Examining the foundations of heterogeneity-based management for promoting plant diversity in a disturbance-prone ecosystem

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Abstract

The conservation of disturbance-prone ecosystems such as rangelands may depend on the spatial and temporal variation in the application of disturbances. Patch-burn management approaches attempt to increase overall landscape biodiversity by creating a mosaic of habitat patches using a patchy application of fire and grazing. Three fundamental assumptions underlay the patch-burn management approach: 1) fire and grazing drive spatial patch differentiation in community structure, 2) species composition of patches diverge through time in response to disturbance, 3) high spatio-temporal variation in fire and grazing results in high compositional variation and thus high landscape-scale diversity. We tested the first two assumptions of the patch-burn approach by comparing the importance of variation in management (changes in fire frequency and grazer species) relative to inherent sources of landscape heterogeneity at the Tallgrass Prairie Preserve in Osage Co., Oklahoma, USA. We sampled 150 square 100 m^2 quadrats on a 1 x 1 km UTM grid. We randomly selected 20 of those quadrats to annually resample for 12-years. We recorded visual cover of all vascular plant species rooted within each quadrat. We used variation partitioning within multiple regression and direct ordination

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frameworks to estimate the relative contribution of classes of variables on species richness and composition respectively.

Our results indicate that there was some support for the two assumptions underlying patch-burn management; however, independent spatial and temporal inherent landscape heterogeneity played a much larger role than management in shaping both plant richness and composition. The strength of inherent landscape heterogeneity on the plant community suggests that fine-tuning the application of fire and grazing is not critical for maintaining this community as long as fire and grazing remain part of the system. More generally, the effects of intrinsic spatiotemporal template on biodiversity may dominate even in disturbance-prone ecosystems.

Keywords: bison, cattle, Flint Hills, Oklahoma, patch-burn, pyric-herbivory, restoration, tallgrass prairie, variation partitioning, vascular plants, vegetation monitoring

Introduction

Natural variability concepts of land management, which promote spatial and temporal variability, are increasingly used in restoration ecology (Palmer et al. 1997, Fuhlendorf et al. 2006, 2009, Winter et al. 2012). Underlying these concepts are two premises: 1) historical conditions and processes can provide guidance for management, and 2) spatial and temporal variability generated by disturbance are vital components of nearly all ecosystems (Landres et al. 1999). Proponents of natural variability concepts believe that managing for historical conditions will benefit species that have evolved in that system and will therefore minimize local extinctions of native taxa (Swanson et al. 1994, Cissel et al. 1999). Additionally, spatial and temporal variability in environmental heterogeneity is thought to maintain biological diversity (MacArthur 1965, Petraitis et al. 1989).

In an effort to restore natural variability to grazing systems, Fuhlendorf and Engle (2001, 2004) suggested the fire-grazing interaction or pyric-herbivory, in which recently burned patches are preferentially grazed, could be used to create a *shifting mosaic* of habitat types when fire is patchy distributed on the landscape in contrast to the traditional homogenous application of fire. They suggested that fire results in higher grazing intensity which promotes short-term dominance of forbs. As time since fire increases, grazing intensity decreases which allows grasses to become dominant and to competitively exclude forbs. They argued that a mosaic of burned and unburned patches more closely approximates the historical variability that would have existed in rangeland ecosystems and will result in higher biodiversity than traditional homogenous management practices. Empirical evidence is beginning to accumulate which suggests that patch-burn management may result in greater community heterogeneity than the homogenous application of fire and grazing but only in certain contexts (McGranahan et al. 2012).

Three important assumptions underlie the application of patch-burn management to promote plant diversity:

I) Fire and grazing drive spatial patch differentiation in species composition and richness,

II) Species composition of local patches diverges through time in response to frequency and time since disturbance, and

III) High spatiotemporal variation in fire and grazing causes high compositional variation and thus high landscape-scale diversity

Tests of the patch-burn approach have thus far examined III by comparing the compositional variability and diversity of management units where fire is either heterogeneously

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or homogeneously applied (results synthesized in McGranahan et al. 2012). The large amount of literature on the effects of fire and grazing on plants suggests that I and II should generally be true in plant communities. However, given that vegetation responses to many drivers simultaneously, it is unclear how important I and II are to explaining variability in grassland community structure and thus how effective the patch-burn approach is likely to be for the objective of promoting plant diversity.

Given that a considerable amount of resources are expended applying fire and grazing in rangeland systems to achieve management goals it is critical that we consider the importance of disturbances relative to *in situ* landscape heterogeneity in shaping community structure. Therefore, we used a long-term observational study at a preserve being managed with a patchy application of fire and free roaming cattle and bison grazers to test assumptions I and II of the patch-burn management approach in a tallgrass prairie plant community.

Methods

Study Site

We conducted our study at the Tallgrass Prairie Preserve (TGPP) which is a 15,700 ha nature preserve that is managed using a patch-burn approach (Hamilton 1996, 2007, Allen et al. 2009). The TGPP is located between 36.73° and 36.90° N latitude, and 96.32° and 96.49° W longitude, in Osage County, Oklahoma and owned by The Nature Conservancy (TNC). Over the course of the 12 year study period (1998-2009), total annual rainfall varied from 494 to 1252 mm. The preserve is situated at the southern extent of the Flint Hills region. The elevation of the preserve ranges from 253 to 366 m, and the underlying bedrock of the region is characterized by soils derived from Permian limestone, sandstone, and shale (Oviatt 1998). Due to the

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proximity of bedrock to the surface and the relatively steep terrain, the Flint Hills region has experienced long-term erosion leaving surface layers of soil that are thin and young. Because of this rockiness the Flint Hills region, including the TGPP, has remained unplowed and has been instead used primarily as rangeland for cattle. Prior to the acquisition of the preserve by TNC in 1989, the majority of the site was managed for cow-calf and yearling cattle production with a 4- to 5-year rotation of prescribed burning and patchy aerial application of broadleaf herbicides (1950-1989) (Hamilton 2007).

Approximately 90% of the TGPP consists of grasslands. The majority of the grasslands are composed of tallgrass prairie habitats dominated by *Andropogon gerardii*, *Sorghastrum nutans*, *Sporobolus compositus*, *Panicum virgatum*, and *Schizachyrium scoparium*. Shortgrass prairie habitat occurs to a lesser extent on more xeric sites and is dominated by *Bouteloua* spp. Despite the application of herbicide earlier in the 20th century, the flora of the preserve appears relatively intact with a total of 763 species of vascular plants (to date) of which 12.1% are exotic (Palmer 2007).

Disturbance regime

The management plan at the TGPP encompasses a wide range of spatial and temporal variation in the application of prescribed fire and cattle or bison grazing (Hamilton 1996, 2007). In 1993, 300 bison were introduced year-round onto a 1,960 ha portion of the preserve. As the bison herd increased in size, the area allotted to the herd was increased eight times to an area of 8,517 ha by 2007 (Fig. 1a, 54% of preserve area). Initial bison stocking rates were increased in 1999 to 2.1 animal-unit months ha^{-1} (see Hamilton 2007 for additional details). Within the bison unit, animals were allowed to range freely and their movement was not obstructed by internal

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fences. Watersheds within the bison unit were considered randomly for burning only if they met the minimum fuel criteria of 900 kg ha^{-1} of fine fuels. Within a given year, the season of burn of the bison unit was split as follows: 40 % dormant spring (March - April), 20 % late growing season (August - September), and 40 % dormant winter (October - December). The remainder of the preserve was seasonally grazed by cattle and typically burned more frequently in the dormant spring season, but some of the cattle pastures were utilized for smaller scale (2,350 ha) patch-burn experiments in which only one-third of a given management unit was burned annually (Hamilton 2007). Stocking within the cattle pastures included both intensive-early stocking and season-long stocking, which contrasted with the year-round stocking in the bison unit.

Data collection

During a three year period (1997- 2000) we collected vegetation and environmental data at every intersection of a 1 km UTM grid for a total of 151 samples (Fig. 1b). However, for our analysis we only used 128 of the samples which had no standing water and less than 20 % of cover by rocks or woody plants to ensure that they were representative of grasslands. We randomly selected 20 of these plots for annual resampling, which continued from 1998 to 2009 (Fig. 1c). All vegetation samples were collected in June (when we could readily identify both early and late-season plants). At each site we recorded species presence/absence for plants rooted within each of the four corners of the 10 x 10 m quadrats at four nested spatial scales: 0.01, 0.1, 1, and 10 m^2 (see McGlinn et al. 2010 for a sampling diagram). At the 100 m^2 spatial scale we visually estimated species percent cover. For the purposes of this study we only report results at the 100 m^2, but analyses at the finer spatial grains (using the corner subplots) yielded qualitatively similar results but higher levels of unexplained variance.

At every sampling event we combined four 15 cm soil cores collected at each corner of the plot. We sent the soil samples to Brookside Labs (New Knoxville, Ohio) to be analyzed for soil cations: P, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, and Al. We recorded topographic data on slope and aspect in the field. We obtained total monthly precipitation data from the Oklahoma Mesonet Foraker weather tower (36.841° N, -96.428° W; elevation: 330 m), which is located on the preserve (McPherson et al. 2007). The resampled vegetation and environmental data are in a public online archive (McGlinn et al. 2010).

Data analysis

Our analysis was composed of two sets of parallel analyses: those on species richness and those on species composition. Additionally we carried out separate analyses on the 128 vegetation samples which were sampled once over a three year period and the 20 samples that were annually resampled over a 12-year period (n = 20 x 12 = 240). We will refer to these separate analyses as the Grid analysis and the Repeat analysis, respectively. The Grid analysis was used to test assumption I and the Repeat analysis was used to test assumption II of the patch-burn approach.

Assumption I asserts that spatial variation in the community should reflect spatial variation in management. To carry out a strong test of this hypothesis we compared the variance explained by management variables relative to inherent environmental heterogeneity captured by soil cations on plant community richness and composition. We quantified variation in soil using the first three axes of a principal components analysis (PCA) on the eleven soil cations. We chose to examine soil variables because previous research at the site indicated that they are good proxies for spatially relevant environmental variation (Palmer et al. 2003).

Assumption II asserts that a space-time interaction, in which community structure changes spatially and temporally, emerges from the independent patch-dynamics that local sites experience in response to past disturbance. To test assumption II we examined the degree to which spatio-temporal changes in richness and composition correlated with changes in management after controlling for inherent site and year specific differences. While the grid analysis examined the effects of key soil variables on species composition, it is possible that unmeasured variables that distinguish one site from another are responsible for intersite differences. Similarly, interannual variation may be inadequately summarized by readily obtainable climatic variables. Thus, the simplest way to completely account for interplot and interyear differences, independent of management, is to use site and year nomial variables to quantify the site and year effects, respectively.

In all the analyses, we quantified management using three variables: years of bison grazing, years since burn, and number of burns in the past five years. Year of bison grazing is meant to capture variation attributed to the differences in bison and cattle management at the preserve. We chose not to include season of burn as an explanatory variable because 83% (67 out of 80) of the prescribed fire events recorded on our study sites took place during the dormant season.

In both the Grid and Repeat analyses, we quantified the variance explained by the competing classes of variables using variation partitioning which estimates the unique and shared fractions of explained variance in species richness and composition (Legendre and Legendre

1998, Peres-Neto et al. 2006). The univariate species richness analyses were carried out using ordinary least squares regression (OLS) and the multivariate compositional analyses were carried out using redundancy analysis (RDA) and canonical correspondence analysis (CCA) direct ordination approaches. We only report the results of the RDA analyses because they were qualitatively similar to the CCA results. For the compositional analyses, we down-weighted the effect of common species using a square root transformation of the cover estimates. Following the recommendations of Peres-Neto et al. (2006), we report the adjusted coefficient of determination R^2_{adj} for each fraction of variance using Ezekiel's adjustment (1930) for the OLS and RDA analyses. We tested if the individual fractions of variation were significantly different than zero using permutation tests with 999 permutations of the rows of the response variable of matrix.

All analyses were conducted in R (R Development Core Team. 2008). The code and data are publically available at an online repository (https://github.com/dmcglinn/tgp_management). The data shared in this manuscript includes the data shared by McGlinn et al. (2010), two additional years of data, and the vegetation and environmental data for the remainder of the plots on the UTM grid.

Results

Grid Analysis – test of spatial management effects

Spatial variation due to differences in soil properties explained the largest proportion of variation in species richness and composition (100% and 67%, respectively, Fig. 2). The

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independent effect of management was negligible on species richness (R^2_{OLSadj} = -0.01, p = 0.59) but not on species composition (R^2_{RDAadj}= 0.02, p = 0.001).

Repeat Analysis – test of space-time management effects

We observed a statistically significant (p = 0.001) space-time interaction attributed to management effects in both richness and composition (Fig. 3); however, relative to site and year effects management explained a small proportion of the total explained variance (6% and 2% of richness and composition, respectively, Fig. 3). The majority of variation in richness and composition was attributed to site specific effects (68% and 82% of the explained variance, respectively). Year effects were intermediate to those of site and management effects. The majority of the variance attributed to management was shared with site effects (Fig. 3).

Discussion

Our findings suggest that the species richness and composition of an intact tallgrass prairie is relatively insensitive to changes in the disturbance regime related to fire frequency and grazer management. Although we observed some statistical support for two fundamental assumptions underlying the patch-burn approach to management, in general variation in management was swamped by the influence of inherent sources of heterogeneity (Fig. 2, 3). Specifically, the Grid analysis demonstrated that management was correlated with spatial variation in species composition (not richness), but that soil heterogeneity explained a much larger portion of overall variance. The Repeat analysis demonstrated that management influenced the space-time interaction as posited by the patch-burn paradigm; however, this was a rather trivial portion of total explained variance in both richness and composition with respect to proportion of inherent spatial and temporal variation (i.e., independent site and year effects).

From a management perspective, our results suggest that fine-tuning a management plan with respect to fire frequency or grazer identity may be of less importance given the potential importance of inherent landscape heterogeneity on the species composition and richness (Knapp et al. 1999). This may be welcome news for land managers because it suggests that intact tallgrass prairie plant communities may be relatively resilient to uncertainty in the prescription of fire frequency and grazer choice as long as some combination of fire and grazing is present on the landscape. Our results also suggest that management plans attempting to harness pyric-herbivory in the context of a patch-burn management scheme to increase community heterogeneity may take time to show a strong effect and that the underlying environmental template should be considered when developing these plans.

At our study site, TNC is utilizing a variable application of prescribed fire to meet several objectives. One objective is to maintain or increase the biological diversity of the plant community (Hamilton 2007). We observed a high overall magnitude of average richness (72.74) and low proportion of exotic species (5-7%) during the 12-year period which suggests that the management decisions are at the very least not detrimental to the plant community. TNC is also attempting to manage for wildlife habitat and diversity. Structural heterogeneity in the vegetation, attributed to the variable application of fire, resulted in the development of suitable habitat for a wider breadth of grassland bird species at the TGPP (Fuhlendorf et al. 2006, Coppedge et al. 2008). These results in conjunction with our findings suggest that the management decisions at the preserve are contributing to important conservation goals, even if their effects on plant richness and composition are slight.

The historical and regional context of our study site likely contributed to the relatively low importance of the disturbance regime. Specifically, prior to TNC's ownership, the site was managed using prescribed burning and cattle grazing (Hamilton 2007). These management practices are common in the Flint Hills region (Malin 1942, Kollmorgen and Simonett 1965) and are likely one of the primary reasons this region has maintained intact tallgrass prairie vegetation (Samson and Knopf 1994). Without this land management legacy, it is likely that we would have observed a much stronger influence of fire and grazing because our study sites would have initially contained higher abundances of disturbance-sensitive species, such as *Juniperus virginiana* (eastern redcedar) which we seldom observed (and only as seedlings) in our sites but has aggressively invaded much of the southern Great Plains due to fire suppression (Briggs et al. 2005).

In a relatively intact tallgrass prairie, the influence of spatiotemporal variation in fire and grazing on plant richness and composition was relatively minor relative to inherent variation between sites. Nevertheless, variation in fire and grazing had significant effects consistent with two basic assumptions of the patch-burning management approach. Given the overriding influence of inherent landscape heterogeneity on the plant community, fine-tuning the application of disturbances that incorporate the variable application of fire and grazing may not be crucial for maintaining biodiversity and composition of plant communities such as the tallgrass prairie.

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Figures

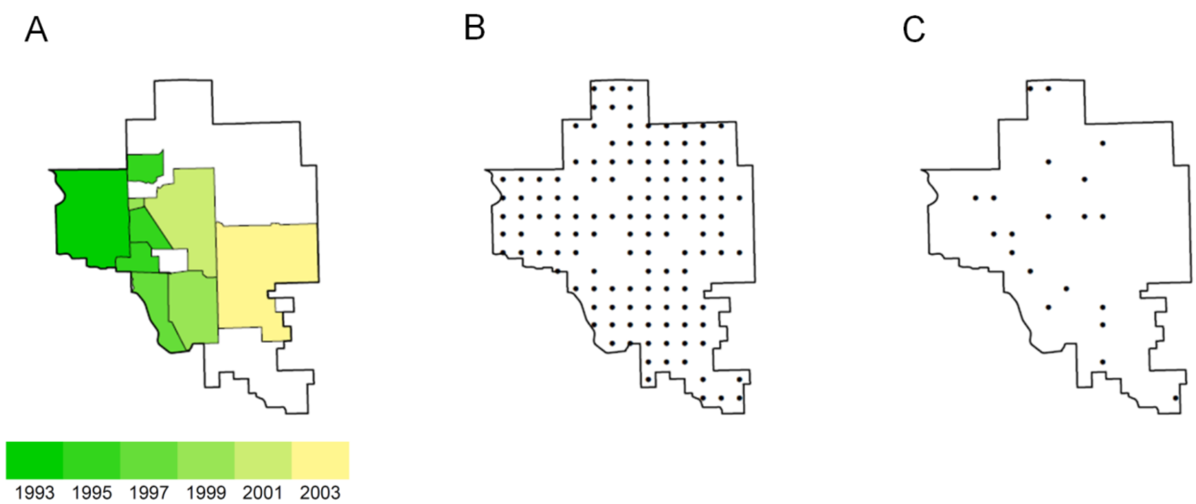

Fig. 1. Maps of the study site the Tallgrass Prairie Preserve. (*A*) The colored area denotes the bison unit which increased in area during the study period (green region to yellow region), and the white area denotes areas grazed by cattle, (*B*) the 128 plots used for the Grid Analysis which were located on a 1 x 1 km UTM grid and were sampled primarily in 1997 and 1998, and (*C*) the locations of the 20 plots used for the Repeat Analysis which were sampled annually from 1998 to 2009.

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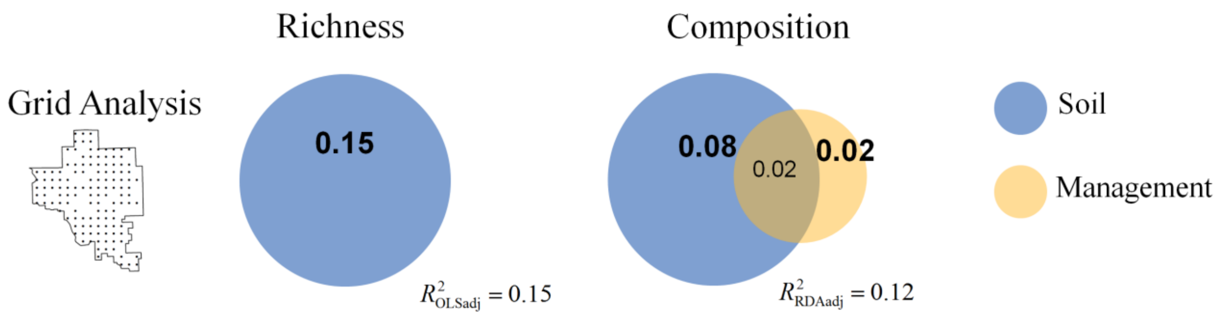

Fig. 2. Venn diagrams display the results of variation partitioning for the Grid analysis on richness and composition as a test of assumption I: management drives spatial variation in community structure. The relative area of the circles and reported statistics represent the adjusted explained variance for richness (from OLS) and for composition (from RDA) attributed to either the soil or management variables. The percentages in bold are statistically significant (p = 0.001). Fractions between -0.01 and 0.009 are not labeled. The overall adjusted explained variance and is reported for each analysis. Note that management explained approximately zero variance in richness.

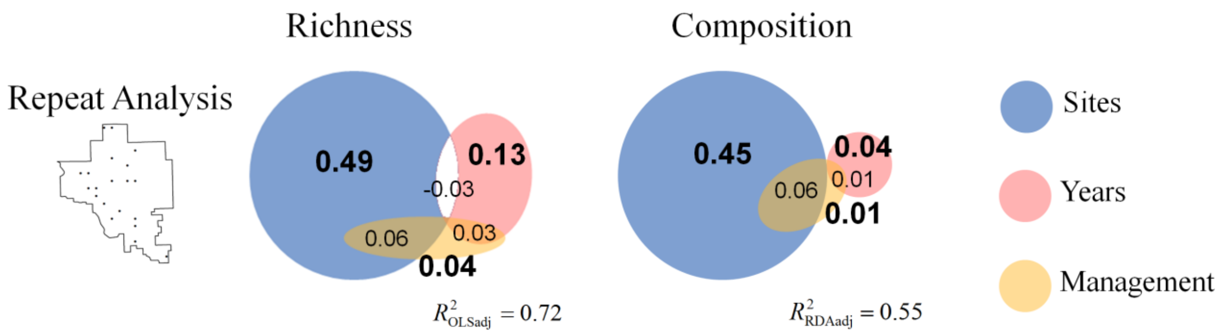

Fig. 3. Venn diagrams display the results of variation partitioning for the Repeat analysis on richness and composition as a test of assumption II: management drives a space-time interaction. See caption of Fig.2 for more details. A negative value of shared explained variance is presented as an unshaded region.

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