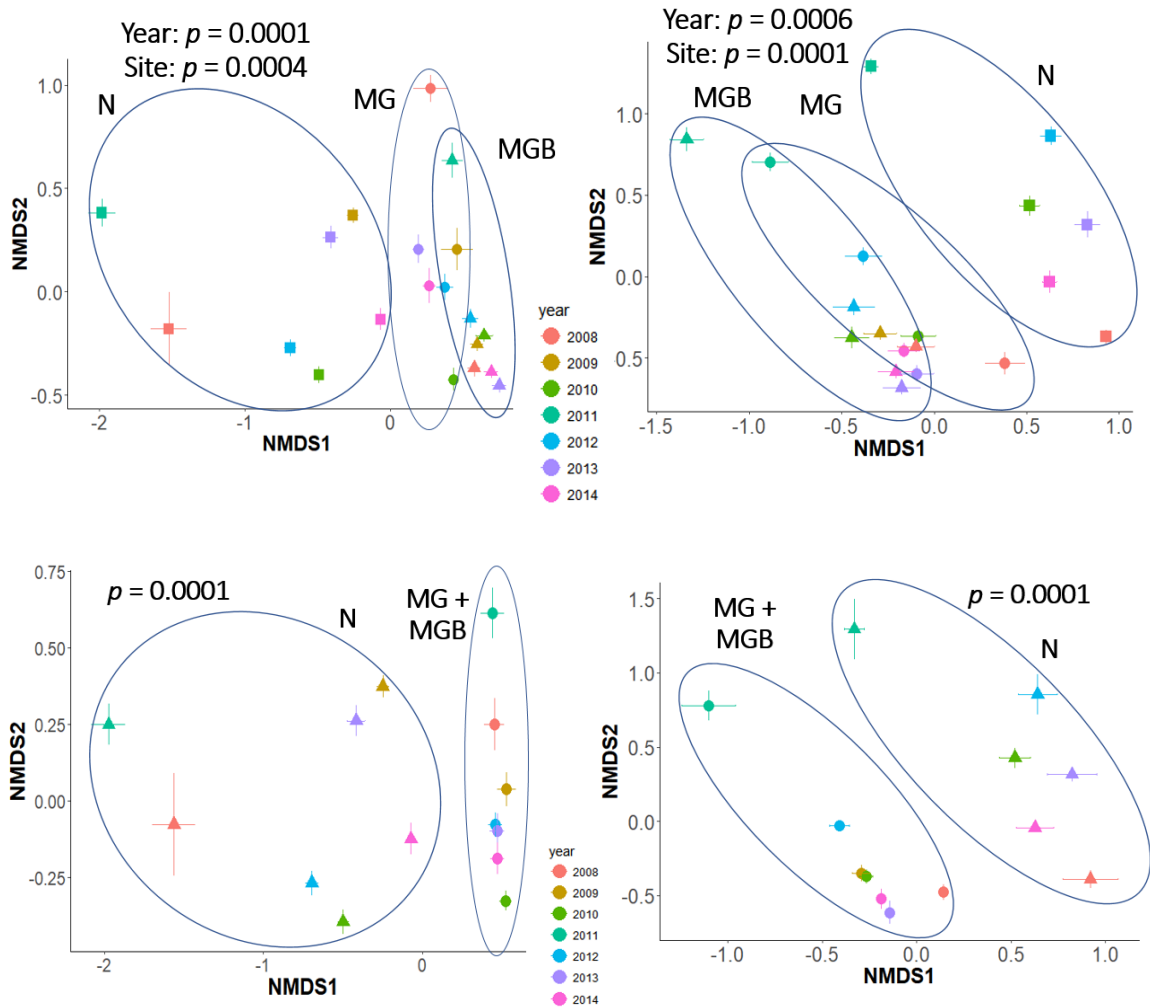


Figure 3. Non-metric multidimensional scaling (NMDS) ordination of plant community composition for each site (mean of all quadrats) in the spring (left) and fall (right) across all sites separately (a) and mixed-grass sites combined (b). Years are separated by color. Hand-drawn ellipses surround sites for clarity, and are labelled by site. NutNet plots were significantly more dispersed than combined MG sites (MG + MGB) for both the spring and fall (p -values show differences in dispersion based on PERMDISP analysis). Error bars are ± 1 SE.

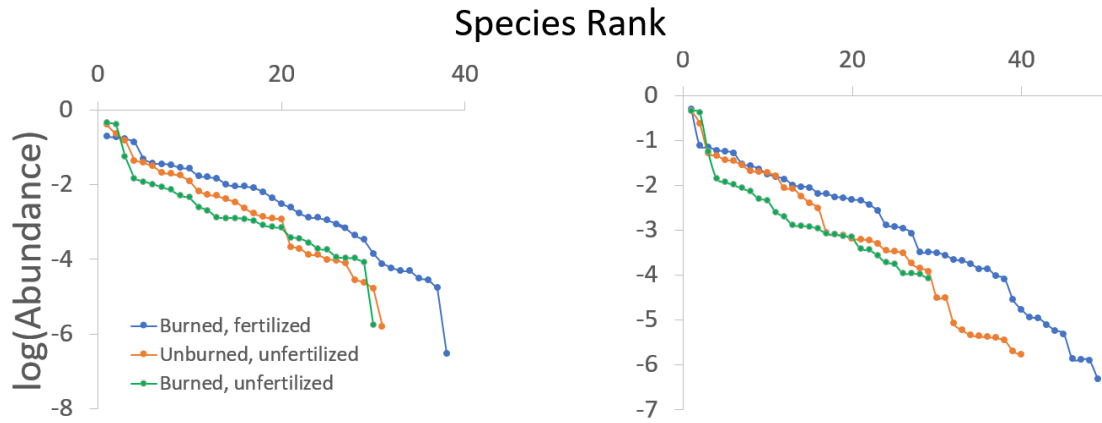


Figure 4. Rank-abundance curves (RACs) for each site. The burned + fertilized site has a greater abundance of less dominant species.

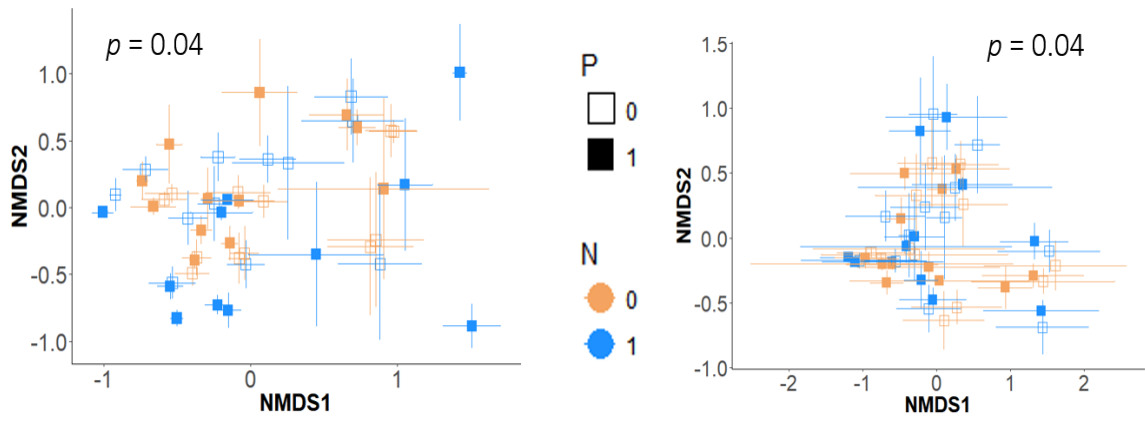


Figure 5. NMDS ordination showing differences in community composition across plots with and without N and P in both the spring (left) and fall (right). Communities with N and P added are more dispersed than plots with P alone in both spring and fall. Error bars are ± 1 SE.

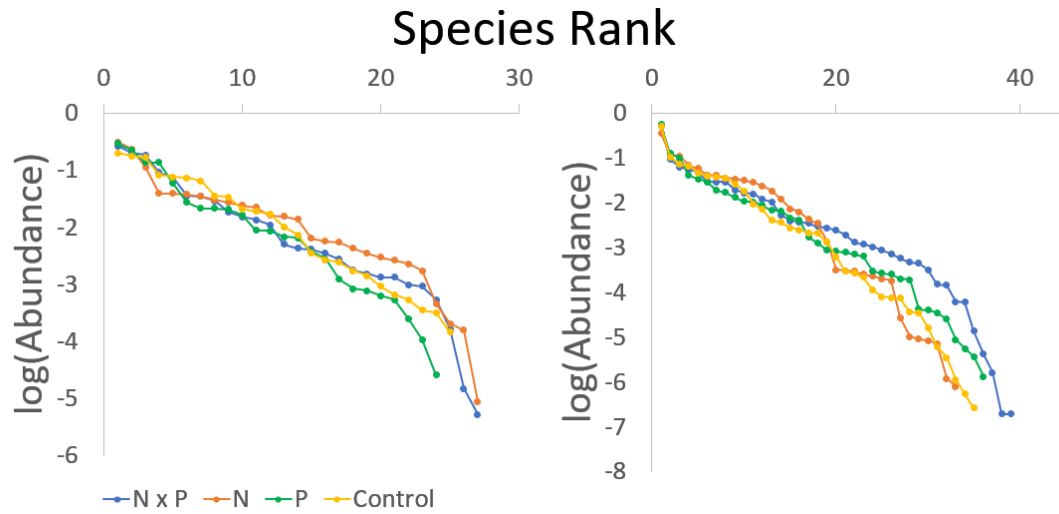


Figure 6. Rank-abundance curves for the NutNet site in plots with nitrogen and phosphorus (N x P), nitrogen only (N), phosphorus only (P), and neither nitrogen or phosphorus (Control) in spring (left) and fall (right). There is a similar number of species on both curves, but a greater abundance of rare species with N added.