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David Gibson

[djgibson@siu.edu](mailto:djgibson@siu.edu)

Southern Illinois University Carbondale <https://orcid.org/0000-0002-0308-7506>

David F. Barfknecht

Southern Illinois University Carbondale

Sara G. Baer

The University of Kansas

Matthew Galliat

Fort Hays State University

Zhe Ren

Purdue University

Jack Sytsma

Kansas State University Division of Biology

Loretta C Johnson

Kansas State University Division of Biology

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## Research Article

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# Dependency of diversity-productivity relationships on ecotypes of the dominant species across a precipitation gradient

David J. Gibson<sup>1</sup> • David F. Barfknecht<sup>1</sup> • Sara G. Baer<sup>2</sup> • Matthew Gallart<sup>3</sup> • Zhe Ren<sup>1,4</sup> • Jack Sytsma<sup>5</sup> • Loretta C Johnson<sup>5</sup>

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<sup>1</sup>School of Biological Sciences, Southern Illinois University Carbondale, Carbondale, IL, USA

<sup>2</sup>Kansas Biological Survey and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, USA

<sup>3</sup>Department of Biological Sciences, Fort Hays State University, Hays, Kansas, USA

<sup>4</sup>Department of Botany and Plant Pathology, Purdue University, West Lafayette, Indiana, USA

<sup>5</sup>Division of Biology, Kansas State University, Manhattan, Kansas, USA

David J. Gibson

[djgibson@siu.edu](mailto:djgibson@siu.edu)

**Author contributions** L.C.J. and S.G.B. designed and established the experiment, L.C.J., S.G.B., M.B.G., and D.J.G. maintained the plots, D.F.B., Z.R., and J.S. collected the data, D.J.G. conceived and conducted the data analysis with assistance from D.F.B. and Z.R., and D.J.G. wrote the manuscript with critical contributions from all the coauthors.

## Abstract

Locally dominant and highly productive species affect diversity through competitive interactions with subordinate species. The relationship between diversity and productivity is commonly unimodal and referred to as the ‘humped-back model’ (HBM). The effect of local adaptation in dominant species on occurrence of the HBM is unknown, particularly among the different aspects of diversity. A reciprocal transplant experiment established across a precipitation gradient in the U.S. Great Plains was used to investigate the effect of variation among ecotypes of the dominant prairie grasses *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indian grass) on expression of the HBM. The information from taxonomic, phylogenetic, and functional diversity metrics on diversity–productivity relationships was compared. The HBM was most common for taxonomic diversity (57% of tests), and when locally sourced (compared with distantly sourced) ecotypes were established in the transplant experiment, reflecting a home-site advantage (local adaptation), especially at the extreme ends of the precipitation gradient. Phylogenetic and functional trait diversity exhibited a less frequent humped-back relationship with productivity (26% and 13%, respectively). The HBM has value in providing insights into diversity-productivity relationships in grasslands restored with different ecotypes of a foundation species but is contingent on local environmental conditions and the ecotype of the dominant grass.

**Keywords** *Andropogon gerardii* • ecotypic variation • grasslands • humped-back model • *Sorghastrum nutans* •

## Introduction

Understanding the relationship between diversity and productivity is relevant to nature-based climate change mitigation (Mori et al. 2021). Typically, represented as species richness, taxonomic diversity is postulated to have a unimodal, concave-down relationship with productivity initially described as the ‘humped-backed model’ (HBM) by Grime and colleagues (Al-Mufti et al. 1977; Grime 1973). Mechanistically, the unimodal relationship of HBMs along productivity gradients is attributed to high stress resulting in low productivity and few species, followed by increased susceptibility to facilitation as improved environmental conditions allow for more species and high productivity until an optimum is reached; subsequently, the stress decreases with decreased diversity as interspecific competition increases with high productivity of dominant species (Michalet et al. 2006). However, while the HBM is globally robust (Fraser et al. 2015), support is context dependent (Catford et al. 2022) due to anthropogenic limitations on the species pool (Adler et al. 2011), aridity (Rey et al. 2016), sampling bias (Oksanen 1996), nutrient limitation (Palpurina et al. 2019), and other abiotic contingencies, such as disturbance or successional progression (Guo 2003; Li et al. 2021; Ónodi et al. 2021). One context of the HBM that has not been explored is whether diversity–productivity relationships are influenced by locally adapted ecotypes of the dominant species that contribute most to productivity. A better understanding of these relationships contributes to understanding the role of the HBM in community assembly (Michalet et al. 2006).

Along regional environmental and productivity gradients, the same species may remain dominant but with a turnover of locally adapted ecotypes (Lowry et al. 2014). If the ecotype of a dominant species affects diversity-productivity relationships, as we suspect, then ecotype selection will have significant effects on community assembly and productivity in restorations

(Baer et al. 2019). The selection of appropriate climate-adapted ecotypes will mediate restoration success. For example, across the climatic precipitation gradient of the U.S. Great Plains grassland, the warm-season perennial grass *Andropogon gerardii* Vitman (big bluestem) has maintained dominance and is represented by a series of local ecotypes (Galliat et al. 2019; Gray et al. 2014; Gustafson et al. 2004; Gustafson et al. 1999; McMillan 1956). While it has been demonstrated that different ecotypes can affect interspecific interactions (Liancourt and Tielbörger 2011), it is unknown whether local ecotypes of dominant species affect diversity-productivity relationships and expression of the HBM. Understanding the role of dominant species in community assembly and diversity-productivity relationships is crucial for understanding and projecting climate change-mediated community shifts (Johnson et al. 2015a; McCain et al. 2010; Polley et al. 2007; Sasaki and Lauenroth 2011).

To fully understand the context dependency or generality of the HBM, it is necessary to investigate a comprehensive suite of diversity metrics beyond taxonomic diversity. While diversity-productivity relationships have been investigated extensively using taxonomic diversity among a variety of plant life forms and taxa (Kessler et al. 2014; Laanisto et al. 2008), additional insight has been provided by investigating other metrics of diversity (Brun et al. 2019; Chalcraft et al. 2009), referred to collectively as attribute diversity (Chao et al. 2014). Phylogenetic diversity incorporates evolutionary relationships among cooccurring species (Barber et al. 2016; Cadotte et al. 2019; Cavender-Bares et al. 2006; Khalil et al. 2017), whereas functional diversity incorporates functional relationships based upon relevant species traits (Khalil et al. 2018; Miller et al. 2019; Petchey and Gaston 2002; Purschke et al. 2013; Spasojevic and Suding 2012). Like taxonomic diversity, which is based upon species richness (the number of taxa in an assemblage), metrics of phylogenetic and functional diversity provide additional insight related

to species dominance and similarity in our experiment (Ren et al. 2023) and patterns of community productivity generally (Cadotte et al. 2009). In brief, in Ren et al. (2023), we reported that taxonomic diversity decreases over time, while phylogenetic and functional diversity remain stable and largely neutral (random). Differences among taxonomic versus phylogenetic and functional diversity were restricted to the plots with the dry ecotype at the wet site. On this basis, we suggest that abiotic filtering (precipitation) is the dominant factor driving diversity and hence diversity-productivity relationships in our system, leading to our expectation of concurrence among diversity metrics. Together, these dimensions of diversity can allow the importance of niche relationships to be incorporated into an understanding of the constraints on productivity (Vega-Álvarez et al. 2019).

In this study, we investigated the effects of the ecotype of dominant species on occurrence of the HBM. We took advantage of a decadal-established reciprocal transplant garden experiment, a particularly valuable approach for detecting the role of local adaptation in grasslands (Johnson et al. 2022) where dominant species were sourced from three different regions across the U.S. Great Plains. Four reciprocal transplant gardens were sown with other native species in each region where ecotypes of the dominant species were collected and at a drier site outside of the collection area. A comparison of the responses across all the sites allowed for a novel regional-scale comparison. Ecotypes of the dominant warm-season perennial grasses *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash were sourced across a 1000 km precipitation gradient from central Kansas to Illinois, U.S. These species are the dominant foundation species comprising up to 80% of the biomass across the North American Great Plains (Epstein et al. 1997; Risser et al. 1981; Weaver and Fitzpatrick 1934). Frequent droughts and strong interannual variation in rainfall characterize grasslands, which are projected to increase with climate change

(Hoover and Rogers 2016; Schoof and Robeson 2016), affecting plant performance and productivity, community composition, and ecosystem functioning (Fraser 2019; Huxman et al. 2004; Mackie et al. 2019; Scott et al. 2010; Wang et al. 2007).

We hypothesized ( $H_1$ ) that locally adapted ecotypes would exhibit the highest productivity at their home sites (home-site advantage sensu Montalvo and Ellstrand 2000), which would suppress diversity and produce more robust HBM curves than would nonlocal ecotypes at each site (Fig. 1). Second, we hypothesized ( $H_2$ ) that the HBM curve would shift to the left as conditions became more arid, with a decrease in peak diversity occurring at dry sites compared to more mesic sites (Fig. 1). We predicted that this effect on the HBM would be demonstrated across the precipitation gradient and through an experimental reduction in precipitation under rainout shelters (Cherwin and Knapp 2012). Third, we hypothesized ( $H_3$ ) that these hypothesized relationships occur between taxonomic, phylogenetic, and functional diversity metrics, indicating that the mechanisms of species relationships related to niche competition and limiting similarity are related to species phylogenetic relationships and functional traits (Barry et al. 2019; Brun et al. 2019).

## **Materials and Methods**

### **Reciprocal transplant garden experiment**

#### **Garden locations**

Reciprocal transplant gardens were established in 2009 at four sites: Colby, KS (driest site), Hays, KS (dry site), Manhattan, KS (moist site), and Carbondale, IL (wet site) (Fig. 2). These sites experienced an increase in mean annual precipitation (MAP) from 520 mm yr<sup>-1</sup> (driest site) to 1201 mm yr<sup>-1</sup> (wet site; 30-year averages) over 1000 km from west to east across the Great Plains of North America. The sites had previously been in agricultural production and were

prepared by light disking in the Fall of 2008. The full details of the reciprocal transplant gardens and their establishment have been previously described (Galliat et al. 2019; Johnson et al. 2022; Wilson et al. 2016) but are summarized below. A comparison of the results across all the sites from the four reciprocal transplant gardens allowed for a regional-scale comparison.

### **Collection of source populations**

*Andropogon gerardii* seeds were collected in Fall 2008 from remnant prairies within an 80 km radius of the three reciprocal transplant garden sites, i.e., the dry, moist, and wet sites. Seeds of *Sorghastrum nutans* were collected from four remnants near the wet site and one near each of the dry and moist sites. Seeds of 8 nondominant prairie species (Table S1) were purchased from a commercial supplier (Ion Exchange, Inc., Harpers Ferry, IA, USA). Seeds were kept in dry storage before planting. The *A. gerardii* sources represent regional ecotypes (i.e., wet, moist, and dry ecotypes) that we have demonstrated to exhibit genetic, phenotypic, fitness, chemical, and forage quality differences (Caudle et al. 2014; Epstein et al. 1997; Galliat et al. 2020; Gan et al. 2012; Gibson et al. 2016; Olsen et al. 2013). In our experimental gardens (see below), strong phenotypic (Johnson et al. 2015b) and genetic differences were observed between ecotypes of *A. gerardii* in 2010 (Gray et al. 2014), and these differences were maintained in 2016 (Galliat et al. 2019). We are currently analyzing data from 2021. The extent of the ecotypic differences among the *S. nutans* sources is understudied but is expected to be similar to that of *A. gerardii* based upon previous studies (Gustafson et al. 2004; McMillan 1959). In 2021, phenotypic distinctions, including the maximum height, weight, and leaf nitrogen content, were quantified among the functional traits of the ecotypes of *S. nutans* (Ren 2022).

### **Garden design**

Four blocks were established at each site, each with four randomized plots seeded with one of the *A. gerardii* and *S. nutans* regional ecotypes (dry, moist, or wet) and one plot (mix) seeded with a mixture of all three ecotypes, allowing H<sub>1</sub> and H<sub>2</sub> to be addressed (Fig. 1, Fig. S1). The local ecotype and mix plots were 4 m × 8 m, and the nonlocal plots at each site were 4 m × 4 m. All plots at the driest site (Colby, KS) were 4 m × 4 m. Plots were seeded in June 2009 with the regional ecotype of *A. gerardii* at 270 live seeds m<sup>-2</sup> and *S. nutans* at 70 live seeds m<sup>-2</sup> combined with seeds of the other species, for a total of 580 seed m<sup>-2</sup> following the restoration guidelines for the U.S. Great Plains grasslands (Packard and Mutel 2005). The plots were separated by 4–6 m buffer strips seeded with *Bouteloua curtipendula* (Michx.) Torr. and *Schizachyrium scoparium* (Michx.) Nash was purchased from a commercial supplier (Ion Exchange, Inc., Harpers Ferry, IA, USA).

To further address H<sub>2</sub>, rainout shelters were installed at dry, moist, and wet sites in spring 2011 in more than half of all plots except for the mixed plots. The design of the shelters followed Yahdjian and Sala (2002), with 2.00 m × 1.88 m clear acrylic, V-shaped plates 2.00 m long, 0.13 m wide, set 20 cm apart, and angled at a 20° slope. At the Kansas sites, runoff rain was collected in barrels and discarded away from plots. In Illinois, rain ran into a gutter at the lower side and away from the plots. The lowest side was 1.5 m above the ground surface to avoid intercepting the vegetation. The shelters were established in late May–early June each year beginning in 2011 after 25% of the growing days had occurred at each site. The shelters were designed to intercept 50% of the precipitation and reduce precipitation under shelters 34–38%, reducing soil moisture 8, 14, and 25% by 2012 (Wilson et al. 2016) and 14.6, 22.8, and 21.3% over the 2021 season (J. Sytsma, unpublished) at the wet, moist, and dry sites, respectively, corresponding to decreased rainfall across the precipitation gradient.

## **Data collection**

Diversity and productivity data were collected for each plot in 2012 and 2021, three and 12 years after the reciprocal transplant gardens were established, respectively, as succession progressed. Canopy cover was visually estimated by observers for vascular plants rooted in four 1 m<sup>2</sup> quadrats per plot in spring and fall of each year, and the maximum cover value retained for each species per plot was retained for analysis. The data from the quadrats were averaged per plot.

## **Productivity**

Like in previous investigations, including meta-analyses of the HBM (Adler et al. 2011; Al-Mufti et al. 1977; Fraser et al. 2015; Guo and Berry 1998), we estimated peak-growing season aboveground biomass as a proxy for productivity (Sala and Austin 2000). Productivity was determined in 2012 and 2021 as the oven-dry weight of live plant biomass of plants that were rooted in four randomly placed 0.1 m<sup>2</sup> quadrats per plot. The plants were clipped at ground level, placed into bags in the field prior to being oven-dried at 60°C for 48 hours and weighed. Litter (including woody shrub stems) was excluded from the analysis because we were not confident in separating the previous year's litter from the current year's litter and wished to avoid an overestimation of productivity. This decision may have led to more conservative HBM fits, as Fraser et al. (2015) reported a better fit to the HBM when litter was included than when it was excluded.

## **Phylogenetic Diversity**

Following surveys conducted in 2012 and 2021 across all sites, maximum likelihood phylogenies (Fig. S2) were constructed for each survey, including all taxa observed in sample plots. Nucleotide *rbcL* and *matK* sequences were retrieved from GenBank ((Benson et al. 2013);

206 <https://www.ncbi.nlm.nih.gov/genbank/>). Following retrieval, the *rbcL* and *matK* sequences were  
207 individually aligned via muscle alignment (Edgar 2004) in SeaView (Ver. 4 Gouy et al. 2010).  
208 The sequences were trimmed, and the *rbcL* and *matK* sequences were concatenated using  
209 Mesquite (Maddison and Maddison 2021). Phylogeny construction for both 2012 and 2021 was  
210 conducted using the IQTree Web Server (<http://iqtree.cibiv.univie.ac.at/>) to compare multiple  
211 substitution models (Nguyen et al. 2015; Trifinopoulos et al. 2016). Final phylogenetic inference  
212 was conducted based on the best substitution model based on the AIC, AICc, and BIC. Analyses  
213 based upon a single phylogeny for 2012 and 2021 together across all sites revealed qualitatively  
214 similar results (pNRI values (two phylogenies) versus pNRI (single phylogeny), correlation =  
215 0.74,  $p < 2.2e^{-16}$  at  $df = 197$ ; fNRI values (two phylogenies) versus fNRI (single phylogeny),  
216 correlation = 0.89,  $p < 2.2e^{-16}$  at  $df = 197$ ).

## 217 **Functional trait diversity**

218 The functional trait diversity was based upon the values of five continuous functional traits (LA:  
219 leaf area ( $\text{cm}^2$ ), SLA: specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ), HI: maximum vegetative height (cm), LNC: leaf  
220 nitrogen content ( $\text{mg g}^{-1}$ ), and SM: seed mass ( $\text{g } 1000^{-1}$ )) and five categorical functional traits  
221 (growth form [GF], life span (LS; annual biennial or perennial), pollination mode (PM; biotic or  
222 abiotic), seed dispersal vector (SD; biotic or abiotic), and clonal reproduction (CD; yes or no))  
223 per species. These traits were chosen to represent important aspects of plant fitness,  
224 reproduction, resource acquisition, and persistence (Pérez-Harguindeguy et al. 2016). Functional  
225 trait values for each species were obtained from measurements following standard protocols  
226 (Cornelissen et al. 2003) using data from Khalil et al. (2019) and Ren (2022) or downloaded  
227 from the TRY database (Kattge et al. 2020). These data were used to construct a functional trait  
228 data frame with taxa as rows and the different traits in columns (Kembel 2010). Unweighted pair

group method with arithmetic mean (UPGMA) dendrograms (Fig. S3) based on these continuous and categorical functional traits were constructed for each survey independently for all taxa using the FD package in R Software (version 4.1) (Laliberté et al. 2014).

The phylogenetic signal of all functional traits across all plots surveyed in 2012 and 2021 were calculated using Blomberg's K and Pagel's lambda ( $\lambda$ ) statistics in the phytools R package (Revell 2012) for continuous traits and Borge's et al. (2019) delta ( $\delta$ ) for categorical traits (Appendix S2).

## **Data analysis**

### **Calculation of Diversity Indices**

A wide range of diversity indices were considered for investigating diversity-productivity relationships, including attribute diversity, using Hill's family of diversity numbers (Chao et al. 2010; Chao et al. 2014; Hill 1973) and a suite of phylogenetic and functional trait indices (Tucker et al. 2017); details in Appendix S1, Fig. S4. Correlations between diversity indices and productivity were investigated using the corrplot package in R (Wei and Simko 2021). The phylogenetic net relatedness index (pNRI) and functional net relatedness index (fNRI) weighted by species abundance were ultimately selected as measures of phylogenetic (PD) and functional diversity (FD), respectively, for investigating diversity-productivity relationships. The pNRI and fNRI were appropriate because their values were uncorrelated with the taxonomic diversity expressed as species richness (T0), albeit positively correlated with each other ( $r = 0.77$ ) (Fig. S3). Both the pNRI and fNRI are informative measures of PD and FD, respectively (Chai et al. 2016; Lv et al. 2022) as they are measures of divergence in species assemblages (Tucker et al.

2017). The pNRI was calculated using the picante R package (Kembel et al. 2010) as the standardized mean nodal distance among plots:

$$NRI = 1 - (x/x_{max}),$$

where  $x$  is the mean nodal distance across the phylogeny and  $x_{max}$  is the maximum value of  $x$  possible for the taxa in the phylogeny (Webb 2000) weighted by species abundance. The phylogenetic distance matrix used in calculating the pNRI was substituted with a functional trait matrix to calculate the fNRI (Kembel 2010). Negative pNRI and fNRI values indicate overdispersion of taxa (cooccurring taxa less closely related or functionally similar than expected), while positive values represent clustering (cooccurring taxa more closely related or functionally similar than expected) (Cadotte and Davies 2016). We interpret overdispersion as indicating greater divergence than clustering of taxa (Tucker et al. 2017).

### **Analyses based on the HBM of Fraser**

Diversity–productivity relationships were analyzed following Fraser et al. (2015). The effects of productivity ( $\log_{10}$  peak season biomass without litter) on taxonomic diversity (T0), phylogenetic diversity (pNRI), and functional diversity (fNRI) were investigated via separate generalized linear model (GLM) regressions at both the regional scale and within sites.

Following Adler et al. (2004) and Fraser et al. (2015), the effect of productivity on species diversity at the regional scale, within sites and among ecotype sources was investigated using Poisson regression in a GLM framework for count data (i.e., species richness counts: T0). A quasi-Poisson model was used to adjust the standard errors when the dispersion parameter from a Poisson model was significantly different from the assumed value of 1. A Gaussian model in the GLM was used for phylogenetic and functional diversity data (i.e., pNRI and fNRI), as these

were continuous and not count data such as species richness. In these GLMs, tests of each site and within sites included the effect of source (3 ecotypes and mixed sources) and year (2012 and 2021), and their interaction was tested as treatments with block as a random effect. Linear and quadratic terms for biomass were included in the models retaining the latter only if significant based upon analysis of deviance chi-square tests used as models of fit (see below). If the linear term alone was not significant, then the relationship was considered nonsignificant. The significance of the model terms, including interactions, was determined based upon chi-square tests calculated from an analysis of deviance (D) and residual deviance (RD) values that sequentially compared smaller models with the next more complex model as variables were added in each step starting with the linear and quadratic production variables. This Type I ANOVA approach allowed us to assess the improvement in model fit following inclusion of source, year, and their interaction provided by significant diversity–productivity models. Separate models were constructed with either Poisson or quasi-Poisson error terms for T0 as a count variable, although the latter was predominantly retained over the former following two-sided dispersion tests. Models with the pNRI and fNRI as continuous variables were constructed using a Gaussian error distribution. Prior to analysis, a constant number was added to the pNRI and fNRI values, and the values were multiplied by 100 to allow these variables to have nonzero integers appropriate for these regressions.

Regional-scale analyses across sites excluded plots under rainout shelters, as they were not established at the driest site or in the mixed plots. A separate analysis including this treatment followed the procedure outlined above and was restricted to the dry, moist, and wet sites excluding the mixed plots.

Following Fraser et al. (2015), significant unimodal relationships were characterized as concave-down, where diversity peaked at intermediate productivity values, and concave-up, where the highest taxonomic diversity was at the lowest and highest productivity levels (Fig. 1). Concave-down unimodal relationships based upon taxonomic richness (T0) are interpreted as consistent with the HBM. By contrast, phylogenetic (pNRI) and functional (fNRI) diversity values as calculated here have an inverse relationship (smaller values have highest diversity), and concave-up unimodal relationships were considered consistent with the HBM. The fit of the diversity–productivity relationships is reported as the amount of deviance accounted for by the models (DE: D-squared with values of 1 indicating perfect fit). The DE values are equivalent to the coefficient of determination (model  $R^2$ ) values reported for linear regression models and interpreted in the same way (Guisan and Zimmermann 2000). In our models, we observed DE values to be either the same as Nagelkerke’s  $R^2$  values or slightly lower; hence, we observed a more conservative estimate of model fit. The predict() function in R was used to predict diversity values to generate diversity–productivity plots for presentation using the saved significant GLM models (quasi-Poisson site, within-site, ecotype source, or rainout shelter regressions).

Diversity-productivity analyses were conducted using the AER, ggplot2, MASS, modEvA, quantreg, Pastecs, and performance packages in R Software (R Core Team 2021), adapting the R code provided in Fraser et al. (2015) and Adler et al. (2011). Independence and a lack of autocorrelation among residuals were tested using the Durbin–Watson test, multicollinearity of model terms was checked by calculation and inspection of the variance inflation factor, and constant error variance (homoscedasticity) for Gaussian models was checked using the Breusch–Pagan test with the Performance R package (Lüdecke et al. 2021). Heteroscedasticity of the phylogenetic diversity values according to the Breusch–Pagan test ( $p < 0.05$ ) was rectified by a

Box–Cox transformation values using the caret R package (Kuhn 2008). The presence of outliers was checked through calculation of Cook’s distance (a measure of influence) (Adler 2004).

## **Results**

Species richness (T0) ranged from 2 to 27 species m<sup>-2</sup> (mean = 8.65, SE ± 0.44), with productivity (live biomass without litter) ranging from 6.6 to 2,091.8 g dw m<sup>-2</sup> (mean = 619.1, SE ± 31.1) across all sites, treatments, and years. The phylogenetic diversity (pNRI) ranged from -2.04 to 3.06 (mean = 0.29, SE ± 0.09), and the functional trait diversity (fNRI) ranged from -0.52 to 3.85 (mean = 1.04, SE ± 0.09).

Seven of the 10 functional traits (three continuous traits and four categorical traits) exhibited a phylogenetic relationship in 2012 compared with 4 in 2021 (one continuous trait and three categorical traits) (Table S2). Among these traits, growth form, and pollination mode exhibited phylogenetic significance in both 2012 and 2021.

## **Regional-scale analyses**

At the regional scale across all sites, there was no relationship between diversity, measured as species richness (T0), phylogenetic diversity (pNRI) or functional diversity (fNRI), and productivity across all sites (Fig. 3). Neither log biomass nor log biomass<sup>2</sup> had a significant effect on the slope of the model when predicting diversity across all sites ( $P > 0.05$ ). Nevertheless, there was a large increase in the variation in these measures of diversity with increasing productivity. For example, the species richness ranged from 5-10 species m<sup>-2</sup> in plots with the lowest productivity to 1-27 species m<sup>-2</sup> in plots with the highest productivity (Fig. 3a).

## **Site effects**

339 Diversity-productivity relationships for species richness were evident at the four sites (Fig. 3a).  
340 At this scale, a concave-down unimodal relationship consistent with the HBM was observed at  
341 the driest and wet sites (deviance explained,  $DE = 0.68$  and  $0.91$ , respectively). There was a  
342 concave-down but nonunimodal relationship at the dry site ( $DE = 0.69$ ), whereas a concave-up  
343 relationship occurred at the moist site ( $DE = 0.85$ ), where multicollinearity between the live  
344 biomass and live biomass quadratic model terms was observed (i.e., high variance inflation  
345 factors  $> 10$ ), suggesting some redundancy in the inclusion of both terms in this model. Source  
346 effects were significant either as a main effect at the wet site (Deviance,  $D = 10.62$ ; Residual  
347 Deviance,  $RD = 100.31$ ,  $df = 3, 26$ ,  $P = 0.0004$ ) or as an interaction with year at the moist site ( $D$   
348  $= 1.91$ ,  $RD = 4.06$ ,  $df = 3, 19$ ,  $P = 0.03$ ). At the wet site, only the wet source exhibited a  
349 significant unimodal concave-down relationship between species richness and productivity ( $DE$   
350  $= 0.99$ ) (Fig. 4a); the linear biomass term was excluded from the model (to avoid autocorrelation  
351 of residuals between linear and quadratic biomass variables), and the quadratic biomass  
352 coefficient was marginally significant ( $D = 3.79$ ,  $RD = 25.08$ ,  $df = 1, 6$ ,  $P < 0.001$ ). Models for  
353 dry and moist sources were unimodal and concave down, but included autocorrelated residuals;  
354 moreover, the corresponding plots (Fig. 4a) were not interpreted. The model of the mixed source  
355 did not include a significant biomass coefficient ( $P > 0.05$ ). At the moist site, there were too few  
356 cases to allow analysis of the source-by-year interaction ( $n = 16$ , 4 per source). However,  
357 analysis of the source effect at the moist site revealed unimodal concave-down relationships  
358 between diversity and productivity for the moist, mixed, and wet sources ( $DE = 0.85$ ,  $0.92$ , and  
359  $0.99$ , respectively; no relationship was shown for the dry source; Fig. 4b), although  
360 autocorrelation of residuals was detected for the wet source even after excluding the linear  
361 biomass variable. The year effect contributing to the source-by-year effect at the moist site was

significant in the moist, mixed, and wet source models (Moist source  $D = 6.01$ ,  $RD = 1.94$ ,  $df = 1,5$ ,  $P = 0.005$ ; Mixed source,  $D = 1.27$ ,  $RD = 0.50$ ,  $df = 1,5$ ,  $P < 0.001$ ; Wet source,  $D = 7.40$ ,  $RD = 1.00$ ,  $df = 1,5$ ,  $P < 0.001$ ). Source effects did not significantly affect the diversity-productivity relationship at the driest or dry sites ( $P > 0.05$ ).

The unimodal concave-up relationships were consistent with the HBM for phylogenetic diversity at the driest, dry, and moist sites ( $DE = 0.90$ ,  $0.76$ , and  $0.63$ , respectively) (Fig. 3b), and for functional diversity at the driest site ( $DE = 0.89$ , Fig. 3c). At these sites, there was a source-by-year interaction effect on phylogenetic diversity at the driest ( $D = 0.70$ ,  $RD = 1.31$ ,  $df = 19$ ,  $P = 0.02$ ), dry ( $D = 6.15$ ,  $RD = 5.31$ ,  $df = 3,19$ ,  $P < 0.0001$ ), and moist ( $D = 4.59$ ,  $RD = 9.08$ ,  $df = 3,19$ ,  $P = 0.02$ ) sites, but no effect of source at the wet site ( $P > 0.05$ ). There was a unimodal concave-up relationship consistent with the HBM between functional diversity and productivity at only the driest site ( $DE = 0.88$ ; Fig. 3c). At this site, there was an effect of source on functional diversity ( $D = 30,456$ ,  $RD = 280,470$ ,  $df = 3,26$ ,  $P = 0.03$ ). At the moist site, there was a unimodal concave-down relationship ( $DE = 0.59$ ) with a significant source effect ( $D = 75558$ ,  $RD = 174317$ ,  $df = 3,26$ ,  $P = 0.003$ ), but the biomass coefficients in this model were not significant ( $P > 0.05$ ).

Within the driest site, phylogenetic diversity exhibited a unimodal concave-up relationship with productivity for wet, dry, and mixed sources ( $DE = 0.87$ ,  $0.98$ , and  $0.92$ , respectively), and a unimodal concave-down downward relationship was shown for the moist source ( $DE = 0.99$ ) (Fig. 4c) (there were too few cases to allow model fitting of the source by time interaction). Within the moist site, phylogenetic diversity exhibited a relationship with productivity only for the mixed source, and this relationship was unimodal and concave-down, which was not

consistent with that of the HBM ( $DE = 0.89$ ) (Fig. 4d). Models for the dry, moist, and wet sources were not significant at this site ( $P > 0.05$ ).

Within the driest site, a significant unimodal concave-up relationship between functional diversity and productivity occurred for only the dry and mixed sources ( $DE = 0.98$  and  $0.97$ , respectively) in models with only the quadratic biomass term (the linear term was dropped to avoid autocorrelation issues) (Fig. 4e). The moist source exhibited a concave-down unimodal response ( $DE = 0.88$ ), and the relationship with the wet source was nonsignificant.

### **Effects of rainout shelters**

At the three sites where rainout shelters were installed (dry, moist, and wet), there was a unimodal concave-down relationship between  $T_0$  and productivity at the wet and dry sites ( $DE = 0.88$  and  $0.70$ , respectively), while a unimodal concave-up relationship occurred at the moist site ( $DE = 0.86$ ) (Fig. 5a). Within sites, the rainout treatment contributed to the models only through interactions between year and rainout treatment at the moist site (year \* treatment  $D = 2.10$ ,  $RD = 9.63$ ,  $df = 1,33$ ,  $P = 0.008$ ) and to a marginal effect at the wet site (year \* treatment  $D = 2.03$ ,  $RD = 20.37$ ,  $df = 1,33$ ,  $P = 0.07$ ). At the moist site, this interaction exhibited a unimodal concave-down relationship in the ambient plots in 2012 ( $DE = 0.99$ ; Fig. 5b) and a concave-down relationship without a modal value within the range of productivity values in 2021 ( $DE = 0.83$ ; Fig. 5c). Both models included a significant ecotype source effect in 2012 and a marginal effect in 2021 (2012:  $D = 0.48$ ,  $RD = 2.37$ ,  $df = 2,7$ ,  $P < 0.0001$ ; 2021:  $D = 1.01$ ,  $RD = 1.81$ ,  $df = 2,7$ ,  $P = 0.07$ ). There was no productivity-diversity relationship in the rainout plots at the moist site ( $P > 0.05$ ). At the wet site, the year-by-treatment interaction showed a unimodal, concave-down relationship in the rainout plots in 2012 ( $DE = 0.86$ , Fig. 5d) and a concave-up relationship in the ambient plots ( $DE = 0.84$ ). The ecotype source effect was marginal in the ambient plots at

the wet site in 2012 ( $D = 1.85$ ,  $RD = 4.37$ ,  $df = 2,7$ ,  $P = 0.08$ ) but not significant in the rainout plots. There was no significant difference in diversity-productivity relationships or effect of the rainout shelter treatment at the wet site in 2021 ( $P > 0.05$ ).

The rainout shelter treatments had no effect on the diversity-productivity relationships according to the phylogenetic (pNRI) or functional (fNRI) diversity at each site (data not shown); i.e., when the rainout shelter treatment was included in the GLMs from the dry, moist, and wet sites, the linear and quadratic biomass coefficients were not significant ( $P > 0.05$ ), except for the linear biomass coefficient for phylogenetic diversity at the wet site (pNRI:  $D = 1.08$ ,  $RD = 9.89$ ,  $df = 1,46$ ,  $P = 0.02$ ). According to this model, the rainout shelter treatment effect was not significant either as a main effect or in combination with year or source ( $P > 0.05$ ).

#### **Summary of diversity-productivity relationships**

A significant diversity-productivity relationship was observed in 95% of the cases tested involving taxonomic diversity but in only 42% and 33% of the cases involving phylogenetic and functional diversity, respectively (Table 1).

Among the attributes of diversity, unimodal models (both concave-up or concave-down) were most frequently observed based on taxonomic diversity (73% of the cases tested) and least common for phylogenetic and functional diversity (37 and 27%, respectively). Among all the indices of diversity, a diversity-productivity relationship consistent with a concave-down unimodal HBM model was observed in 57% of the taxonomic diversity tests, a concave-up unimodal HBM model was observed in 26% of the phylogenetic diversity tests, and 13% of the functional diversity tests that were conducted (Table 1).

## Discussion

### General diversity-productivity patterns fit the HBM

The high frequency of fits of the HBM in our study (i.e., concave-down unimodal fits for taxonomic species richness and concave-up unimodal fits for phylogenetic and functional trait diversity) support its value as a null model for diversity–productivity relationships. There was a significant diversity-productivity relationship in our reciprocal transplant gardens in 95% of tests based upon taxonomic diversity, 57% of which exhibited humped-back models (HBMs; i.e., concave-down unimodal diversity-productivity curves). This frequency of HBMs was less than the 68% reported by Fraser et al. (2015) across 28 sites. The occurrence of HBM fits based on phylogenetic and functional diversity was lower than that based upon taxonomic diversity. Nevertheless, the lower frequency of these measures of diversity consistent with the HBM than with taxonomic diversity suggests that the mechanisms governing diversity–productivity relationships include multiple evolutionary and trait relationships (Cadotte et al. 2019); we discuss these below.

The occurrence of diversity-productivity relationships consistent with the HBM may indicate a shift in the response of species from stress tolerance to competitive dominance along the productivity gradient. Under these conditions, a peak in diversity occurs at a midpoint along the productivity gradient (Al-Mufti et al. 1977; Fraser et al. 2015; Grime 1973). However, in our study, we observed the HBM to be context dependent (Catford et al. 2022) and to be most common in reciprocal gardens at extremes of the precipitation gradient, i.e., the driest and wet sites for taxonomic diversity, only at the driest site for functional diversity, but at all but at the wet site for phylogenetic diversity. Concurrence with the HBM for taxonomic diversity at the

most extreme sites suggested that the interplay of abiotic (moisture stress) and biotic (competition from dominants) factors most clearly occurred at these very dry and very wet sites (Brose and Tielbörger 2005). These findings suggest that the mechanisms that drive the HBM related to competitive exclusion and stress limitation (Al-Mufti et al. 1977; Grime 1973) are most important at the ends of environmental gradients. Practitioners restoring grasslands in extreme habitats would benefit from designing seed mixes while taking the implications of the HBM into account. For example, the unimodal envelope described by the HBM represents an upper boundary on diversity constrained by productivity that needs to be recognized when considering seed additions in restorations (Foster et al. 2007; Pierce 2014).

We show elsewhere (Galliat et al. 2020) that the local ecotypes are adapted to their home site where they show their best performance compared with when grown at other sites. The moist ecotype is a generalist compared to the other ecotypes, does comparatively well across the precipitation gradient and, as we show here, exhibits an HBM relationship at its home site. The biomass of plants in the plots seeded with the moist ecotype at the driest site was greater than that in the other plots, but the biomass of *A. gerardii* in these plots was less than its biomass in the dry ecotype plots (Sytsma, unpublished), consistent with the home-site advantage hypothesis.

Within sites, we hypothesized (Fig. 1;  $H_1$ ) that a home-site advantage (sensu Montalvo and Ellstrand 2000) of local ecotype sources causes competitive exclusion of species at the high end of the productivity gradient, leading to agreement with the HBM by the local ecotype when sown at its local site. This hypothesis was supported for the wet and moist ecotypes at their respective home sites. At these sites, the local ecotype is well adapted, produces high biomass, and drives down local species richness (Wilson et al. 2016), as also found in related studies of local adaptation, e.g., Joshi et al. (2001). In addition, the results for the mixed plots sown with equal

amounts of each ecotype were consistent with those for the HBM in the moist site. Genetic analyses indicate that the mix plots are dominated by the dry ecotype at the driest and dry sites, a mix of ecotypes at the moist site, and the wet ecotype at the wet site (Galliat et al. 2019).

Deviations from the HBM null model were likely related to nonlocal ecotypes at nonlocal sites being maladapted and not competitive enough to drive down the diversity of subordinate species, especially at sites at intermediate points along the precipitation gradient, i.e., dry and moist sites. The degree to which community dominants are locally adapted affects the strength of interspecific interactions and thereby local diversity (Germain et al. 2022). The lack of agreement between the local ecotype and the HBM at the dry site showed that the home-site advantage effect on the diversity of the surrounding community was not expressed across the precipitation gradient. At the most xeric end of the gradient, it may be that even the local ecotypes are not well adapted; indeed, the driest site was established west of the native range of *Andropogon gerardii*, the dominant species, which formed the focus of our study. At these xeric sites, the productivity gradient may not be long enough to allow the full range of stress–response and competitive dominance interactions to be expressed (Mount et al. 2023). At the western end of the gradient in the Great Plains grasslands, species diversity is lower than that at sites further to the east (Ren et al. 2023; Wilson et al. 2016), and the regional species pool may be too limited to allow sufficient species colonization for the HBM to be expressed among local ecotype sources of the dominant taxa (Foster et al. 2004; Pierce 2014; Zobel 2016).

In support of our second hypothesis (Figs. 1, 3; H<sub>2</sub> a shift of the HBM curve to the left with decreased precipitation), we observed lower productivity and taxonomic diversity consistent with the HBM at the driest site than at the wet site. These relationships occurred irrespective of the ecotype source at the wet site, suggesting the generality of this response of *A. gerardii* and *S.*

*nutans* as dominant species to subordinate species, consistent with mass ratio effects in grasslands (Grime 1998; Smith et al. 2020) and observations that diversity-productivity relationships vary with resource availability (Palpurina et al. 2019; Wang et al. 2022). These relationships were less clear under the experimental reduction in precipitation provided by the rainout shelters and limited to the earliest surveys of taxonomic richness (i.e., 2012 compared with 2021) at the moist and wet sites, consistent with other effects of this manipulation on our system (Ren et al. 2023); see below.

### **Insights from phylogenetic and functional diversity**

Our analyses are among the first to consider phylogenetic and functional diversity as useful metrics for investigating diversity-productivity relationships and the HBM. To the best of our knowledge, diversity-productivity relationships have not been investigated in terms of phylogenetic or functional trait diversity. HBM fits (i.e., concave-up unimodal fits for phylogenetic and functional trait diversity) were less frequent, but when they occurred, they were similar to taxonomic diversity HBM patterns and indicated a congruent role of evolutionary and niche relationships in diversity-productivity relationships (Cadotte et al. 2019). Indeed, in support of our third hypothesis (H<sub>3</sub> concurrence of taxonomic, phylogenetic, and functional trait diversity indices), concave-up unimodal fits of phylogenetic diversity and functional trait diversity coincided with taxonomic HBMs at the dry and driest sites, suggesting the establishment of evolutionarily and functionally similar species at these points along the productivity gradient.

Previous studies have shown that taxonomic, phylogenetic, and functional trait diversity peaks do not necessarily coincide along gradients (Brun et al. 2019; Erdős et al. 2022), including

in grasslands (Venail et al. 2015). Rather, an alternate hypothesis proposes that niche complementarity among species may allow phylogenetic and functional diversity to increase with productivity rather than exhibiting a unimodal relationship consistent with the HBM shown for taxonomic diversity (Brun et al. 2019). In our study, phylogenetic and functional trait diversity did not consistently increase with productivity, as reported by Brun et al. (2019). We purposely chose phylogenetic and functional trait diversity metrics (pNRI and fNRI, respectively) that were uncorrelated with taxonomic richness precisely to provide the opportunity to obtain additional insights.

Phylogenetic diversity provides an additional mechanistic understanding not necessarily revealed by taxonomic diversity (expressed as richness) in grasslands (Barber et al. 2016; Forrestel et al. 2014; Khalil et al. 2017), including in our system (Ren et al. 2023). We found similar diversity-productivity relationships between the phylogenetic and taxonomic diversity of the HBMs only at the driest end of the precipitation gradient. This precipitation limitation suggests that the evolutionary relevance of the diversity-productivity HBM relationship was limited by the conditions under which annual productivity was constrained and the regional species pool was low. Community assembly processes associated with productivity limitations and the availability of species, especially the establishment and abundance of dominant grasses, thus drove phylogenetic diversity in our grassland restorations (Jones et al. 2019). The dominant grasses, especially *Andropogon gerardii* and *Sorghastrum nutans*, had the highest biomass at the wet end of the precipitation gradient where an HBM for phylogenetic diversity was not observed. In contrast, the biomass of these grasses was lower than that of other taxa at drier sites, and HBM was evident. In summary, phylogenetic diversity was a useful metric indicating the importance of evolutionary relationships among taxa in productivity-diversity relationships.

In contrast to phylogenetic and taxonomic diversity, functional trait diversity had few HBM fits, suggesting that the 10 aboveground functional traits we tested did not drive diversity-productivity relationships in the manner predicted by the HBM. However, in one instance, functional trait diversity was consistent with that of the HBM, and this was at the driest site mirroring the results for taxonomic and phylogenetic diversity and, in this case, was related to the dry ecotype source. At the driest site, the aboveground functional traits we included in the functional trait diversity represent the saturation of functional trait space, which moderates the colonization of species across the productivity gradient (Galland et al. 2019). The inclusion of belowground functional traits, including root and rhizome traits, may be an important predictor of aboveground productivity (Klumpp and Soussana 2009) and may have contributed more to humped back diversity-productivity relationships if species interactions were predominantly belowground and at more mesic sites across the gradient represented by our transplant gardens. Nevertheless, belowground functional traits are infrequently studied in grasslands, and future studies are needed to understand their potential role in driving diversity-productivity relationships. In summary, functional trait diversity provided limited additional information for understanding diversity-productivity relationships across the precipitation gradient represented by our sites, despite the occurrence of a phylogenetic signal for traits associated with light competition and interspecific trait variation (specific leaf area and height), nutrient acquisition (leaf nitrogen) in 2012 (Gruntman et al. 2017; Loomis 1997), and traits associated with life history (Growth Form and Pollination mode) and climate (seed mass and seed dispersal) in 2021 (Zheng et al. 2017).

#### **Few effects of experimental rainout shelters**

An experimental reduction in soil moisture under rainout shelters to simulate climate-change projections for the Great Plains (Lant et al. 2016; Schoof and Robeson 2016) led to a loss of the HBM diversity-productivity relationship in terms of taxonomic richness compared with ambient plots at the moist site in 2012 and 2021 and wet site in 2012. At the moist site, rainfall reduction led to the loss of a HBM relationship between taxonomic richness and productivity (Fig. 5b, c). At this site, more so than at the other sites, the interspecific dominance of the general-purpose moist ecotype may be most susceptible to drought. By contrast, this response to imposed drought was reversed at the wet site (Fig. 5d) unrelated to ecotype source. No other rainout shelter treatment effects on diversity-productivity relationships were observed. This lack of an effect of reduced precipitation on aboveground productivity compared with a precipitation addition response (which we did not test) has been reported in a meta-analysis synthesis of grassland experiments (Wilcox et al. 2017). Taken together, our results suggest that the lower evenness among species observed at drier sites in response to reduced soil moisture early in our experiment (Wilson et al. 2016) was not maintained (Ren et al. 2023) and did not contribute to changes in diversity-productivity relationships. This result suggested that changes in assembly rules did not occur in response to experimental reductions in precipitation (except at wet and moist sites), suggesting potential ecological resistance or resilience to climate change under arid conditions (Ratajczak and Ladwig 2019). Nevertheless, management of grassland remnants or restoration may consider strategies such as assisted migration of the dry ecotype to the current moist and wet sites to be useful strategies to consider if climate change projections are realized (Bucharova 2017).

## **Conclusions**

Our experiment demonstrated the relative importance of local and regional processes affecting the role of ecotypes of dominant species in controlling the diversity of subordinate species (Ricklefs 1987). Like in many ecological phenomena, the expression of the HBM is mechanistically context dependent (sensu Catford et al. 2022) based upon local conditions and, as we show, the ecotype source of dominant species. The appreciation of the contextual dependency of ecological phenomena, including diversity-productivity relationships (Mori et al. 2021) and the effects of species interactions (Chamberlain et al. 2014), has particular relevance for selecting sources for restorations and needs to be incorporated into management decisions (Baer et al. 2019; Klopff et al. 2014) in light of ongoing climate change effects in grasslands (Gibson and Newman 2019).

**Supplementary Information** The online version contains supplementary material available at TBD

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**Availability of data and materials** The dataset used and analyzed during the current study will be placed in a public archive upon acceptance of the manuscript.

**Code availability** The code used during the analysis was adapted from code published by Adler et al. (2011) and Fraser et al. (2015) and is available from the corresponding author upon reasonable request.

## Declarations

**Conflicts of interest** The authors declare no conflicts of interest.

**Ethics approval** This article does not contain any studies with human participants or animals performed by the authors.

**Consent to participate** Not applicable

**Consent for publication** Not applicable

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927 of Vegetation Science 27:8-18. doi: <https://doi.org/10.1111/jvs.12333>  
928

929 **Table 1** Number of concave-down and concave-up diversity-production relationships found to be consistent with a unimodal, humped-  
930 back model (HBM) for tests at four common gardens with four ecotype sources in 2012 and 2021. ‘Other’ includes significant positive  
931 and negative linear or quadratic relationships that were not concave-down or concave-up. Diversity was calculated as taxonomic  
932 species richness, phylogenetic diversity, and functional diversity (see Appendix S1 for details). %HBM refers to the percentage of  
933 significant models that fit either concave-down for taxonomic diversity or concave-up for phylogenetic and functional diversity,  
934 consistent with expectations of the HBM.

935

| Diversity                 | Taxonomic (% HBM) | Phylogenetic (%) | Functional (%) |
|---------------------------|-------------------|------------------|----------------|
| Concave-down              | 11 (57)           | 2                | 2              |
| Concave-up                | 3                 | 5 (26)           | 2 (13)         |
| Other positive            | 0                 | 1                | 1              |
| Other negative            | 4                 | 0                | 0              |
| Not-significant           | 9                 | 27               | 30             |
| Total tested <sup>1</sup> | 19                | 19               | 15             |

936

937 <sup>1</sup>. The total tested depended upon the hierarchical testing procedure used; i.e., within-site tests were only carried out when a significant  
938 ecotype source effect was observed in regional tests across all sites.

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940

## Figures

**Fig. 1.** Schematic diagram showing the effects of ( $H_1$ ) locally adapted ecotypes and ( $H_2$ ) increased aridity on the humped back model unimodal relationship between productivity and diversity. The null model is the solid line, and the proposed changes in response to locally adapted ecotypes and increased aridity are shown by comparison to the null model by the dashed and dotted yellow, red, and blue lines.  $H_1$  was tested by comparisons among ecotypes within sites and regionally across sites (dot-dashed yellow line) and predicts an increase in diversity with a decrease in productivity.  $H_2$  was tested across the precipitation gradient regionally among sites (dotted red line) and experimentally using rain-out shelters within sites (dashed light blue line), predicting a decrease in diversity and productivity.  $H_3$  concurrence among taxonomic, phylogenetic, and functional diversity indices is shown by the dashed and dotted lines depicting departure from the null model (solid dark blue line) for  $H_1$  and  $H_2$  (i.e., taxonomic, phylogenetic, and functional diversity lines, if shown, would overlap).

**Fig. 2.** Map showing the locations of reciprocal garden sites and seed collection sites across the US Great Plains. Modified from Galliart et al. (2019).

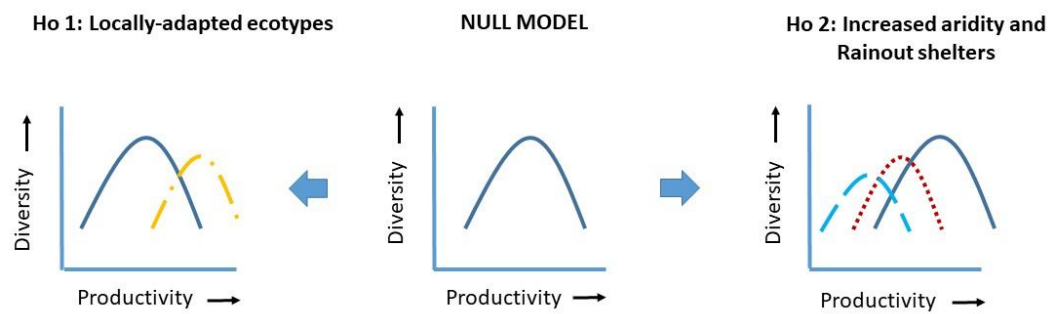
**Fig. 3.** Model fits testing the regional-scale site effects of production (live biomass) over all years on (a) taxonomic diversity (T0), (b) phylogenetic diversity (BoxCox-transformed pNRI), and (c) functional diversity (fNRI) at transplant garden sites (driest, dry, moist, wet). Nonsignificant model fits are not shown.

**Fig. 4.** Model fits testing the effect of production (live biomass) by ecotype (dry, moist, wet, or mixed sources) within sites overall years: (a-b) diversity measured by species richness, T0; (c-d) phylogenetic diversity (pNRI); and (e) functional diversity (fNRI). Nonsignificant relationships

between production and diversity within sites are not shown (i.e., TO at the driest and dry sites; pNRI at the dry and wet sites; and fNRI at the dry, moist, and wet sites).

**Fig. 5.** Effect of rainout shelter treatment on species richness (TO) diversity-production relationships (a) across 3 sites in which rainout shelters were installed, (b, c) in ambient plots at the moist site in 2012 and 2021, and (d) at the wet site in 2012. Nonsignificant rainout shelter treatment effects on diversity-production relationships are not shown. Rainout shelter treatment had no effect on phylogenetic diversity or functional diversity-productivity relationships.

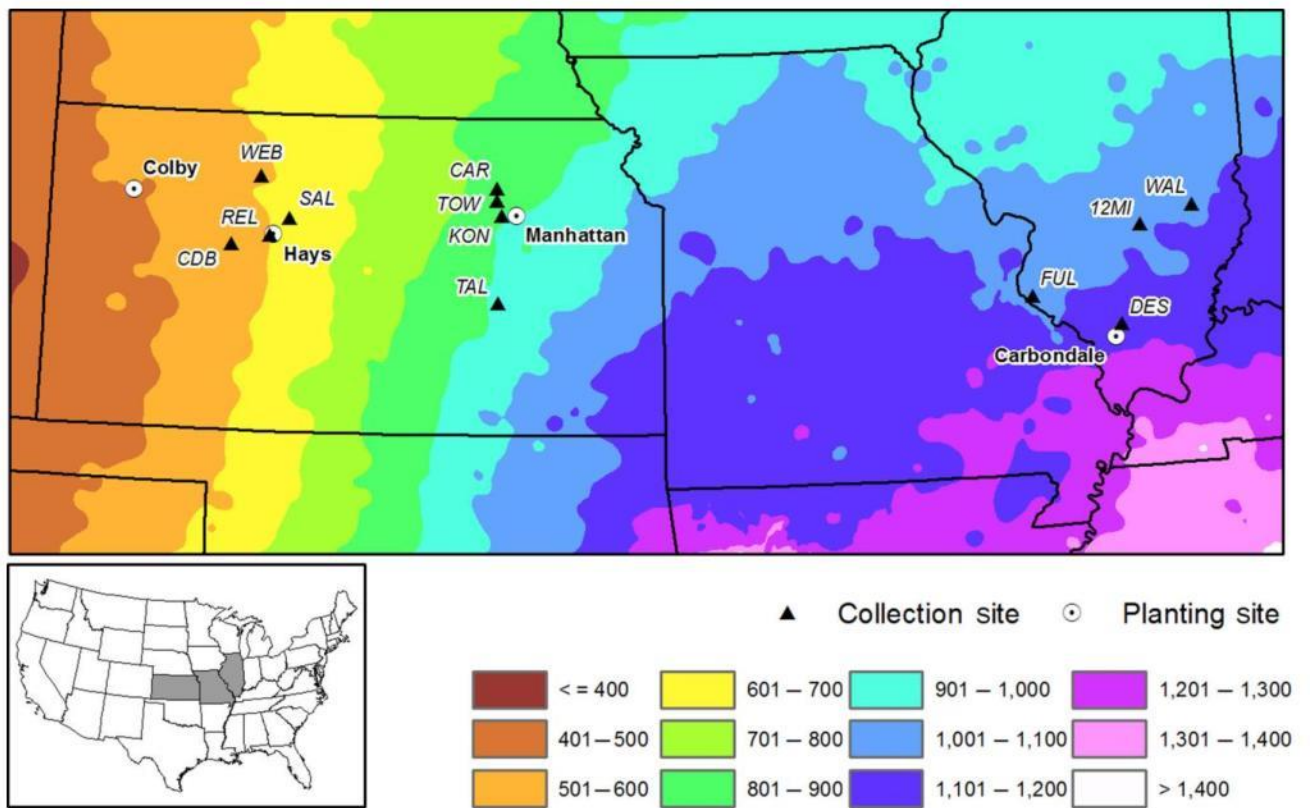
972 **Fig. 1**



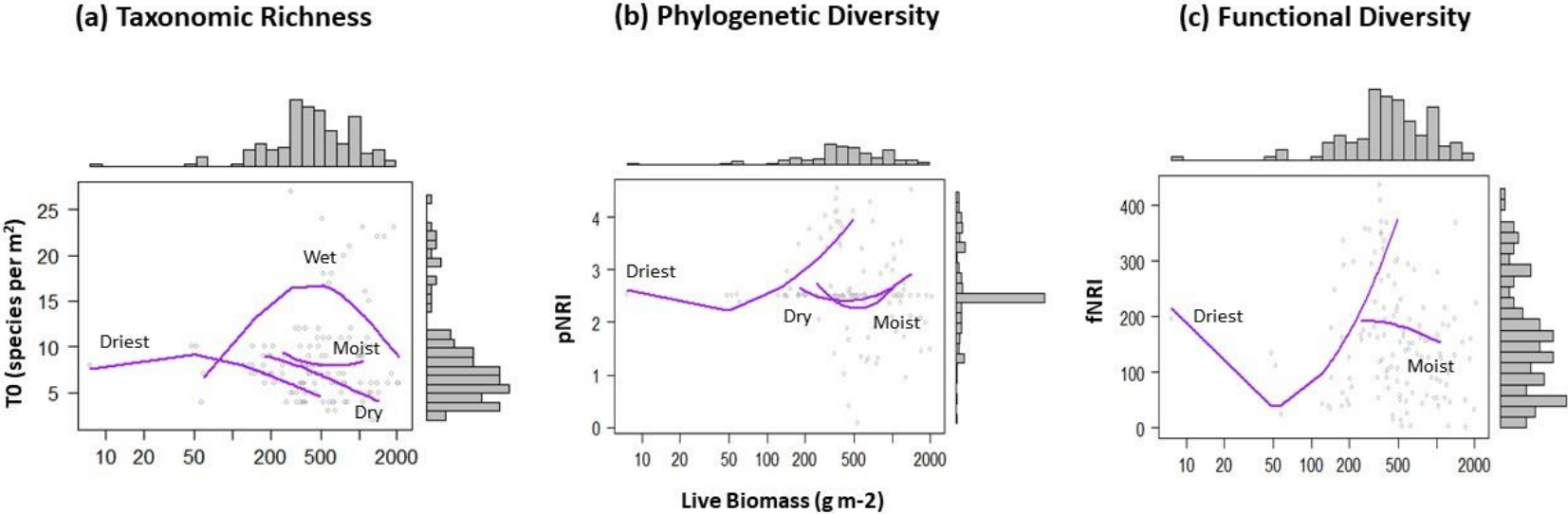
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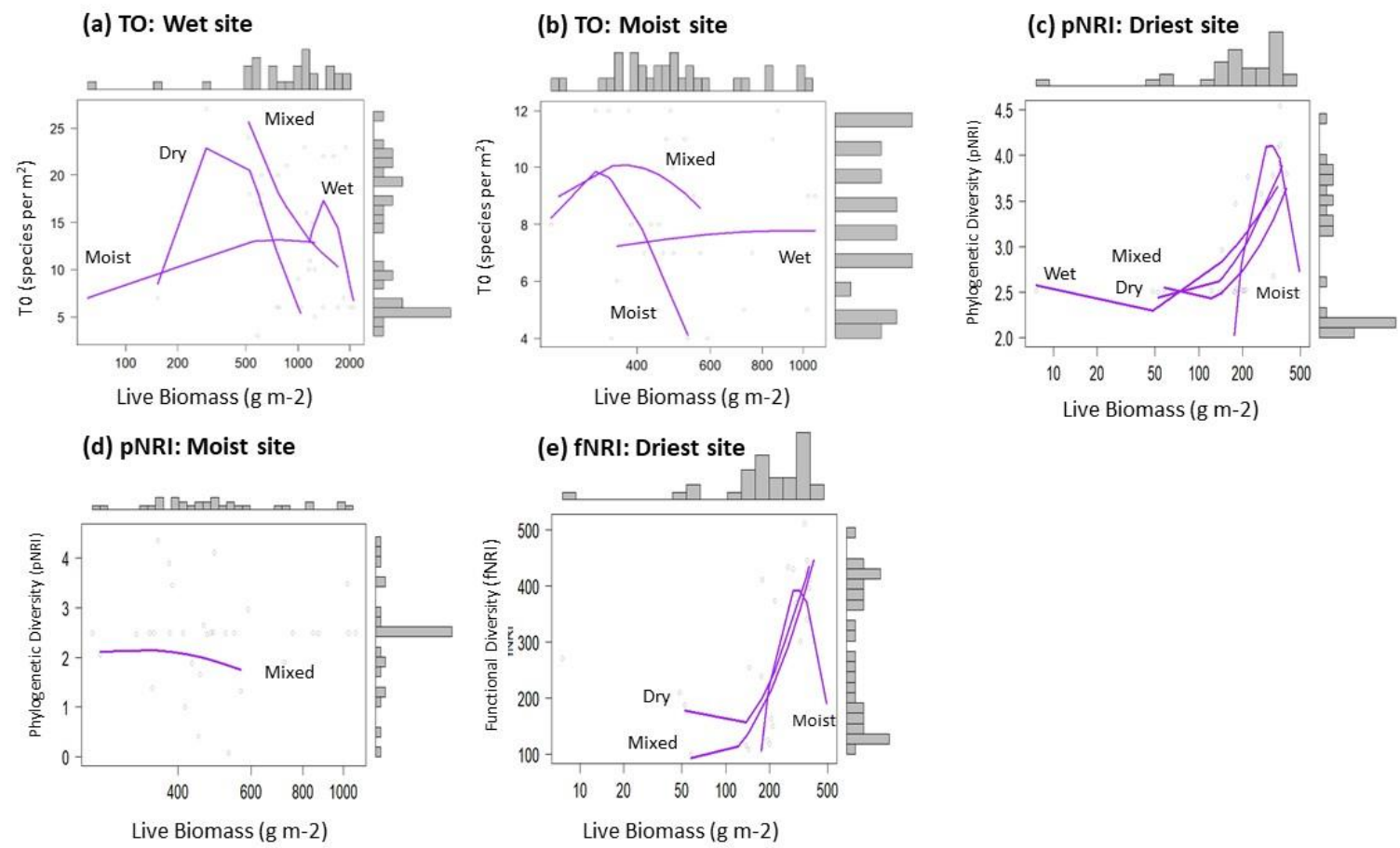
975 **Fig. 2.**



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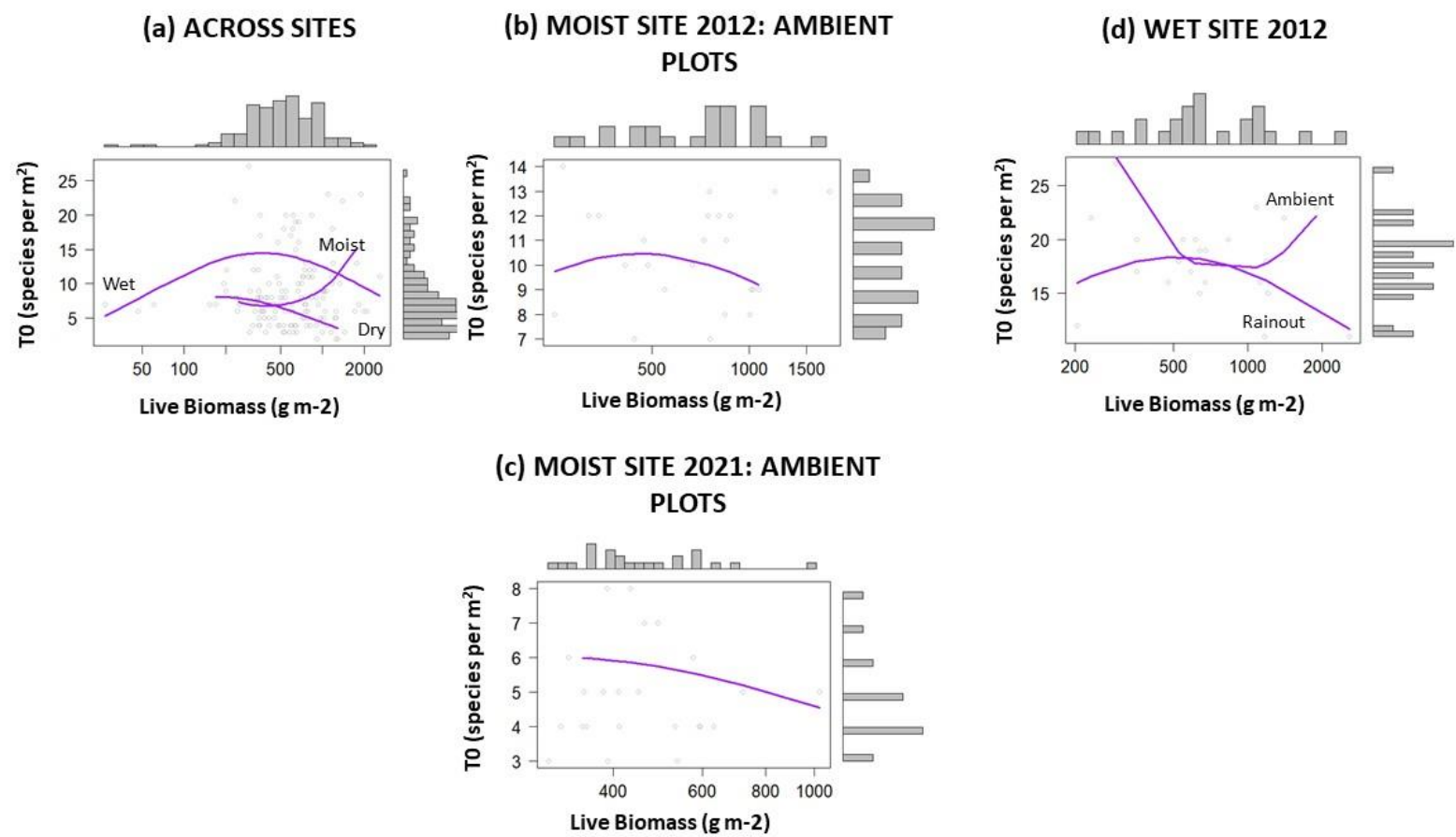
979 **Fig. 4.**



980

981

982 **Fig. 5.**



983

## Supplementary Files

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