Functional dependence underlies a positive plant-grasshopper richness relationship

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Abstract

A central focus of ecology is identifying the factors that shape spatial patterns of species diversity and this is particularly relevant in an era of global change. Positive relationships between plant and consumer diversity are common, but could be driven by direct responses of each trophic level to underlying environmental gradients, or indirectly where changes in environmental conditions propagate through food webs. Here we use structural equation modeling to examine the relative importance of soil resource availability and disturbance (fire) in mediating relationships between plant and grasshopper richness in insular grasslands. We found a positive relationship between plant and consumer richness that became stronger after accounting for disturbance, despite unique responses of plants and consumers to the two environmental gradients. Plant richness responded to an underlying gradient in soil resource availability. Time since the last fire had a direct positive effect on grasshopper richness but had no effect on plant richness. This work supports that plant and consumer richness are functionally linked, rather than having similar responses to environmental gradients. By disentangling the direct and indirect processes underlying a positive relationship between plant and consumer diversity in a natural system that spans multiple environmental gradients, we demonstrate the importance of investigating biodiversity through explicit multivariate models.

Keywords: Ozarks; Glades; Indirect relationships; Herbivores

Introduction

A central focus of ecology is determining how environmental factors underlie changes in species diversity across space

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plant and consumer diversity could both respond directly to disturbance (e.g., fire) or other environmental variables. Alternatively, if consumers respond directly to plants but not to an environmental variable, the environment may still affect consumer diversity indirectly through changes in the plant community.

Highly controlled experiments often support that more plant species support more herbivore taxa—i.e., the functional dependence hypothesis—suggesting that specialization of consumers on their plant resources is a primary driver of multitrophic diversity relationships in North American tallgrass prairies (Haddad et al. 2009). Similar findings have been reported in experimental European grasslands (Scherber et al. 2010), but there have been few attempts to test mechanisms underpinning positive relationships between plants and consumers in natural systems where environmental variation and disturbance could have strong confounding influences on diversity patterns. Consumer diversity may also be related to plant productivity rather than diversity per se (Srivastava & Lawton 1998; Joern & Laws 2013), although most previous research has focused on, and supported as summarized above, diversity-diversity relationships.

Resource availability and fire are well-documented drivers of both plant and arthropod diversity patterns in grasslands, with both positive and negative—and direct and indirect—effects in different contexts (Cavender-Bares & Reich 2012; Joern & Laws 2013; Kirkman, Mitchell, Helton, & Drew 2001; Swengel 2001). Moreover, plant and arthropod responses to these environmental variables may be linked; for instance, fire can indirectly influence arthropod diversity by changing plant species richness, vegetation structure, or tissue quality (Kim & Holt 2012; Van Der Plas et al. 2012). Simultaneous direct and indirect effects are also possible; for example, fire could directly and negatively affect consumer diversity via increased mortality while simultaneously having an indirect and positive effect mediated through changes in the diversity or productivity of the plant community. Thus, considering only direct effects when examining how plant and insect communities are structured can lead to spurious results (Grace 2006). Understanding the mechanisms regulating patterns of diversity between multiple trophic levels necessitates analytical techniques that fully account for direct and indirect community drivers, since these drivers may otherwise mask multitrophic relationships.

In this paper we use structural equation modeling to investigate relationships between plant and consumer richness, and plant productivity and consumer abundance, after considering direct and indirect influences of disturbance and resource availability. We conducted this study in dolomite glades (rocky grasslands) in the Missouri Ozarks, USA (Fig. 1), which support a diverse flora and arthropod fauna (Nelson 2005). Glades are typically embedded in a woodland matrix and range in size from <1 to >100 ha (Nelson 2005). These grasslands are a fire-adapted ecosystem, with historic fire return intervals ranging from one year to several decades (Batek et al. 1999; Guyette & McGinness 1982). Grasshoppers are generalist herbivores that often show strong preferences for certain plant species or families (Chapman & Joern 1990). They are diverse and abundant in grassland ecosystems (Capinera, Scott, & Walker 2005) including glades (Hill & Dakin 2011), and regulate many ecosystem processes such as nutrient cycling (Belovsky & Slade 2000) and transferring energy to higher trophic levels (Chapman & Joern 1990). Grasshopper abundance can respond to fire, usually by decreasing immediately following a fire and recovering in the years thereafter (Branson & Sword 2010; Joern 2005). Fire

![Fig. 1. Photograph of one of our dolomite glade study sites, Spurgeon Hollow, in Shannon County, Missouri. Photo credit: J.E.D. Miller.](image-url)
can kill active grasshoppers and may also destroy grasshopper eggs laid on plants or in the soil (Branson & Vermeire 2013; Evans 1984; Swengel 2001). Similarly, grasshopper abundance can be limited by physical properties of the soil, such as soil moisture, which can effect egg survival (Stauffer, Hatle, & Whitman 2011).

We predicted that a positive relationship would emerge between herbaceous plant richness and consumer (grasshopper) richness because higher herb richness would provide more host plants for herbivores (i.e., support for the functional dependence hypothesis). Specifically, we hypothesized that consumer richness would be more strongly influenced by herb richness than by site productivity, and that consumer richness would respond more strongly to herb richness than consumer abundance does. We hypothesized that herb richness would respond to fire history and soil resource availability, as previous research has shown in this system (Miller, Damschen, Harrison, & Grace 2015) and others (Massad et al. 2013, 2015; Massad et al., 2013). Finally, we hypothesized that grasshopper richness would also respond directly to disturbance history, and indirectly to soil resource availability and fire via their effects on plant richness (Fig. 2).

**Materials and methods**

**Study system and site selection**

We selected 15 glades on public conservation lands in southern Missouri for study. We consulted with land managers to locate glades that are managed with prescribed fire. Prescribed fires occurred during the dormant season—usually in the later winter in February or March. All of the glades we sampled have been managed with prescribed fire on approximately 3–6 year intervals, and none of the glades have experienced any wildfires since management began. We used management records to calculate the time since the most recent fire. Time since fire ranged from 0 to 6 years (mean = 2.2). We also avoided sampling glades that are believed to have been intensively grazed by domestic livestock in the past, and none of the study glades had been grazed by livestock in recent decades. All glades occurred within mostly natural landscapes. Within our study glades, soils ranged from clay soils with high organic matter content to less fertile, sandier soils. Our study was conducted during a relatively wet year (129% of average annual precipitation over the last 20 years at NOAA’s weather station on Hwy. 1 in Eminence, Missouri).

**Plant surveys**

We sampled herbaceous plant communities using one 100 m² (2 x 50 m) modified Whittaker plot within each glade. Plot locations were randomly chosen within a glade, but had to be more than 5 m from grassland edges and more than 50 m from roads. Study glades were >500 m apart, in all cases, and usually much farther (median pairwise distance between plots = 23 km, Q1 = 15 km, Q3 = 107 km). Plant surveys were conducted twice during the growing season, once in the spring and once in the late summer, to identify both early and late
blooming species. We combined data from these visits to construct a master species list for each glade. Plants were identified according to the Flora of Missouri (Yatskievych 1999, 2006, 2013). See Miller et al. (2015) for additional details on glades and plant surveys.

**Grasshopper sampling**

We sampled grasshoppers (families Acrididae and Tetrigoniidae) using sweep nets. Sweep net sampling is the most common method used to measure grasshopper community composition (Belovsky & Slade 1995; Evans 1984; Joern 2005). We sampled each glade by vigorously sweeping through vegetation while walking a transect along the edge of the 2 × 50 m plot (hereafter “transect”) for a 10 minute period. This resulted in approximately 3–4 passes along each transect. Sampling was conducted from 12–15 August 2013, between 10:00–17:00 during sunny and calm weather. Time of day did not affect total grasshopper abundance ($F_{1,12} = 0.8, P = 0.38$) or grasshopper richness ($F_{1,12} = 0.3, P = 0.62$). Grasshoppers were stored on ice immediately after collection and kept frozen until they were identified. We identified grasshoppers to species using regional taxonomic guides (Capinera et al. 2005). Nymphs were identified to genus. Voucher specimens were deposited in the Insect Research Collection of the Department of Entomology at the University of Wisconsin-Madison.

**Environmental variables**

We collected soil samples on the first (spring) visit to each glade. We used a trowel to dig samples of the top 15 cm of soil from six evenly spaced locations along the 50 m transect which were combined and analyzed at the glade level. Soils were analyzed for texture and organic matter content by Brookside labs in New Knoxville, Ohio. We chose soil organic matter and clay content to represent soil resource availability because these variables are known to be strong predictors of plant species richness in Ozark glades as well as other systems (Miller et al. 2015; Miller & Damschen 2017). These variables are correlated with soil water-holding capacity, which can be a strong predictor of plant diversity patterns (Brady & Weil 2007; Kirkman et al. 2001). Soil organic matter ranged from 3.4 to 9.3%, and soil clay content ranged from 2 to 33%. We performed a principal component analysis (PCA) of soil organic matter and clay content and used the first axis from this PCA to represent soil resource availability in the model in the present study. This axis explained 85% of variation in soil organic matter and clay content (axis loadings: 0.82 with organic matter and 0.57 with square-root transformed clay content). We used time since fire to represent fire history because it has been shown to affect plant and arthropod diversity in grasslands (Joern 2005) and it was available for all of our study glades.

To estimate glade productivity, we downloaded 4-band National Agricultural Imagery Program (NAIP) landscape imagery from the Missouri Spatial Data Information Service. We calculated the Normalized Daily Vegetation Index (NDVI) in ArcGIS 10 (ESRI 2011).

**Statistical analysis**

We began analysis by examining correlations among variables of interest (grasshopper richness, grasshopper abundance, plant richness, NDVI [representing glade productivity], time since fire, and soil resource availability). We examined variable distributional properties and linearity of bivariate relationships. To meet assumptions of homogenous variances and normal distributions, we log-10 transformed time since fire and square-root transformed soil clay content and grasshopper abundance.

We used structural equation modeling (SEM) to test our hypotheses about multivariate controls on multitrophic relationships. We began by constructing a meta-model that included all hypothesized relationships (Fig. 2); this model had two exogenous variables (time since fire and soil resource availability) and two endogenous variables (herb species richness and grasshopper species richness). We included only two variables—soil resource availability and fire history—as external influences on plant and grasshopper richness to keep model complexity appropriate for the size of our dataset per the recommendations of Grace (2006). Resource availability and fire are known to be two of two of the most important factors that affect both plant and grasshopper richness in a variety of systems including the Ozark glades (Massad et al. 2013; Miller et al. 2015). Following procedures for hypothesis testing with SEM described by Grace (2006), we then modified the meta-model to create a parameterized model by removing non-significant paths. We performed SEM analyses in the lavaan package (Rosseel 2012) in R version 3.1.2 (R Core Team 2016).

To compare the relative influence of plant productivity and species richness on the grasshopper community, and to compare the relative responses of grasshopper abundance and richness, we performed three additional SEM analyses. We used the same structure as the meta model described above, except for the following changes: (1) Glade productivity (NDVI) replaces herb species richness, (2) grasshopper abundance replaces grasshopper species richness, and (3) glade productivity (NDVI) replaces herb species richness and grasshopper abundance replaces grasshopper species richness. We present the complete models without removing non-significant paths, though removing non-significant paths does not qualitatively change the results.

**Results**

We found 145 total herb species across all glades, with glade-level richness ranging from 14 to 62 species. We found
a total of 16 grasshopper species (Table A.1) and grasshopper richness at the glade level ranged from 3 to 15. Grasshopper richness and abundance were correlated (R = 0.48, P = 0.044), as were plant richness and NDVI (R = 0.71, P = 0.003). Grasshopper richness and herb richness were marginally correlated (R = 0.45, P = 0.089).

Our final SEM provided an adequate fit to the data ($\chi^2 = 1.574$, model $P = 0.455$, model df = 2; Fig. 2) and explained 56% of the variation in grasshopper richness. Grasshopper richness increased with increasing time since fire (path coefficient = 1.33; Fig. 3A) and increasing herb richness (path coefficient = 1.02; Fig. 3B). The SEM explained 46% of variation in herb richness; herb richness increased as soil resource availability (clay and organic matter content) increased (path coefficient = 0.68; Fig. 3C). The hypothesized paths between fire history and herb species richness and between soil resource availability and grasshopper richness were not significant, so we removed them for the final model. Soil resource availability indirectly affected grasshopper richness via plant richness (Fig. 2). The three supplemental SEMs showed that glade productivity was not a significant predictor of grasshopper richness or abundance, and that herb richness was not a significant predictor of grasshopper abundance (Fig. A.1). These supplemental SEMs also did not explain as much variation in grasshopper richness or abundance as did the main model (10–42%; Fig. A.1).

**Discussion**

Our results show that a positive relationship between plant and consumer (grasshopper) diversity is driven through direct effects of plant diversity and disturbance (fire) on consumer diversity, as well as indirect effects of changes in soil resources, which affected consumer diversity through changes in plant diversity. Specifically, our model rejects the hypothesis that both plants and consumers respond directly to the same environmental variables (resource availability and fire). Rather, the bottom-up influence of soil resource availability on plants affected grasshopper species richness indirectly. Similarly, grasshopper richness responded to time since fire whereas plant richness did not, indicating that plants and grasshoppers respond to different underlying environmental gradients. Although glade productivity was correlated with herb species richness, it did not have a significant effect on either grasshopper richness or abundance, indicating that total plant biomass is likely not a limiting factor for grasshopper diversity or abundance in glades. The importance of plant richness but not glade productivity for grasshoppers suggests that the presence of particular plant species that occur only in more productive glades may drive the grasshopper diversity there.

The mechanisms generating functional linkages between plant and grasshopper richness could arise through the effects of host plant availability, effects of structural or habitat complexity provided by plant diversity, or both. For instance,
greater plant diversity could support a more diverse insect assemblage (Dyer et al. 2007; Novotny et al. 2006) because different grasshopper species exhibit substantially different diets (Joern 1979). Changes in structural complexity associated with increased plant richness could alter grasshopper behavior because grasshoppers spend much of their time resting, thermoregulating (Belovsky & Slade 1986; Joern et al. 1986), or avoiding predators (Schmitz, Bechman, & Brien 1997). Therefore it is possible that increasing structural complexity could increase grasshopper richness (Joern 2005) by accommodating more behavioral niches. We were unable to distinguish between the mechanisms driving these functional linkages, and this remains an area that is ripe for future experimental tests.

In our study, the positive relationship between plant and grasshopper richness was partially masked before the influence of fire was controlled for statistically. By identifying the major direct and indirect drivers of plant and consumer diversity, our results highlight the importance of studying relationships between the plant and consumer richness in a multivariate context where environmental variables—such as resource availability and disturbance history—are explicitly considered. Future experiments should manipulate these underlying gradients, in addition to plant diversity, and measure the effects on the diversity of higher trophic levels. Research in heterogeneous environments could elucidate other nuances of diversity relationships across trophic levels. In addition, future studies should work to disentangle reciprocal relationships between richness at multiple trophic levels, since herbivory may feedback to affect plant community composition (Deraison, Badenhausser, Börger, & Gross 2015).

Maintaining biodiversity is a primary conservation priority in an era of rapid biodiversity loss and anthropogenic influences (e.g., grazing domestic animals) can weaken positive multitrophic relationships (Klink et al. 2015; Manning et al. 2015). Management efforts often focus on restoring vegetation structure and diversity; our results support that such management approaches may provide a foundation for supporting biodiversity of organisms at higher trophic levels (Hahn & Orrock 2015; Panzer 2002). Previous research has found that prescribed fire can be an important tool for restoring and maintaining glade plant and animal diversity (Templeton, Robertson, Brisson, & Strasburg 2001). However, because grasshopper communities appear to take several years to recover after fire, providing unburned refuges for fire-sensitive organisms within managed glade landscapes might help maximize the benefits that glade communities receive from prescribed fire.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baee.2017.06.001.

References


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