1   *Running head*: partitioning sources of heterogeneity

2   Inherent spatiotemporal variation trumps fire and grazer effects in an Oklahoma tallgrass prairie

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1   **Abstract**

2   Prescribed fire and grazing influences plant species richness and composition in many ecological

3   communities. However, the majority of knowledge of such effects is largely based upon fine-

4   scale or short-term manipulative studies, which are not ideally suited to quantify the importance

5   of management relative to inherent landscape heterogeneity. The purpose of our study was to

6   quantify the importance of fire and grazing by bison and/or cattle relative to inherent site and

7   year effects on the vascular plant community. Our study system is the Nature Conservancy's

8   Tallgrass Prairie Preserve in Osage County, Oklahoma, which we monitored for 11 years with 20

9   permanent 100 m^2 plots.

10 The management objectives of the preserve are to maintain community heterogeneity through the

11 application of randomized burning and freely-ranging grazers. We used multiple regression and

12 canonical ordination to perform variation partitioning on species richness and species

13 composition respectively. Site effects, probably edaphic in origin, explained the majority of

14 variation in richness and composition. Year effects, related to seasonal precipitation, were more

15 strongly correlated with variation in richness than composition. Interannual variation in fire and

16 grazer species was unimportant relative to inherent site and year effects with respect to both

17 richness and composition. Nevertheless, the effects of fire and grazer variables were significant

18 and interpretable, and bison management was positively correlated with plant richness. The

19 strength of inherent landscape heterogeneity on the plant community suggests that fine-tuning

20 the application of fire and particular grazer is not critical for maintaining this intact tallgrass

21 prairie plant community as long as fire and grazing remain part of the system.

22 *Keywords*: bison, Flint Hills, Oklahoma, restoration, tallgrass prairie, variation partitioning,

23 vascular plants, vegetation monitoring

1 **Introduction**

2   Natural variability concepts of land management, which promote spatial and temporal

3 variability, are increasingly used in restoration ecology (Palmer et al. 1997, Fuhlendorf et al.

4 2006). Underlying these concepts are two premises: 1) historical conditions and processes can

5 provide guidance for management, and 2) spatial and temporal variability generated by

6 disturbance are vital components of nearly all ecosystems (Landres et al. 1999). Proponents of

7 natural variability concepts believe that managing for historical conditions will benefit species

8 that have evolved in that system and will therefore minimize local extinctions of native taxa

9 (Swanson et al. 1994, Cissel et al. 1999). Additionally, spatial and temporal variability in

10 environmental heterogeneity is thought to maintain biological diversity (MacArthur 1965,

11 Petraitis et al. 1989). Although these concepts are grounded in ecological theory, as Palmer et al.

12 (1997) note, the importance of managing for natural variability is rarely examined

13 experimentally.

14   The application of natural variability concepts is relevant to the conservation and

15 restoration of the North American tallgrass prairie ecosystem. In this ecosystem, fire and grazing

16 were important components of the pre-Columbian North American disturbance regime

17 (Anderson 1990) and still are today (Daubenmire 1968, Abrams et al. 1986, Collins 1992).

18 Although historically the region was grazed by bison (*Bison bison*) and was burned in a variety

19 of seasons (Higgins 1986, Howe 1994, Allen et al. 2009), presently much of the remaining

20 tallgrass prairie ecosystem is managed for cattle with annual spring burns (Fuhlendorf and Engle

21 2001). The purpose of annual spring burning is to maximize yields of palatable C4 grasses

22 (Towne and Owensby 1984). Howe (1994) also noted that many restoration efforts on prairie

23 remnants promote production of C4 grasses with spring season burning and a lack of grazing.

1 These management practices may be a threat to the ecosystem's biodiversity by only benefiting

2 one competitively superior plant functional group and by homogenizing an entire region's

3 disturbance regime (Howe 1994, Fuhlendorf and Engle 2001, Nekola and White 2002).

4   In an effort to restore natural variability to grazing systems, Fuhlendorf and Engle (2001,

5 2004) suggested the interaction between fire and grazing could be used in a more variable

6 manner in space and time to create a *shifting mosaic* in contrast to the traditional homogenous

7 application of these management tools. They argued that a mosaic of burned and unburned

8 patches more closely approximates the historical variability that would have existed on the

9 landscape and will result in higher biodiversity than traditional homogenous management

10 practices (annual spring burning). This hypothesis is guiding the management of The Nature

11 Conservancy's Tallgrass Prairie Preserve (TGPP), one of the largest tallgrass prairie preserves

12 (Hamilton 1996, 2007, Allen et al. 2009).

13   The scale of the TGPP (15,700 ha) coupled with the spatially and temporally varying

14 application of fire, the usage of both native and exotic grazers, and intact native vegetation

15 provides both important opportunities and challenges for experimentally evaluating aspects of

16 the natural variability hypothesis. Specifically, the TGPP is an ideal setting for conducting a

17 long-term observational study on the relative importance of variation in grazing and fire in an

18 unplowed tallgrass prairie ecosystem that is presumably in somewhat of a more pre-Columbian

19 state. This opportunity is valuable because the majority of our knowledge on tallgrass prairie

20 ecology either originates from relatively small scale experiments (e.g., Hulbert 1988) or from

21 strictly controlled watershed treatments (e.g., Knapp et al. 1998).

22   Controlled studies are valuable for elucidating ecological mechanisms, but are less useful

23 for examining multiple driving factors of community change within a broader ecological context.

1 This can be better achieved by a properly-designed observational study (Hobbs et al. 2007,

2 Weiher 2007). Examining more than two or three treatments at several levels requires more

3 replication than is typically feasible in long-term ecological research; however, the effect of

4 several factors can be statistically separated in an observational study with relatively few

5 replicates. Furthermore, in many conservation contexts certain landscape scale experimental

6 manipulations may be unethical or conflict with overall management goals (e.g., permanently

7 unburned or ungrazed treatments is contrary to the objectives of the TGPP, Allen et al. 2009),

8 and in such contexts an observational study is the only method of examining the response of the

9 biota to management (Farnsworth and Rosovsky 1993, Marsh and Kenchington 2004).

10 Due to the long-term observational nature of our study, differences due to variation in fire

11 and grazing within sites are likely to be confounded by year-to-year variation in climate

12 (Anderson 1982, Gibson and Hulbert 1987, Adler and Levine 2007) and between sites by

13 variation in soil (Critchley et al. 2002) and topography (Abrams and Hulbert 1987, Briggs and

14 Knapp 1995). However, these confounding differences can be statistically controlled and

15 separated from one another using variation partitioning (Borcard et al. 1992, Økland and

16 Eilertsen 1994). Variation partitioning provides estimates of the independent and shared

17 importance of several groups of variables relative to one another.

18 In this study, we apply variation partitioning to quantify the importance of variability in

19 prescribed burning and grazer species (i.e., cattle vs. bison) on plant species richness and

20 composition at the TGPP relative to *in situ* site and year variation. Our goal is not to directly test

21 whether or not variation in fire and grazing are effective tools for meeting specific conservation

22 targets, but rather to examine the relative influence that variation in these variables has on the

1   plant community. Lastly we wish to examine the implications of our findings for management

2   practices.

3   **Methods**

4   *Study Site*

5   The TGPP is a 15,700 ha nature preserve located between 36.73° and 36.90° N latitude,

6   and 96.32° and 96.49° W longitude, in Osage County, Oklahoma and owned by The Nature

7   Conservancy (TNC, Allen et al. 2009). Over the course of the 11 year study period (1998-2008),

8   total annual rainfall varied from 490 to 1250 mm. The preserve is situated at the southern extent

9   of the Flint Hills region. The elevation of the preserve ranges from 253 to 366 m, and the

10 underlying bedrock of the region is characterized by soils deriving from Permian limestone,

11 sandstone, and shale (Oviatt 1998). Due to the proximity of bedrock to the surface and the

12 relatively steep terrain, the Flint Hills region has experienced long-term erosion leaving surface

13 layers of soil that are thin and young. Because of this rockiness the Flint Hills region, including

14 the Tallgrass Prairie Preserve, has remained unplowed and has been instead utilized primarily as

15 rangeland for cattle. Prior to the acquisition of the preserve by TNC in 1989, the majority of the

16 site was managed for cow-calf and yearling cattle production with a 4- to 5-year rotation of

17 prescribed burning and aerial application of broadleaf herbicides (1950-1989) (Hamilton 2007).

18   Approximately 90% of the TGPP consists of grasslands. The majority of the grasslands

19 are composed of tallgrass prairie habitats dominated by *Andropogon gerardii*, *Sorghastrum*

20 *nutans*, *Sporobolus compositus*, *Panicum virgatum*, and *Schizachyrium scoparium*. Shortgrass

21 prairie habitat occurs to a lesser extent on more xeric sites and is dominated by *Bouteloua* spp.

22 Despite the application of herbicide earlier in the 20th century, the flora of the preserve appears

1   relatively intact with a total of 763 species of vascular plants (to date) of which 12.1% are exotic

2   (Palmer 2007).

3   *Management Plan*

4   The management plan at the TGPP encompasses a wide range of spatial and temporal

5   variation in the application of prescribed fire and cattle or bison grazing (Hamilton 1996, 2007).

6   In 1993, 300 bison were introduced year-round onto a 1,960 ha portion of the preserve. As the

7   bison herd increased in size, the area allotted to the herd was increased eight times to an area of

8   8,517 ha by 2007 (Fig. 1, 54% of preserve area). Initial bison stocking rates were increased in

9   1999 to 2.1 animal-unit months ha^{-1} (see Hamilton 2007 for additional details). Within the bison

10   unit, animals were allowed to range freely and their movement was not obstructed by internal

11   fences. Watersheds within the bison unit were considered randomly for burning only if they met

12   the minimum fuel criteria of 900 kg ha^{-1} of fine fuels. Within a given year, the season of burn of

13   the bison unit was split as follows: 40 % dormant spring (March - April), 20 % late growing

14   season (August - September), and 40 % dormant winter (October - December). The remainder

15   of the preserve was seasonally grazed by cattle and typically burned more frequently in the

16   dormant spring season, but some of the cattle pastures were utilized for smaller scale (2,350 ha)

17   patch-burn experiments in which only one-third of a given management unit was burned

18   annually (Hamilton 2007). Stocking within the cattle pastures included both intensive-early

19   stocking and season-long stocking, which contrasted with the year-round stocking in the bison

20   unit.

21   *Data collection*

22   The management units were spatially aggregated and temporally variable; therefore, a

23   spatially stratified semi-random sampling design was necessary to ensure that samples were

1   representative of the broader variation in grassland communities across the preserve (Palmer

2   1995). We selected twenty 100 m^2 plots to resample through time (Fig. 1) from a set of 157

3   permanent plots that were located on a 1-km UTM grid within the TGPP (Palmer et al. 2002).

4   The only criteria that we imposed on the selection of the resample plots were that they had no

5   standing water and less than 20 % cover of woody plants or exposed rock. We opted to annually

6   resample the sites to observe the vegetation at a given site in multiple management states (e.g.,

7   one year post burn, bison vs. cattle grazed), and to provide information on inherent year-to-year

8   variation.

9   Each year we combined four 15 cm soil cores collected at each corner of the plot and sent

10   these to Brookside Labs (New Knoxville, Ohio) to be analyzed for soil cations, pH, and other

11   variables. We recorded topographic data on slope and aspect in the field. We obtained total

12   monthly precipitation data from the Oklahoma Mesonet Foraker site (36.841° N, -96.428° W;

13   elevation: 330 m; Fig. 1), which is located on the preserve (McPherson et al. 2007). We

14   calculated total precipitation for three arbitrarily defined season variables (four months each):

15   June through September (summer), October through January (winter), and February through

16   May (spring).

17   To examine the importance of variation in fire and grazing we employed three variables:

18   years of bison grazing, years since burn, and number of burns in the past five years, from a GIS

19   database that we developed based on TNC's recorded burn and grazing history. We recognize

20   that the number of burns in the past five years is negatively correlated with years since last burn

21   (see Appendix A) and reflects somewhat of an arbitrary cutoff point (five years), but we chose to

22   include this variable in our models despite these shortcomings because we wished to quantify the

23   short-term burn history of a site which is not captured by "years since burn". Additionally the

1   detailed fire record does not extend beyond five years prior to the beginning of the study. We

2   chose not to include season of burn as an explanatory variable because 83% (67 out of 80) of the

3   prescribed fire events recorded on our study sites took place during the dormant season.

4   It is important to note two aspects of the fire and grazer variables: 1) the application of

5   fire and grazer was heterogeneous in space and time (i.e., there were no fixed treatments), and 2)

6   the variables "time since fire" and "number of burns in the past five years" are inherently

7   temporally variable (i.e., even if a site had experienced a fixed fire-return interval, these

8   variables would display variation through time).

9   We grouped species into five functional groups to aid in the ecological interpretation of

10   patterns of species richness and composition we observed. The functional groups were forbs,

11   legumes, C3 grasses, C4 grasses, and shrubs.

12   All of the data used in this study are archived and available to the public online (McGlinn

13   et al. 2010).

14   *Data analysis*

15   Our goal when modeling richness and species composition was to develop explanatory

16   models and not predictive models, *sensu* Mac Nally (2000). Therefore, we were primarily

17   concerned with comparing the explanatory strength of variables that were chosen *a priori* rather

18   than developing a single most accurate or necessarily most parsimonious model. We coded site

19   and years as dummy variables to quantify site and year effects relative to fire and grazing

20   variables. We then performed a post-hoc examination of the specific environmental variables

21   (described in *Data collection*) that we believed may explain the site and year effects. Given the

22   observational nature of this study, many of our environmental variables (e.g., soil cations, total

23   spring rain) were strongly collinear and likely act as proxy variables. Therefore, to increase the

1   clarity of our results, we only examined a small number of environmental variables. Additionally

2   we note that the primary objectives of this study did not depend on elucidating the specific

3   environmental sources of spatial and temporal heterogeneity. We selected calcium as the soil

4   variable to examine because previous work indicated it acted as a proxy for limestone (rather

5   than sandstone) derived soils and was strongly correlated with richness (Palmer et al. 2003,

6   Brokaw 2004). We included field measurements of slope and aspect in the analysis which we

7   expect to reflect variation in the degree of moisture and solar exposure. Aspect was converted to

8   an index of northness [northness = cos(aspect)] (Roberts 1986). We did not include a

9   corresponding index of eastness as exploratory results indicated it was unimportant (not shown).

10   We first used ordinary least squares (OLS) and generalized least squares (GLS) to dissect

11 relationships between species richness and our various explanatory variables. OLS is ideal for

12 providing interpretable estimates of variance explained; however, exploratory analyses revealed

13 the presence of year-to-year temporal autocorrelation in richness which violates one of OLS's

14 assumptions. We therefore used first-order autoregressive GLS models to correct for the

15 temporal autocorrelation. First-order autoregressive models are some of the simplest models of

16 temporal autocorrelation, and they attempt to correct for short-term autocorrelation between

17 samples within a site (Pinheiro and Bates 2000, p. 228-229). The GLS models were fit with a

18 restricted maximum likelihood algorithm, which is the preferred method for generating unbiased

19 estimates of variance in models that have a relatively large number of parameters (Diggle et al.

20 1994). The R package *nlme* version 3.1-90 (Pinheiro et al. 2008) was used to carry out all GLS

21 model fitting and diagnostics.

22   We used variation partitioning (or commonality analysis) to estimate the unique and

23 shared fractions of explained variation in three groups of variables (or factors), sites, years, and

1 fire and grazing on richness (Legendre and Legendre 1998, Peres-Neto et al. 2006). Sites and

2 years were coded as dummy variables and the fire and grazer group was composed of the three

3 fire and grazer variables described above. The independent component of variation attributable

4 to fire and grazer should be interpreted as variation within-sites which was independent of

5 specific years and was associated with temporal changes in the fire and grazer variables that

6 occurred over the study period. For example, over the course of the study, seven of the sites

7 changed from cattle grazed to bison grazed. The analysis associated changes in these sites after

8 their change in grazer that was independent of a specific year effect with the variable "years of

9 bison grazing". In contrast, if a site remained in the cattle unit for the duration of the study then

10 the variable "years of bison grazing'' would not have been associated with explained temporal

11 variance at that particular site.

12 We carried out partitioning with OLS as well as with GLS multiple regressions. For each

13 fraction of the OLS analysis, we report both the coefficient of determination and its adjustment

14 for number of variables, R^2 and R^2_{adj} respectively. For the GLS fractions we calculated a

15 generalized formulation of the coefficient of determination, R^2_{GLS}, that is appropriate for GLS

16 models (Nagelkerke 1991). We used approximate, conditional (type III) F-tests to assess if a

17 group or variable explained a significant amount of variance in richness.

18 In all analyses we treated species richness as a continuous variable with normally

19 distributed error. We recognized that in some modeling contexts it is more appropriate to

20 consider richness as a Poisson distributed variable (Candy 1997, Palmer and Hussain 1997).

21 However, because the normal distribution provides a good approximation of a Poisson random

22 variable when the mean is larger than approximately 20; we feel that our usage of normal errors

23 (instead of Poisson) is justified given that richness was never below 48 in our samples. We also

1 recognize that some authors consider richness to only be one facet of grassland biodiversity and

2 that other diversity indices can yield more insight into the ecology of the system (Wilsey et al.

3 2005, Chalcraft et al. 2009). However, in this study richness was so strongly correlated with all

4 of the indices examined in Wilsey et al. (2005) that additional analyses on various diversity

5 indices would have yielded little additional insight (see Appendix B).

6   We used both indirect and direct gradient analyses to examine species composition. Prior

7 to all ordinations, we square-root transformed all species cover data to decrease the influence of

8 the most abundant species on the analysis, and we down-weighted rare species. Detrended

9 Correspondence Analysis (DCA; Hill and Gauch 1980) was used to display directionality of

10 change in the plant composition through time and to illustrate the magnitude of temporal

11 variation relative to spatial variation. Results from non-metric multidimensional scaling (NMS)

12 were qualitatively similar to those of DCA and had identical interpretations, and are therefore not

13 shown.

14   We carried out variation partitioning using partial canonical correspondence analysis

15 (pCCA) (Borcard et al. 1992, Økland 1999) to assess species composition. The groups used in

16 the variation partitioning were as defined above for richness. We calculated Peres-Neto et al.'s

17 (2006) formulation of the adjusted fraction of variation explained in CCA using a permutation

18 approach (R^2_{CCAadj}). To our knowledge, correlational models for the residuals have not been

19 theoretically developed within the direct ordination context and therefore these methods were not

20 applied in our analysis of species composition. However, when testing the importance of

21 dependent variables that accounted for the within-site variability in species composition, we

22 conducted a toroidal shift Monte Carlo test (Legendre 1993, ter Braak and Šmilauer 2002b).

23 This method of permutation maintains the observed order of the samples within a site while

1 nullifying the temporal relationship of samples between sites. When the constraining variable

2 was site specific, we carried out permutations that randomly shuffled samples only within their

3 year of occurrence to conform with our assumption of spatial independence between sites but not

4 years. All randomization tests were conducted with 999 iterations to determine significance of

5 all canonical axes for all partial CCA axes under the reduced model (Legendre and Legendre

6 1998, p308). As in the analysis on richness, we constructed models to examine the importance

7 of specific explanatory variables with estimates of variation explained and conditional *F*-tests.

8 We performed multivariate analyses with CANOCO version 4.5 (ter Braak and Šmilauer 2002a)

9 and the R package *vegan* version 1.15-1 (Oksanen et al. 2008, R Development Core Team.

10 2008). A total of 25 tests were performed, and to minimize our Type I error rate we used the

11 Bonferroni alpha level of 0.002 (= 0.05/25) to judge significance.

12 **Results**

13 *Variance in species richness*

14 The average species richness over the 11 year study at the 100 m^2 grain was 76.24 (±

15 0.86) of which between 5-7% were exotic species. The between-year variance ($\sigma = 9.13$) in

16 richness was approximately equal to the between-site variance ($\sigma = 8.93$). There were not strong

17 directional changes in total richness or in the five functional groups through time (Fig. 2). Forbs

18 were more species-rich than all other functional groups. Variation partitioning of the unbiased

19 OLS estimate of variance explained (R^2_{adj}; Table 1), indicated that between-site differences

20 accounted for the majority of variance in richness ($R^2_{adj} = 0.48$), followed by year-to-year

21 differences ($R^2_{adj} = 0.13$). However, after within-site temporal autocorrelation was considered

22 (using a first-order auto-regressive term), the strength of site identity relative to year identity was

23 diminished substantially according to Nagelkerke's (1991) generalized definition of the

1   coefficient of determination. In both OLS and GLS based variation partitioning, the fire/grazer

2   class of variables accounted for a much smaller percentage of explained variance in richness (2–

3   4 %) than the site and year variables, but still contributed a significant amount of explained

4   variation (Table 2). There was a large shared fraction of variation (R^2_{GLS} = 0.25) between site and

5   year that was only apparent after correcting for the inherent temporal autocorrelation. The

6   shared fractions of variance between the fire/grazer class of variables and each of the other

7   groups were approximately equal to the independent effect of the fire/grazer group (2-4%).

8   The strongest correlate for explaining site-to-site differences in richness was log Ca,

9   which was negatively correlated with richness (standardized coefficient, $\hat{\beta}$ = -0.42) (Table 2).

10   Topography did not seem to have a strong influence on richness as neither slope nor northness

11   explained much variation in richness.

12   Temporal variation in richness within the sites was attributable to both climate and fire

13   and grazing variables. The most important seasonal rainfall variable was summer rain, which

14   was negatively correlated with richness ($\hat{\beta}$ = -0.19); winter rain and spring rain appeared equally

15   important and both were positively associated with richness ($\hat{\beta}$ = 0.15 and 0.14, respectively).

16   The single most important fire and grazing variable was years of bison, which was positively

17   associated with richness ($\hat{\beta}$ = 0.46). Both years since burn and number of burns in the past five

18   years were negatively associated with richness but neither variable was found to explain

19   significantly more variation in richness than due to chance at the Bonferroni corrected alpha

20   level of 0.002 (Table 2).

21   *Variance in species composition*

22   The DCA scatterplot did not illustrate a strong directional change in species composition

23   (Fig. 3). Furthermore, sites remained relatively separate from one another in ordination space,

1   which indicates that among-site variation in species composition was greater than temporal

2   variation within sites, despite a dynamic fire regime. There was not a strong difference in

3   sample scores between sites that were bison- versus cattle-grazed along the first through fourth

4   DCA axes (third and forth axes not shown). Furthermore, when samples switched from cattle to

5   bison, their trajectory through time did not change substantially. The results of the NMDS (not

6   shown) corroborated these qualitative results.

7   Variation partitioning based upon pCCA indicated that site effects explained the majority

8   of the variation in species composition ($R^2_{\mathrm{CCAadj}} = 0.46$, Fig. 4). Year and fire and grazing effects

9   on species composition were negligible after adjustment, but both were still found to be

10   significant in randomization tests at the 0.05 level (Table 3). There was a relatively large shared

11   site and fire and grazing fraction ($R^2_{\mathrm{CCAadj}} = 0.08$) of explained variation. The pCCAs that

12   considered site specific explanatory variables after factoring out year and fire and grazing effects

13   indicated that log Ca was the most important site specific variable ($R^2_{\mathrm{CCAadj}} = 0.07$; Table 3).

14   The pCCA biplot displays only the 90 most abundant species (although all 307 species

15   were included in the analysis) with respect to the three fire and grazing variables after factoring

16   out year and site effects as dummy variables (Fig. 5). Although the variation explained by these

17   variables was slight (Table 3), it was interpretable. It appeared that both C3 and C4 grasses

18   (open and filled black circles on biplot respectively) appeared to decrease in cover with increased

19   years of bison grazing. *Lespedeza cuneata* (sericea lespedeza), an invasive species, was

20   positively correlated with years of bison grazing. However, this species is a target for spot

21   herbicide application by the TNC so care must be taken in interpretation of this result. Annual

22   and ruderal species, such as *Chamaesyce nutans* (eye bane), *Plantago virginica* (Virginia

1 plantain), *Ambrosia artemisiifolia* (annual ragweed), and *Andropogon virginicus* (broomsedge

2 bluestem), all were positively associated with the number of burns in the past five years.

3 **Discussion**

4 The purpose of our study was to examine the influence of variation in fire and grazing on

5 plant richness and composition relative to intersite and interyear variability. Our results suggest

6 that the grasslands of the TGPP are not undergoing strong directional changes in richness or

7 composition through time (i.e., they do not appear to be on a clear trajectory). Rather, sites

8 appear to maintain their differences over time. This is not to say that the effects of variation in

9 fire and grazing on richness and composition independent of site and year were irrelevant and

10 uninterpretable, but simply that fire and grazing were relatively unimportant relative to inherent

11 temporal and spatial heterogeneity.

12 *Role and drivers of site-to-site variation*

13 The bulk of the variation in richness and composition was due to differences between

14 sites, which we believe primarily reflects belowground environmental differences. We found

15 that soil calcium explained the predominant amount of site-to-site variability in both richness and

16 composition (Table 2). We interpret calcium's importance to be due to its role as a proxy

17 variable for many other soil properties which are generally indicative of limestone derived soils

18 (Palmer et al. 2003, Brokaw 2004). Using the same 20 sites analyzed in this study (only for the

19 year 2002), Brokaw (2004) found that out of a set of 12 different soil nutrients and total carbon

20 that the two most important variables for explaining plant composition (using pCCA) were total

21 carbon and residual phosphorus. These two variables were strongly positively correlated with

22 the majority of soil nutrients and calcium which Brokaw (2004) interpreted as general indicators

23 of limestone parent materials. These findings suggest that the important role that calcium, as an

1   indicator of bedrock, played in our study does not necessary contradict the body of work that

2   suggests that below ground nutrients other than cations are the predominant drivers of plant

3   richness and composition in tallgrass prairie ecosystems (Turner et al. 1997, Burke et al. 1998,

4   Baer et al. 2003, 2004).

5   Why was the relationship between calcium and richness negative? The positive

6   relationship between calcium and soil nutrients (that Brokaw [2004] found in our samples)

7   suggests one possible explanation. If soils high in calcium are the productive, nutrient rich sites,

8   then plant species at these sites may experience stronger competitive exclusion and therefore

9   have lower richness (Grime 1973, Tilman 1982). Pärtel's (2002) species pool hypothesis offers

10   an alternative hypothesis for the negative correlation between richness and calcium. The species

11   pool hypothesis postulates that negative correlations between richness and pH (or calcium given

12   their tight correlation) will occur in regions in which habitats high in pH were evolutionarily

13   scarce. Palmer et al. (2003) found that the data from the Tallgrass Prairie Preserve (including

14   this study's sites as well as many others) appeared to support Pärtel's (2002) hypothesis in the

15   grasslands but not in the woodlands.

16   *Role and drivers of year-to-year variation*

17   Year-to-year variation was more influential for richness than species composition. This

18   indicates that year-to-year changes in richness were primarily by rarer species that were not

19   strongly positively associated with one another. Year effects explained almost equal amounts of

20   variation in richness as site effects (21% compared to 25%, respectively) with 9 fewer

21   parameters. With respect to species composition, year effects were much less than the site

22   effects and were more comparable with the small influence of the fire and grazer effect (both

23   were < 1%).

1   Climatic variability is the most obvious candidate for a driver of year-to-year variation

2 (that is independent of fire and grazing effects). In grassland plant communities, water is

3 typically viewed as an important limiting resource, and it is generally positively associated with

4 richness (Cornwell and Grubb 2003, Adler and Levine 2007, Wilson 2007). In our study,

5 richness was positively correlated with the winter and spring seasonal precipitation variables, but

6 negatively correlated with the summer precipitation variable. In fact the negative correlation

7 between richness and summer rainfall resulted in the strongest partial correlation (Table 2).

8 Following Adler and Levine (2007), increased precipitation may act on richness directly by

9 making the environment more benign and thus allowing more species to coexist. However, if

10 this was generally true, then it is difficult to explain the strong negative correlation observed for

11 summer rainfall. An alternative season specific hypothesis that may explain the negative

12 relationship with summer rainfall is that increased precipitation in the summer previous to

13 sampling yields higher aboveground cover of C4 grasses. High yields of aboveground biomass

14 could act to both inhibit germination of annuals and biennials at the beginning of the next

15 growing season as well as increase asymmetric light competition due to increased litter (Grace

16 2001). The positive influence of spring and winter rains may also be explained by the critical

17 role that rainfall plays in stimulating germination in the annuals and biennials during the dormant

18 seasons. To be clear in both of these explanations precipitation is viewed as a non-resource

19 variable that indirectly influences richness by increasing aboveground primary productivity the

20 summer prior to sampling and/or by influencing germination of species-rich plant groups (Grace

21 2001, Adler and Levine 2007).

1   *Fire and grazer effects*

2   Fire and grazer effects explained a significant component of the variance we observed in

3   richness and composition, but these effects appeared relatively unimportant compared to

4   contextual spatial and temporal heterogeneity. The historical and regional context of our study

5   site may have contributed to this result. Specifically, prior to TNC's ownership, the site was

6   managed using prescribed annual burning and cattle grazing (R. Hamilton, *personal*

7   *communication*). These management practices are common in the Flint Hills region (Malin

8   1942, Kollmorgen and Simonett 1965) and are likely one of the primary reasons this region has

9   maintained intact tallgrass prairie vegetation (Samson and Knopf 1994). Without this land

10   management legacy, it is likely that we would have observed a much stronger influence of fire

11   and grazing because our study sites would have initially contained higher abundances of

12   disturbance-sensitive species, such as *Juniperus virginiana* (eastern redcedar) which we seldom

13   observed (and only as seedlings) in our sites but has aggressively invaded much of the southern

14   Great Plains due to fire suppression (Briggs et al. 2005). Additionally, we did not compare our

15   samples to control sites that received no burning and/or grazing, although some of our sites went

16   as long as 10 years without fire. We expect that longer periods without fire (than typically

17   observed in our study) would have resulted in both increased cover of woody plants (as

18   described above) and a stronger negative correlation between time since fire and richness due to

19   the gradual accumulation of litter which would have suppressed richness (e.g., Lamb 2008).

20   Therefore, in light of the fact that our study site represents a relatively intact tallgrass prairie with

21   a long history of fire and grazing; it is not necessarily surprising that landscape soil heterogeneity

22   and climatic variation had a stronger influence.

1   Although the fire and grazing variables explained little variation overall, years of bison

2   grazing had a strong positive relationship with richness (Table 2). This suggests that TNC's

3   system of bison management at the TGPP is having a positive influence on plant species

4   richness. We stress bison *management* rather than the influence of bison directly because the

5   average fire-return interval was generally longer and the season of burn was more variable in the

6   bison units when compared with the cattle units (Hamilton 2007). In addition, the bison units

7   were grazed year round, while the cattle units were only seasonally grazed. Therefore, we are

8   fairly confident bison *management* is having a positive effect on richness, but we are less

9   confident that this is due to the presence of bison in comparison to cattle.

10   Other authors have proposed that bison may indirectly increase plant richness because

11   they show grazing preference for graminoids rather than forbs (in contrast to cattle which behave

12   more as generalists) (Coppedge et al. 1998b, Knapp et al. 1999). This dietary behavior may

13   release forbs from competitive exclusion due to the dominant C4 grasses. In our study, years of

14   bison grazing was negatively correlated with the cover of the majority of C3 and C4 species (Fig.

15   5). The increase in richness and decrease in graminoid cover in the bison managed sites lend

16   modest support to the hypothesis that bison may increase richness of tallgrass prairie by

17   decreasing the cover of graminoids relative to sites that were grazed seasonally by cattle.

18   Towne et al. (2005) undertook a more controlled approach to investigating the effects of

19   bison and cattle grazing on plant richness and composition at the Konza Prairie LTER over a 10

20   year period in annually burned pastures. They also found that overall the differences between

21   bison and cattle were slight but that bison grazed patches had a higher cover of some forb species

22   and gained forb species at a more rapid rate through time. They concluded the differential

23   responses of vegetation to bison or cattle grazing may be predominately due to differences in

1   management of these grazers rather than inherent differences in their biology. A similar effect

2   may be taking place at our study site as well.

3   Years since last burn was most strongly correlated with changes in species composition

4   (Fig. 5), but the other two fire and grazing variables explained comparable amounts of variation

5   (Table 3). Other studies have noted the strong positive relationship between the cover of

6   legumes and C4 grasses with frequency of dormant season burning (Hulbert 1988, Towne and

7   Knapp 1996, Coppedge et al. 1998a, Peterson et al. 2007), although 84% of the burns in our

8   samples occurred during the dormant season, there was not a clear relationship between fire

9   frequency and either of these functional groups (Fig. 5). We found anecdotal evidence that

10   ruderal species were positively associated with the number of burns in the past five years (Fig.

11   5), which is to be expected given that these samples were likely to have higher grazing pressure

12   due to their more nutritious regrowth (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001).

13   *Management implications*

14   The results of our study demonstrated that plant richness and composition may be

15   relatively insensitive to fire frequency and grazer type in an intact tallgrass prairie with a long

16   legacy of prescribed fire and grazing. This suggests that fine-tuning a management plan with

17   respect to fire frequency or grazer identity may be of less importance given the potentially large

18   sources of inherent landscape heterogeneity on the landscape (Knapp et al. 1999). This may be

19   welcome news for land managers because it suggests that intact tallgrass prairie plant

20   communities may be relatively resilient to uncertainty in the prescription of fire frequency and

21   grazer choice as long as some combination of fire and grazing is present on the landscape.

22   Although our study did not examine long-term unburned and/or ungrazed sites, it is worth

23   noting that tallgrass prairie landscapes managed in this way are likely to experience increased

1 woody encroachment (e.g., Briggs et al. 2002), in which case decisions about fire frequency and

2 grazer species may become critical to restoring the plant community (Peterson and Reich 2001,

3 Peterson et al. 2007, Papanastasis 2009).

4 At our study site, TNC is utilizing a variable application of prescribed fire to meet several

5 objectives. One goal is to maintain or increase the biological diversity of the plant community

6 (Hamilton 2007). The non-directional changes in species richness and composition coupled with

7 the high overall magnitude of average richness and low proportion of exotic species we observed

8 during the 11-year period, suggest that the management decisions are at the very least are not

9 detrimental to the plant community. TNC is also attempting to manage for wildlife habitat and

10 diversity. Structural heterogeneity in the vegetation, attributed to the variable application of fire,

11 resulted in the development of suitable habitat for a wider breadth of grassland bird species at the

12 TGPP (Fuhlendorf et al. 2006, Coppedge et al. 2008). These results in conjunction with our

13 findings suggest that the management decisions at the preserve are contributing to important

14 conservation goals, even if their effects on plant richness and composition are slight.

15 *Conclusions*

16 In a relatively intact tallgrass prairie the influence of spatiotemporal variation in fire and

17 grazing on plant richness and composition was relatively minor relative to inherent variation

18 between sites and years. Nevertheless, variation in fire and grazing had significant and

19 interpretable effects, and we detected a significant positive correlation between bison

20 management and plant richness. Given the overriding influence of inherent landscape

21 heterogeneity on the plant community, fine-tuning management prescriptions that incorporate the

22 variable application of fire and grazing may not be crucial for maintaining native tallgrass prairie

23 plant communities.

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12

1 **Tables**

2 Table 1. Variation partitioning of species richness into its components for site, year, and

3 fire/grazer variables. Note that the groups: site, year, and fire and grazer consist of q explanatory

4 variables. The site and year groups were coded as dummy variables (see *Methods* for

5 explanation). The partitioning was conducted with respect to the unadjusted and adjusted OLS

6 coefficients of determination (R^2 and R^2_{adj} respectively) as well as coefficients of determination

7 for GLS models (R^2_{GLS}) incorporating a single autoregressive term.

Explanatory Groups (q)	Covariable Groups	OLS		GLS (AR1)
		R^2	R^2_{adj}	R^2_{GLS}
site (19)	year + fire/grazer	0.48	0.48	0.27
year (10)	site + fire/grazer	0.13	0.13	0.18
fire/grazer (3)	site + year	0.04	0.04	0.02
site + year	fire/grazer	0.01	-0.02	0.25
site + fire/grazer	year	0.05	0.05	0.04
year + fire/grazer	site	0.08	0.07	< 0.01
site + year + fire/grazer	NA	-0.01	-0.02	< 0.01
Total (32)		0.77	0.74	0.77

8

9

1   Table 2. The conditional explanatory power of specific variables on species richness estimated

2   with the GLS autoregressive models. The classes site, year, and fire and grazer consist of q

3   explanatory variables. Each model incorporated only a single autoregressive term. Provided are

4   the standardized regression coefficient ($\hat{\beta}$) indicating strength and direction of the response of

5   richness, an estimate of variation explained (R^2_{GLS}), and the results of conditional F-tests

6   (approximate tests).

Explanatory Variables	Covariables	$\hat{\beta}$	R^2_{GLS}	F-ratio	p-value
Groups (q)					
site (19)	year + fire/grazer	NA	0.27	11.53	< 0.001
year (10)	site + fire/grazer	NA	0.18	13.17	< 0.001
fire/grazer (3)	site + year	NA	0.02	6.40	< 0.001
Site Specific Variables					
log Ca	slope + northness + year + fire/grazer	-0.42	0.04	25.39	< 0.001
slope	log Ca+ northness + year + fire/grazer	-0.12	< 0.01	1.88	0.172
northness	log Ca + slope + year + fire/grazer	0.17	0.01	4.02	0.047
Year Specific Variables					
summer rain	winter rain + spring rain + site + fire/grazer	-0.19	0.03	26.65	< 0.001
winter rain	summer rain + spring rain + site + fire/ grazer	0.15	0.02	15.47	< 0.001
spring rain	summer rain + winter rain + site + fire/ grazer	0.14	0.01	11.43	0.001
Fire/Grazer variables					
years of bison	years since burn + # of burns in 5 years + site + year	0.46	0.01	12.00	< 0.001
years since burn	years of bison + # of burns in 5 years + site + year	-0.14	< 0.01	5.67	0.018
# of burns in 5 years	years of bison + years since burn + site + year	-0.15	< 0.01	2.82	0.095

7

1 Table 3. The results of Monte Carlo randomization tests using the results of pCCA under the

2 reduced model. Each randomization test was conducted with 999 iterations. The groups site,

3 year, and fire and grazer consist of q explanatory variables. Cells marked as "**--**" indicate that

4 their values are identical to cells above.

Explanatory Variable	Covariables	Randomization Type[*]	R^2_{CCA}	R^2_{CCAadj}	F-ratio	p-value
Groups (q)						
site (19)	year + fire/grazer	random shuffle	0.50	0.46	13.471	0.001
year (10)	site + fire/grazer	toroidal shift	0.04	< 0.01	2.248	0.001
fire/grazer (3)	site + year	random shuffle	0.01	< 0.01	2.145	0.001
--	--	toroidal shift	--	--	--	0.001
Site Specific Variables						
log Ca	slope + northness + year + fire/grazer	random shuffle	0.13	0.12	19.735	0.001
slope	log Ca+ northness + year + fire/grazer	random shuffle	0.03	0.03	8.152	0.001
northness	log Ca + slope + year + fire/grazer	random shuffle	0.02	0.01	5.219	0.001
Fire/Grazer Variables						
years of bison	years since burn + # of burns in 5 years + site + year	random shuffle	< 0.01	< 0.01	2.314	0.001
--	--	toroidal shift	--	--	--	0.001
years since burn	years of bison + # of burns in 5 years + site + year	random shuffle	< 0.01	< 0.01	2.102	0.001
--	--	toroidal shift	--	--	--	0.001
# of burns in 5 years	years of bison + years since burn + site + year	random shuffle	< 0.01	< 0.01	1.616	0.001
--	--	toroidal shift	--	--	--	0.021

5 * random shuffle permutations were constrained to occur within a year, toroidal shifts were
6 constrained within a given a site and preserved the temporal order of samples (see *Methods* for
7 more explanation)
8

1 **Figure Legends**

2 Fig. 1. A map of the Tallgrass Prairie Preserve. The shaded area denotes the bison unit which

3 increased in area during the study period. The Mesonet tower where the climate data was

4 recorded is marked on the map as a star (★). The twenty plots sampled each year of this study

5 are displayed on the map. The sites that were bison at the beginning of the study (1998) are

6 displayed with filled triangles (▲), those that transitioned during the study from cattle to bison

7 are denoted by unfilled triangles (∆), and the other cattle grazed samples are denoted by unfilled

8 circles (○). *Area of bison unit is as of 1 May 2008.

9 Fig. 2. The average species richness of five functional groups: forbs (that are not legumes),

10 legumes, C3 graminoids (grasses, sedges, and rushes), C4 graminoids (grasses), and shrubs

11 (woody plants) over the course of the study. The error bars display $\bar{x} \pm 1$ standard error.

12 Fig. 3. DCA scatterplot displaying the 20 sites from 1998 to 2008. The eigenvalues were 0.152

13 and 0.108 for the first and second axis respectively. The time series is indicated by a line

14 segment (—) with joints at each year, a black line joins years in which the plot experienced bison

15 grazing and a grey line demarcates years in which the plot experienced cattle grazing. The 1998

16 samples are indicated by circles (●) and the 2008 samples are indicated by squares (□).

17 Fig. 4. A Venn diagram displaying the R^2_{CCAadj} (followed by R^2_{CCA} in parentheses) of each fraction

18 resulting from the variation partitioning of species composition using pCCA. The three groups

19 (classes of explanatory variables) were sites, years, and fire and grazing. Note that R^2_{CCAadj} in this

20 context should not be interpreted as the fraction of explained variance but rather as the fraction

21 of explained inertia. For the shared fractions we only report the unbiased R^2_{CCAadj} values.
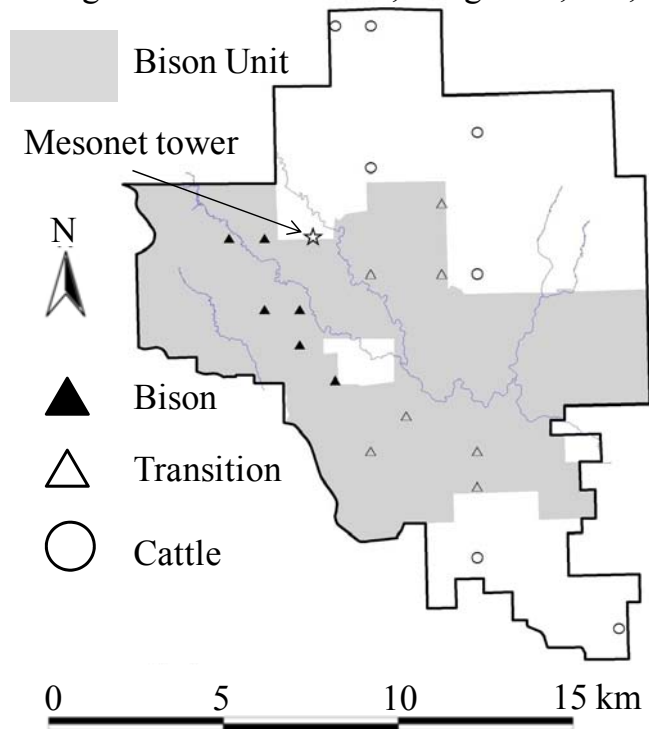
22 Fig. 5. A pCCA biplot displaying the influence of the fire and grazer variables with the sites and

23 years as covariables. The fire and grazer variables in the model are indicated by black arrows.

1   Only the 90 most abundant species of the 307 total are displayed for clarity. Abbreviations

2   represent the first four letters of the genus and the first four of the letters of the species (see

3   Appendix C). The symbol of each species depends on which functional type it belongs to (see

4   legend).

5

1   **Figures**

The Nature Conservancy's
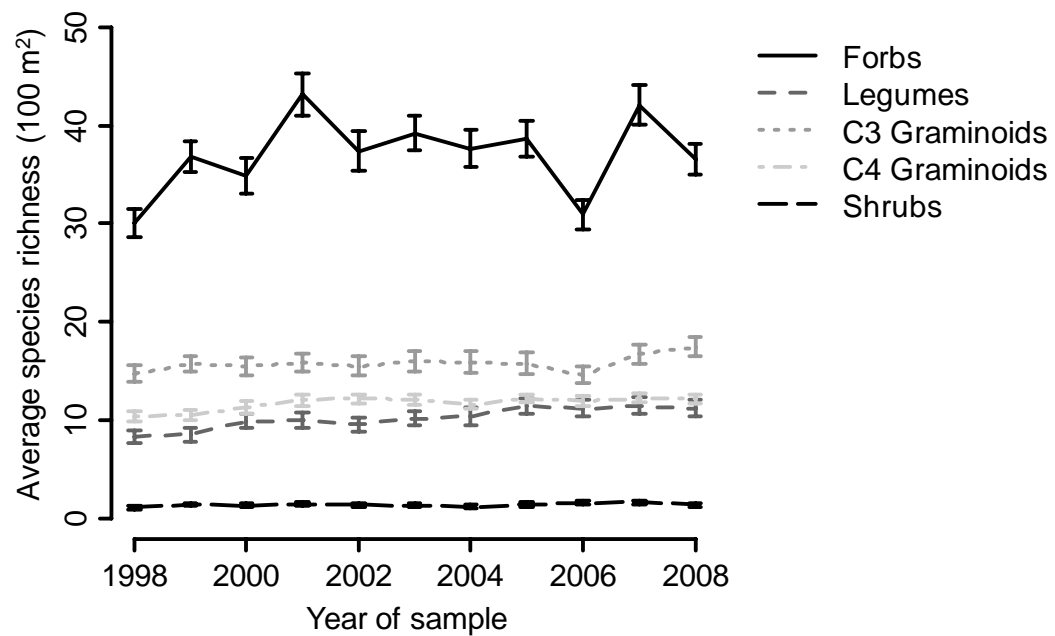Tallgrass Prairie Preserve, Osage Co., OK, USA

Bison Unit

Mesonet tower

N

▲ Bison

△ Transition

○ Cattle

0   5   10   15 km

Preserve Area ≈ 15,700 ha
Bison Unit Area ≈ 8,500 ha (54%)*

2

3   Fig. 1.

1

2   Fig. 2.

1

2   Fig. 3.

Site + Year

0.46 (0.50)
Site

0.03

0.00 (0.04)
Year

0.00

0.08

0.00

Site + Fire/Grazer

0.00 (0.01)
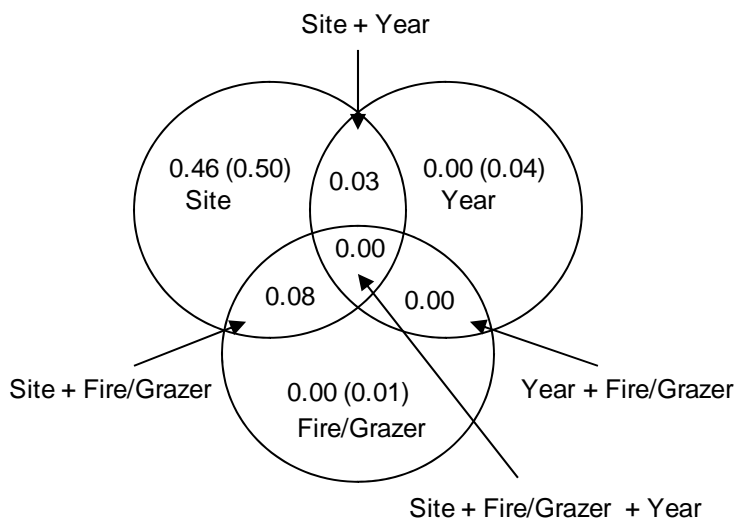Fire/Grazer

Year + Fire/Grazer

Site + Fire/Grazer + Year
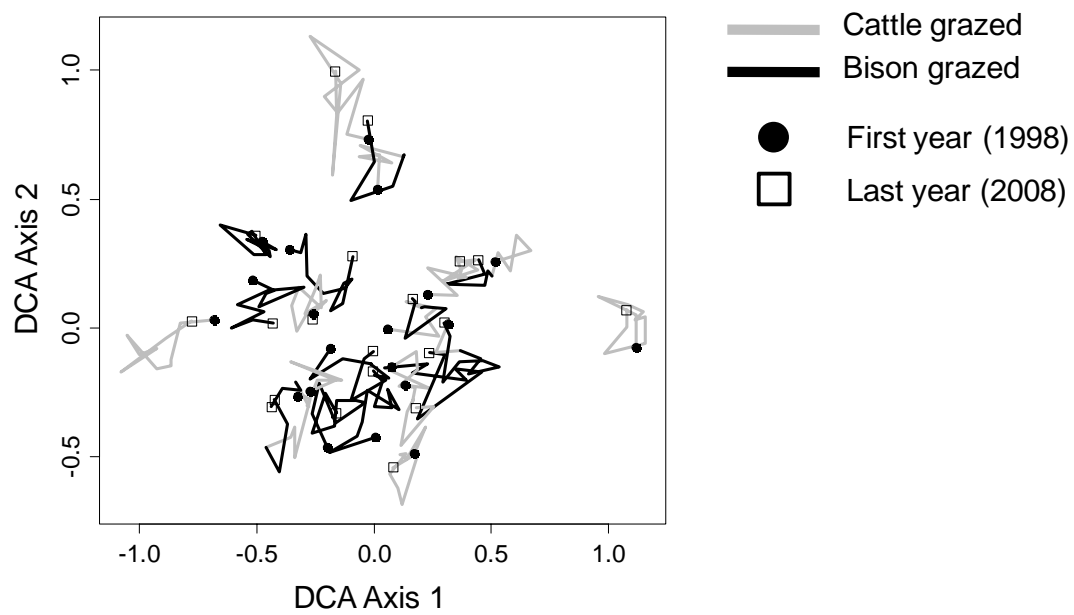
Total inertia = 1.48
$R^2_{CCAadj} = 0.57 (0.63)$

1

2   Fig. 4.

Fig. 5.