Exploring the impacts of drought on spatial beta diversity in grassland plant communities

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Note: This document is a pre-analysis plan

Abstract

Understanding how drought impacts species diversity in communities and ecosystems is an important focus of ecological research. However, research on this topic has historically focused on alpha diversity (i.e. local scale diversity) at the 1m^2 scale. Beta diversity - the heterogeneity of landscapes - is important for the stability of metacommunities and ecosystems, limiting local extinctions, and is also the scale at which many management decisions and activities take place. In this study, we will use data from the Drought Network's International Drought Experiment (IDE) to test the impact of experimental drought on spatial beta diversity at experiment sites around the world. We will incorporate numerous site-level attributes to understand *Are drought-induced changes to spatial beta diversity attributable to species turnover or changes in abundance?, Do impacts of drought on spatial beta diversity increase or decrease with drought duration* , and *To what extent do biotic vs abiotic characteristics of sites moderate the effect of experimental drought on spatial beta diversity?*

Background

Biodiversity plays an important role in ecosystem function and services, such as productivity, invasion resistance, and nutrient cycling (Dee et al. 2019, Souza et al. 2011, Lohbeck et al. 2016). However, biodiversity in terrestrial ecosystems around the world face threats from increasing duration and severity of droughts (Chen et al. 2025). Drought has the capacity to reshape the structure and function of plant communities by modifying resource availability and altering diversity at multiple spatial scales all aspects of which are related to the duration and intensity of the drought event. Though studies at numerous sites have reported that species richness and evenness at local scales (1m^2) was unaffected by drought treatments (Batbaatar et al. 2022, Castillioni et al. 2020, Alon and Sternberg 2019), other studies have reported losses of species richness and Shannon's diversity in drier sites (Wheeler et al. 2021, Korell et al. 2021). Beta diversity - the degree of difference in community composition among replicates, on the other hand has been shown to decrease under drought conditions in food webs of artificial ponds (Chase 2007) but studies on the effects of drought on diversity in grasslands rarely test for or report impacts on beta diversity.

Drought may have negative or positive impacts on beta diversity in grasslands via contrasting mechanisms. Drought may decrease spatial beta diversity by imposing a strong environmental filter on the assembly of alpha diversity. Though a regional species pool (gamma diversity) may be diverse, drought could limit assembly of plant communities to only those species that are tolerant to drought (i.e. an environmental filter; Kraft et al. 2015). Alternatively, drought may increase beta diversity by amplifying pre-existing differences among communities (e.g. community dispersion, divergence; Houseman et al. 2009). For example, if replicates across space have similar species but differing abundances of those species, a drought treatment that reduces abundance of the rarest (i.e. least abundant) species will result in replicates that are more different from each other than before since they will no longer have as many species in common. Complete loss of species (i.e. turnover) may drive either of these mechanisms, but changes to the abundance of species without loss can drive changes to beta diversity, such as severe reductions in dominant species cover. Therefore, to gain an understanding of the mechanisms driving changes in beta diversity, we must also consider how numerous facets of beta diversity change.

Changes to spatial beta diversity can be attributed to species turnover or changes to the abundance of species. With species turnover, species are either completely lost (i.e. not present) and/or new species are gained. Turnover of species is common in drought experiments, primarily via loss of species (Avolio et al. *in prep*), though species losses and gains in response to perturbation are most often concentrated in transient species at low abundances (Wilfhart et al. 2021). Conversely, responses of dominant and/or common species to perturbations can drive community changes often without total loss of species (Wilfhart et al. 2021, Wilfhart et al. 2023). By comparing the responses of both turnover-based and abundance-based beta diversity indices to drought treatment, we can determine whether observed changes are due to species turnover or shifts in abundance.

Regardless of the mechanisms of change, the impact of drought on beta diversity is likely tied to the duration of drought. The effect of drought duration on plant communities can be positive (i.e. increasing over time), diminishing (i.e. decreasing over time), or null (i.e. no change over time). Whether drought has a positive or negative impact on beta diversity, this effect could be magnified over time. For example, if drought decreases beta diversity through environmental filtering for drought tolerant species, greater duration of drought should impose a stronger filter. Conversely, if drought increases beta diversity by amplifying differences among replicates (plots), greater duration of drought might continue to amplify those differences.

Furthermore, many site-specific factors may contribute to the direction or magnitude of change in beta diversity exhibited as a response to drought. Sites with greater gamma diversity (regional diversity) have large pools of species possible for recruitment in community assembly which may result in greater beta diversity in response to drought as a greater number of drought-tolerant species could be available to persist or colonize across a landscape. Similarly, the nestedness of a community is a measure of the extent to which replicates in a community are subsets of the most diverse replicates compared to turnover across space. More nested communities may have greater decreases in beta diversity in response to drought as more-nested communities have limited opportunities for recruitment of species. Additionally, greater dominance within a community may alter the effect of disturbance on beta diversity as negative impacts on dominant species increases the stochastic assembly of subordinate species (Ohlert et al. 2025). Finally, mean annual precipitation is an important climatic characteristic of ecosystems that has been linked to sensitivity of ANPP to precipitation (Huxman 2004), and facets of alpha diversity (Smith et al. 2022, Korell et al. 2019). Just as these ecosystem functions and diversity are more sensitive in drier ecosystems (those with low mean annual precipitation), beta diversity may also be more impacted by drought in dry ecosystems.

In this study we will use data from sites in the Drought Network's International Drought Experiment (IDE) to answer the following questions:

Are drought-induced changes to beta diversity attributable to species turnover (e.g. loss) versus changes in abundance?

Previous study of beta diversity of pond communities under drought have been done(Chase 2007), but no similar study exists in grassland systems. We expect that drought will reduce beta diversity and based on Avolio et al. (*in prep*) which reports species losses, but not rank abundance changes, under drought, we expect that reduction of beta diversity will be predominately due to changes in species identity (i.e. turnover).

Do impacts of drought on beta diversity increase or decrease with drought duration?

Housemann et al. (2009) suggests that greater magnitude of perturbation, including perturbation duration, will increase beta diversity and Fukami (2015) provides stochastic priority effects and the consequent historical contingency as a mechanism. Therefore, we expect that the impact of drought effects on beta diversity will increase as drought duration increases.

Do biotic vs abiotic attributes moderate heterogenous treatment effects on beta diversity? (i.e. further explain variation in beta diversity changes)

We expect that some site-level variables will moderate the relationship between drought and beta diversity. We expect that sites with greater relative abundance of annuals (versus perennials) prior to treatment will incur greater changes to beta diversity, particularly species turnover, as annuals are more sensitive to short-term changes in climatic conditions. We also expect that higher nestedness of communities prior to treatment will result in greater negative changes to beta diversity as rarer species are more likely to be lost from plots, leaving more-similar species across plots. We also expect that responses of beta diversity will differ across a gradient of mean annual precipitation (MAP). For drier sites (those with lower MAP; approximately 400 mm or less) for which water is the most limiting resource, experimental drought may impose a more effective environmental filter and therefore, we expect dry sites to show greater decreases in beta diversity with drought treatment than at wetter sites.

Analysis plan

IDE and data selection

The Drought Network's International Drought Experiment (IDE) is a globally distributed network of experiments that use passive rainout shelters to induce drought in plant communities. Treatments are imposed with a passive rainout shelter design that diverts a percentage of ambient rainfall determined by the historical variability of precipitation and targets a 1-in-100 year drought event given exactly average annual precipitation (Smith et al. 2024). In this study, we will use grassland sites from this network with at least one year of treatment and include up to four treatment years as was the original design of the experiment. For inclusion in analyses, sites must also have at least five control and five treatment plots. As beta diversity is a measure of variation among replicates, fewer than five plots may introduce considerable noise into the calculation of beta diversity.

Drought treatment variable

Treatments will be quantified as the rainfall received by a treatment in the previous 0-365 days prior to data collection, relative to mean annual precipitation for the site.

$Precip_{c,d}$ – MAP / MAP

Where $Precip_{c,d}$ is the annual precipitation in either the control or drought treatment plots and MAP is the site's mean annual precipitation. This metric has been called "drought severity" in previous manuscripts of the IDE (Smith et al. 2024), however, as we are calculating this metric for both control and drought treatment plots, we have renamed it "relative rainfall" to reflect that this value is not only used to classify the drought treatment and will often be positive (e.g. annual rainfall is greater than mean annual precipitation). As a measure of the relative difference in annual rainfall compared to mean conditions, this metric has been shown to be a useful predictor of ANPP responses to drought treatment (Smith et al. 2024) and therefore is a useful measure of water conditions generalizable across global ecosystems.

<u>Beta diversity indices</u>

For each site/treatment/year combination, we will calculate two forms of beta diversity: Jaccard (presence-absence based) and Bray-Curtis (abundance based) (Schroeder and Jenkins 2018). We recognize that many beta diversity indices exist in the literature and have chosen two that represent distinct categories of beta diversity indices which, when compared, will clarify the dynamics driving changes in beta diversity.

<u>Approach for each question</u>

Are drought-induced changes to beta diversity attributable to species turnover (e.g. loss) or changes in abundance?

We will assess the direction of change in beta diversity with relative rainfall (i.e. increasing or decreasing with drought) along with whether presence-absence and abundance based measures of beta diversity detect the same direction of change. We will test one model for each of the beta diversity indices: feols(Jaccard beta diversity ~ relative rainfall | site), feols(Bray-Curtis beta diversity ~ relative rainfall | site). The first model detects changes to species turnover (i.e. species gains and losses), while the second model is more sensitive to changes in the abundance of species whether or not species are entirely lost or gained.

Do impacts of drought on beta diversity increase or decrease over time?

The effect of treatment time will be quantified in two ways: first, the relative rainfall averaged over a given time period prior to the data collection and second, treatment year as an integer. For each beta diversity index, we will test the models: feols(beta diversity ~ average relative rainfall | site) and feols(beta diversity ~ treatment(binary) * treatment year | site). The first model assumes that the effect of treatment is captured by the relative rainfall averaged over the chosen time period and the second model assumes that the treatment effect is captured in a binary drought/control designation.

Do biotic vs abiotic attributes moderate heterogenous treatment effects on beta diversity? (i.e. further explain variation in beta diversity changes)

We expect that the impact of drought on beta diversity will differ across space based on site-level attributes including mean annual precipitation, nestedness of the community pretreatment, gamma diversity, pretreatment dominance, and percent of annual species cover. To test these ecological hypotheses, we will report the results of the following models, one for each of the above moderating variables: feols(beta diversity ~ relative rainfall + relative rainfall:attribute | site). The same analyses will be replicated for both beta diversity indices.

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