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Research

Diversity patterns from sequentially restored grasslands support the 'environmental heterogeneity hypothesis'

Drew A. Scott and Sara G. Baer

D. A. Scott (https://orcid.org/0000-0003-0361-9522) ✉ (dascott@siu.edu) and S. G. Baer, Dept of Plant Biology and Center for Ecology, Southern Illinois Univ., 1125 Lincoln Drive, Mailcode 6509 Carbondale, Carbondale, IL 62901, USA.

The 'environmental heterogeneity hypothesis' (EHH) has been proposed as a mechanism that enables species coexistence through resource partitioning. In accordance with this hypothesis, plant diversity is predicted to increase with variability in resources, but there has been weak support for this hypothesis from experimental studies. The objectives of this research were to 1) characterize how resource availability and heterogeneity (coefficient of variation) change as plant communities develop using sequentially restored grasslands, 2) determine if resource heterogeneity relates to plant diversity (effective number of species, richness and evenness) and 3) reveal if the strength of resource heterogeneity–diversity relationships is different among levels of resource availability. We quantified means and coefficients of variation in soil nitrate and light availability in grasslands established on former agricultural lands for different times and their relationship to plant diversity using a geostatistically-informed design. Nitrate availability decreased exponentially with restoration age, but no directional change in nitrate heterogeneity across the chronosequence occurred due to high resource variability in some restorations. Light availability also decreased exponentially across the chronosequence, but there was no directional change in light heterogeneity. Nitrate heterogeneity was positively correlated with both plant richness and plant effective number of species at high levels of nitrate availability. However, no nitrate heterogeneity correlation was detected at low levels of nitrate availability. Light heterogeneity was positively correlated with plant effective number of species at low levels of light availability. However, no light heterogeneity correlation was detected at high levels of light availability. Plant evenness was not correlated with resource heterogeneity at any resource availability level. These results support the positive heterogeneity–diversity relationship predicted by EHH, and uniquely that this relationship develops within a decade of plant community development, but can be obscured by resource availability.

Keywords: nitrate, photosynthetically active radiation, plant community structure, plant species richness, tallgrass prairie

Introduction

The 'environmental heterogeneity hypothesis' (EHH) hypothesizes that variation in resources promotes species coexistence (MacArthur 1965, 1966, Pianka 1966, Murdoch et al. 1972). The hypothesis, developed from the relationship between structural heterogeneity of plants affecting animal diversity, was first applied to plant communities by correlating openness gradients in tropical and temperate forests with changes in the variability in light and soil nutrients (Ricklefs 1977). Mechanisms underlying the opportunity for species to exploit resource heterogeneity include local communities connected by dispersal (metacommunities; Leibold et al. 2004), differential response of competing species under varying levels of resource availability (spatial storage; Chesson 2000), and varying coexistence outcomes determined by minimum resource requirements and resource use rates under varying resource supply in space (resource ratio hypothesis; Tilman 1982). For example, highly connected metacommunites lead to homogenization of communities and lower local diversity (Shippers et al. 2015), neighborhood competition experiments and models that incorporate environment-competition covariance show spatial storage results in higher regional diversity (Chesson 1985), and community evenness increases with decreasing total resource supply in mixed communities (Gamfeldt and Hillenbrand 2011).

Support for the hypothesis in grasslands has come from observational studies (reviewed by Huston 1979, Bakker et al. 2003) and theoretical modeling (Golubbski et al. 2008), but only weak effects have been detected in experimental manipulations (Eilts et al. 2011, Baer et al. 2016). Limited support for the EHH in experimental manipulations (reviewed by Lundholm 2009) has been attributed to lack of considering propagule limitations and inappropriate scales of environmental manipulations, e.g. large expanse of genets (genetic individuals of clonal grasses; Lundholm 2009, Eilts et al. 2011). Additionally, studies have not considered that heterogeneity in a resource may be modulated by the resource's mean availability.

The EHH has been tested in the context of restoring diversity in grassland that has been largely homogenized through conversion to agriculture. Restored tallgrass prairies often contain less diverse plant communities than never-cultivated prairie (Sluis 2002, Baer et al. 2004, Camill et al. 2004, Carter and Blair 2012), and cultivation caused homogenization of soil resources has been hypothesized to contribute to this general phenomenon (Baer et al. 2003, 2005). At the onset of community development in long-term cultivated systems, soil conditions are fairly homogeneous in contrast to native ecosystems (Haas et al. 1957, Pan-González et al. 2000). As plant communities develop in formerly cultivated soils, they influence nutrient availability and light availability. Plant diversity has been shown to decline with nutrient availability and increase with light availability in the initial years of community development in formerly cultivated soil (Baer et al. 2003, 2004). In natural never-cultivated grassland,

Bakker et al. (2003) found that plant community diversity was positively related to light heterogeneity, but not heterogeneity in soil nitrogen availability. Other studies have found that soil nutrient heterogeneity was related to plant diversity but did not consider light heterogeneity (Golubbski et al. 2008, Eilts et al. 2011).

The objectives of this study were to 1) quantify how resource heterogeneity changes during ecosystem development following long-term disturbance, 2) examine whether resource heterogeneity correlates with plant community diversity (effective number of species, richness and evenness) and 3) reveal if the strength of resource heterogeneity–diversity relationships is different among levels of resource availability. This was accomplished by quantifying the availability and heterogeneity of light and inorganic nitrogen availability in grasslands restored for different periods of time and at scales comparable to an established long-term test of the EHH in grasslands (Baer et al. 2016). We used a geostatistically-informed design to calculate the minimum distance for plot independence within the same restoration. We modeled changes in resource heterogeneity during grassland restoration and examined whether plant community diversity was related to resource heterogeneity. We hypothesized the availability and heterogeneity of light and nitrogen availability would decrease with increasing restoration age as clonal grasses increase in dominance (Sluis 2002, Carter and Blair 2012, Baer et al. 2016). We also hypothesized plant diversity would be positively correlated with resource heterogeneity. We predicted that light heterogeneity would be more strongly correlated with the plant community than soil nitrate heterogeneity because a study that analyzed both factors found that only light heterogeneity influenced plant richness (Bakker 2003). We were not able to distinguish cause and effect, however, because plants influence environmental heterogeneity.

Methods

Site description and field sampling

This research was conducted at the Konza Biological Station and Long-Term Ecological Research site (KNZ), located 9 km south of Manhattan, KS. The 30-year average annual precipitation is 835 mm year^{-1} (75% received during the April–September growing season). The restored prairies were located on a lowland Mollisol soil characterized as a Reading Silt loam 0–1% slope (mesic Typic Arguidoll), formed from alluvial and colluvial deposits. All prairie restoration sites were located within 0.5 km of each other.

We measured nitrate, photosynthetically active radiation (PAR; wavelengths of light used by plants to fix carbon), and plant species composition in independently restored prairies that varied in time since restored (1, 3, 5 and 7 years) and a cultivated agricultural field (0 years restored). All fields were in continuous cultivation for >50 years prior

to restoration. The common agricultural practice has been a corn–soybean–wheat rotation. Prior to restoration, each site was field-cultivated to loosen soil and increase soil-seed contact. The restored prairies were sown with 60% grasses (20–1100 live seeds m^{-2}) and 40% forbs (8–500 live seeds m^{-2}; Manning and Baer 2018), with seeding rates varying by species. Six grass species (*Andropogon gerardii, Sorghastrum nutans, Schizachyrium scoparium, Bouteloua curtipendula, Panicum virgatum* and *Elymus canadensis*) and 14 forb species (*Amorpha canescens, Baptisia autralis, Dalea purpurea, Dalea candida, Dalea multiflora, Desmanthus illinoiensis, Echinacea angustifolia, Helianthus pauciflo-rus, Lespedeza capitata, Liatris punctata, Oenothera macro-carpa, Rosa arkansana, Silphium integrifolium, Oligoneuron rigidum*) were included in the mix (nomenclature follows USDA Plants Database).

Four plots were established in each field. Plots were 6 × 8 m containing 12 subplots (2 × 2 m). The plot dimensions were based on the design of Baer et al. (2003); the scale at which a long term test of the EHH has been conducted at Konza Prairie (Baer et al. 2016). Plots within each field were positioned such that sampling points among different plots would be at least 10 m apart to satisfy spatial independence based on a pilot geospatial analysis (Fig. 1) using data from Baer et al. (2016) to construct a semivariogram of soil nitrate availability. This dataset was chosen because it was recent and had relatively few missing values. Coordinates (x and y distance in meters from most

southern and western corners of plots) were assigned with the sp package (Pebesma and Bivand 2005, Bivand et al. 2013) in R (<www.r-project.org>). Nitrate and coordinate data were transformed to z scores to remove anisotropy (i.e. directionality) and normalize the attribute data (Isaaks and Shrivastava 1989). The range was then estimated with a variogram model using an unweighted (ordinary least squares) fit method to preserve heterogeneity in the vari-ance estimates. A Spherical model was fitted in the R pack-age gstat (Pebesma 2004). The estimated range was then back transformed using the average of x- and y-values, resulting in a range of 10 m (3.3 before back transforma-tion). Pilot analysis indicated plots within the same field needed to be placed 10 m or more apart to maintain spatial independence.

Each subplot contained two 0.5 × 0.5 m quadrats where N, light and plant species composition were measured in 2016. Anion exchange resin bags were used to determine rela-tive nitrate availability (Binkley and Matson 1983) over one growing season. One anion exchange resin bag was buried in each 0.25-m^2 quadrat arranged northwest and southeast from the center of each subplot. Resin bags were prepared by placing 5 g of a strongly basic anion exchange resins (Dowex 1X8, 50–100 μm mesh) in a double layer of nylon hosiery attached to zip-ties (Baer et al. 2003, 2016). These resin bags were buried approximately 10 cm deep in the soil in late May and collected in early September. Photosynthetically active radiation (PAR) was measured in the same quadrats where species composition was measured in early September (cul-tivated field not recorded). Photosynthetically active radia-tion was measured above and below the plant canopy using a ceptometer. Proportion of light available at the soil surface was calculated by dividing PAR at the soil surface by PAR above the canopy. In each restored field, vascular plant species were identified in each quadrat in late May and September. Presence/absence data for each quadrat were converted to fre-quency of occurrence at the plot level by dividing the number of quadrats where each species occurred by the total number of quadrats per plot (24).

Lab analyses

Resin bags were rinsed with deionized water to remove excess soil then extracted with 25 ml of 2 M KCl in 0.1 M HCl. The extracts were filtered with 0.4 μm HTTP Isopore Membrane Filters and analyzed on an OI Analytical Flow Solution IV for nitrite + nitrate-N. Nitrate was reduced to nitrite with cadmium metal. The nitrite reacted with sulfanilimide and then coupled with N-(1-naphthyl)ethylenediamine dihydro-chloride to produce colored solution (azo dye) detected at 540 nm (absorbance). The average of blanks (one for each batch of resin bags analyzed) was subtracted from all sam-ples. Nitrogen collected on resin bags represents an index of relative nitrate availability, which is reasonable to compare across co-located sites that all experienced the same climate conditions.
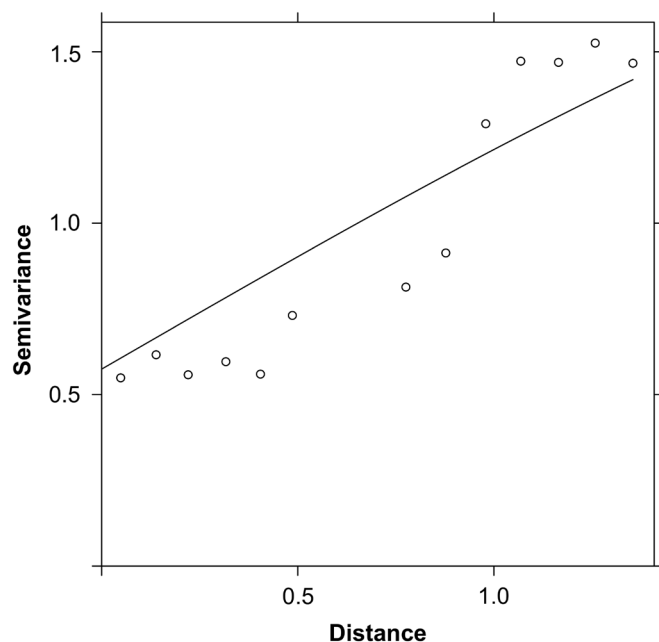

Figure 1. Semivariogram analysis used to determine distance required to satisfy independence between plots (z-transformed data presented). Analysis was based on resin bag exchangeable nitrate data from a 16 year-restored prairie located at Konza (Baer et al. 2016). The untransformed range = 1.4, approximating 10 m follow-ing back-transformation.

Statistical analyses

Means and coefficients of variation (CV; standard deviation/mean × 100) were calculated for soil nitrate and proportion of PAR available at the soil surface for each plot. A useful property of CV is that it is unrelated to the mean. Relationships between mean soil nitrate (nitrate availability), mean proportion of PAR available (light availability), CV of soil nitrate (nitrate heterogeneity) and CV of proportion of PAR available (light heterogeneity) with restoration age were explored using linear and non-linear models (e.g. linear regression, low-order polynomial [third order or less], 3-parameter Gaussian, exponential rise-to-max and exponential decay) in R (<www.r-project.org>). We used this limited suite of candidate models because they are commonly used to describe temporal dynamics of resources and communities in restored systems. Only models that appeared to fit the data were tested to avoid over fitting a model. All significant linear and polynomial models and all converging non-linear models were compared by AIC and BIC values to determine the most parsimonious model. Non-linear models were tested for significance by comparison to a null model, where the most significant parameter was dropped.

Exponent of Shannon's diversity ($e^{H'}$; effective number of species), Pielou's evenness (J) and richness (S) were tested for a positive Pearson correlation (one-sided) with CV of nitrate and CV of PAR at high (greater than 50th percentile) and low (less than 50th percentile) levels. This was accomplished using the cor.test function. Effective number of species was used because Shannon diversity can lead to misleading results (Jost 2006, 2007, Morris et al. 2014). These relationships were displayed in a scatterplot.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tj11c86> (Scott and Baer 2019).

Results

Mean soil nitrate and mean proportion of PAR available at the soil surface decreased with restoration age according to an exponential decay model (Fig. 2A and C). There was no directional change in CV of available nitrogen or CV of proportion of PAR available at the soil surface with restoration age (Fig. 2B and D).

Sixty-one species were encountered; *Andropogon gerardii* was the most frequently encountered species. Nitrate heterogeneity was positively correlated with both plant richness
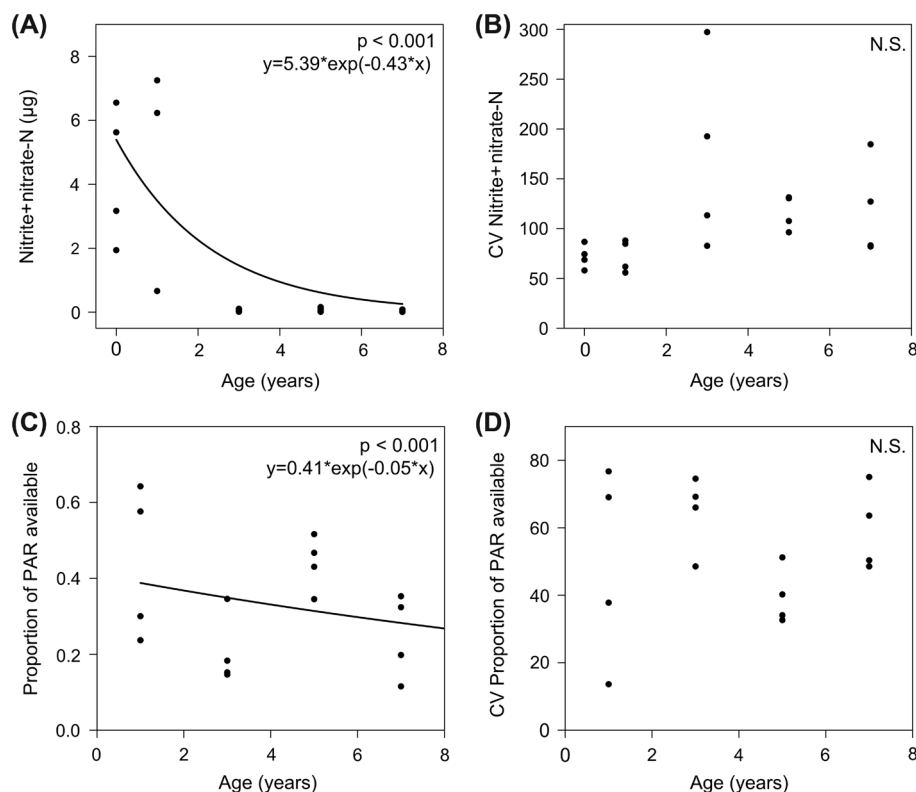

Figure 2. Relationships between the mean and coefficient of variation (CV) of each environmental variable with restoration age: (A) mean soil nitrate level, (B) CV of soil nitrate (i.e. nitrate heterogeneity), (C) proportion of photosynthetically active radiation available at soil surface (i.e. light level), (D) CV of proportion of photosynthetically active radiation available at soil surface (i.e. light heterogeneity). Each point represents a measurement from each spatially independent plot. The lines represent an exponential decay regression based on fitted parameter estimates (displayed as constants in equations on panels).
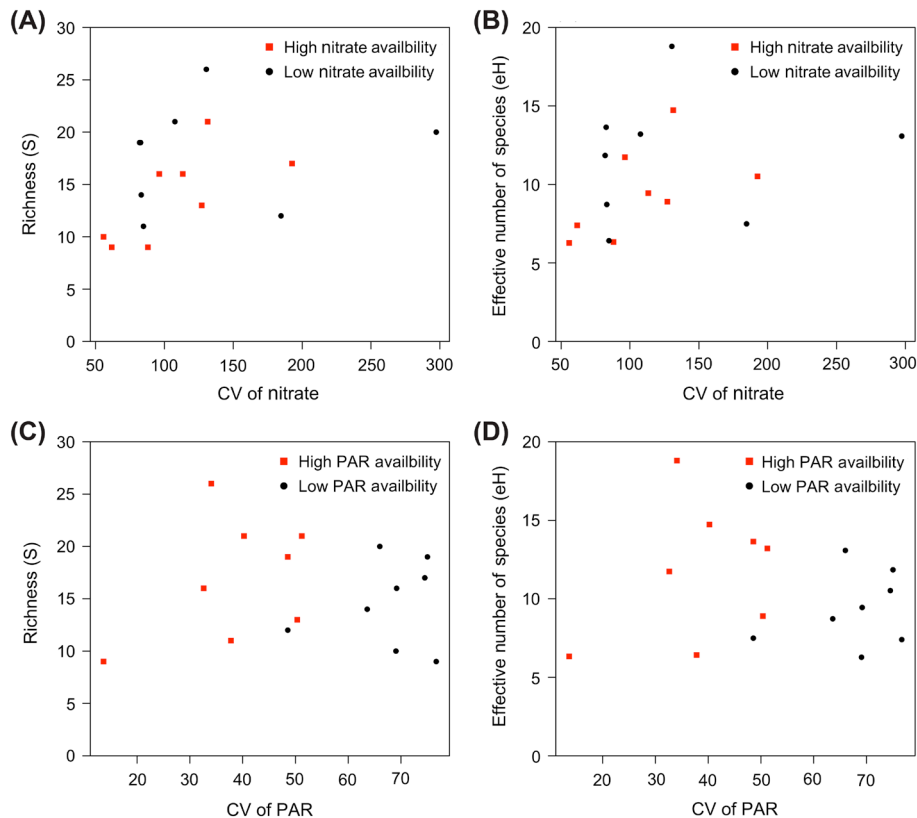
Figure 3. Relationship of resource heterogeneity with plant diversity metrics with color-coding representing availability of resources (above or below 50th percentile): (A) CV of soil nitrate (i.e. nitrate heterogeneity) with plant richness, (B) nitrate heterogeneity with plant effective number of species, (D) CV of proportion of photosynthetically active radiation available at soil surface (i.e. light heterogeneity) with plant richness, (D) light heterogeneity and plant effective number of species.

(r = 0.72, p = 0.021; Fig. 3A) and plant effective number of species (r = 0.64, p = 0.043; Fig. 3B) at high levels of nitrate availability. However, no correlation was detected at low levels of nitrate availability (richness: r = −0.24, p = 0.719; effective number of species: r = −0.23, p = 0.708). Light heterogeneity was not positively correlated with plant richness (r = 0.59, p = 0.060; Fig. 3C), but there was a positive relationship with effective number of species (r = 0.62, p = 0.049; Fig. 3D) at low levels of light availability. No correlation was detected at high levels of light availability (richness: r = 0.56, p = 0.074; effective number of species: r = 0.56, p = 0.074). Plant evenness was not correlated with resource heterogeneity at any resource availability level (p > 0.05).

Discussion

The 'environmental heterogeneity hypothesis' is an explanation for species coexistence through variability in resources that can be partitioned (Ricklefs 1977) and for plants in tallgrass prairie two key resources for growth are N and light. This hypothesis has been supported by multiple observational studies (reviewed by Huston 1979, Bakker et al. 2003, Golubbski et al. 2008, Eilts et al. 2011), but experimental

tests have found weak (Baer et al. 2016) or no support for the hypothesis (reviewed by Lundholm 2009). This study used the same scale as the Baer et al. (2016) experiment and found stronger support for EHH, suggesting that it is difficult to experimentally manipulate environmental heterogeneity to mimic reference ecosystems. Alternatively, this discrepancy between observational support and lack of experimental evidence could be because plants induce and respond to heterogeneity during community development (Greig-Smith 1979, Gibson 1986, 1988a, b).

As hypothesized, light availability and soil nitrate availability changed with restoration age. The exponential decrease in growing-season soil nitrate availability with increasing restoration age was consistent with a previous study that measured extractable soil nitrate (Rosenzweig et al. 2016). The exponential decrease in nitrate was expected because of lower mineralization rates compared to never-cultivated prairie (Rosenzweig et al. 2016) and frequent burning promoting lower mineralization rates (Turner et al. 1997). The exponential decrease in light availability was also expected because frequent burning promotes dominance of productive grasses (Myers and Harms 2011). Inconsistent with our predictions, heterogeneity in light and soil nitrate did not show a directional change with increasing restoration

age. This suggests that it might be difficult to maintain high diversity plant communities in grassland restorations without augmenting or managing drivers that promote environmental heterogeneity (Baer et al. 2012).

Richness and effective number of species were positively related to resource heterogeneity at some levels of resource availability. A positive relationship of richness and effective number of species with nitrate heterogeneity only occurred at high levels of nitrate availability. This relationship could pose challenges to restoring diverse grasslands because N becomes progressively limited during grassland restoration (Baer et al. 2003, Baer and Blair 2008, Rosenzweig et al. 2016). Unlike nitrate heterogeneity, light heterogeneity had a stronger relationship with plant richness/effective number of species at low levels of light availability. In contrast to native (never-cultivated) grazed prairie, we did not find light heterogeneity was more strongly related to plant richness than N heterogeneity (Bakker et al. 2003). Resource heterogeneity was not related to evenness, suggesting that the relationship between effective number of species and heterogeneity was mostly due to richness rather than evenness.

Metacommunities might influence local diversity of grassland restorations from agriculture because they often exist in fragmented landscapes. Local diversity might decrease, according to the mass-effect paradigm of metacommunity theory, if there is a dominant species and few propagules of other species or an efficient disperser has much higher propagule supply in the local community (Leibold et al. 2004). Because we did not measure propagule dispersal, we cannot evaluate this mechanism. A conceptual framework that combines spatial and non-spatial mechanisms, as suggested by Leibold et al. (2014), could improve species coexistence and diversity predictions.

Our results suggest that resource ratio theory and spatial storage both contribute to maintenance of plant diversity. Differing resource ratios among species within communities can act as a simple form of spatial storage to promote regional diversity (Pacala and Tilman 1994). Spatial storage theory was developed from spatially explicit studies of plant populations (Bolker and Pacala 1999, Bolker 2003). However, few studies have examined resource availability and heterogeneity simultaneously as it relates to species diversity. Our results demonstrate that resource availability influences resource heterogeneity–plant diversity relationships, suggesting that resource ratio theory and spatial storage are not mutually exclusive, in agreement with the theoretical work by Chesson (2000).

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