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Moderate Grazer Density Stabilizes Forage Availability More Than Patch Burning in Low-Stature Grassland

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Abstract: Spatially patchy fire creates landscape-level diversity that in turn stabilizes several rangeland ecosystem services, including forage production and habitat availability. To enhance biodiversity and livestock production, efforts are underway to restore fire regimes in rangelands throughout the Great Plains. However, invasive species such as tall fescue *Schedonorus arundinaceus* syn. *Festuca arundinacea*, initially introduced for forage production, hamper prescribed fire use. Grazer density, or stocking rate, modulates the effect of patchy fire regimes on ecological patterns in invaded, semi-natural rangeland pastures. We compare three diversity–stability responses—temporal variability in aboveground plant biomass, portfolio effects among plant functional groups, and beta diversity in plant functional group composition—in pastures managed with two different fire regimes through three periods of heavy, light, and moderate stocking rate in southern Iowa, USA. Pastures were either burned in patches, with one-third of the pasture burned each year, or completely burned every third year. The period of moderate grazer density had the least temporal variability in aboveground plant biomass, regardless of fire regime. We also found statistical evidence for a portfolio effect under moderate stocking, where diversification of plant communities through varying cover of functional groups can stabilize communities by reducing year-to-year variability. Beta diversity among plant functional groups was greatest during the moderate grazer density period as well. The short stature of tall fescue prevented the patch-burning regime to create contrast in vegetation structure among patches, and there was no difference in any diversity–stability mechanism response across the two different patterns of burning. Although longitudinal, these data suggest that temporal variability in aboveground plant biomass declines with diversity–stability mechanisms that underlie ecosystem function. Our results also support a decades-old principle of range management: moderate grazing intensity enhances diversity and stability, which has been shown to buffer forage shortfalls during drought.

Keywords: diversity–stability; fire–grazing interaction; great plains; temporal variability

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1. Introduction

Rangelands of the North American Great Plains evolved under a distinct disturbance regime characterized by the interaction of fire and grazing by bison (*Bison bison*) [1]. The fire regime of the eastern part of the region, the mesic tallgrass "prairie peninsula", has long been attributed to Native American activity [2]. The interaction between fire and grazing produced dynamic landscape-level patterns in vegetation structure, a shifting mosaic of patches defined by a time-since-fire temporal gradient [3]. Short vegetation and extensive bare ground characterize recently burned patches; post-fire regrowth is the highest-quality forage in the landscape, which attracts grazers and maintains the low, open vegetation stature [4,5]. Grazers avoid unburned patches in which vegetation grows tall and litter accumulates, creating dense cover for wildlife and an ideal fuelbed for future ignitions [6,7].

The tallgrass prairie region was transformed into a landscape of production agriculture, the legacies of which complicate efforts to restore pre-colonial ecological structure and function. By the end of the 19th century, European-American colonization of the Great Plains effectively eliminated bison grazing and pre-colonial fire regimes [8], which decoupled the interaction between fire and grazing [1]. Recognizing that fire is important to control woody plant cover and a shifting mosaic akin to the pre-colonial landscape is critical to a breadth of native biodiversity [9], there is a "rising Great Plains fire campaign" in which land managers use prescribed fire [10]. However, simply reintroducing fire is difficult when the nature of the vegetation has been altered by socio-ecological developments undertaken since fire was initially removed from the system. Today, reconstructed and even native prairie parcels are often highly invaded by non-native plant species introduced for their forage value in intensive grazing systems such as tall fescue (*Schedonorus arundinaceus* syn. *Festuca arundinacea*) [11], which despite its common name grows substantially shorter than native tallgrass species and precludes patch contrast in vegetation structure [7].

Restoring fire regimes and landscape-level heterogeneity in grassland ecosystems dominated by low-stature forage species like tall fescue is challenging [12]. Tall fescue alters prairie fuelbeds and reduces fire spread, making the initial application of effective prescribed fire difficult [13,14]. Furthermore, evidence suggests that *stocking rate*—the density of livestock on a pasture over a grazing period—is an important modulator of spatial heterogeneity in wildlife resources in tall fescue-dominated rangeland [7,15]. However, this relationship between grazer density and patch contrast has yet to be explicitly explored [16], although producers appear willing to alter stocking rates to advance conservation goals [17].

The characteristic patchiness of pre-colonial landscapes can be recreated through patch burn grazing, and several properties of plant community ecology at the stand level are associated with patch contrast at the landscape level [9]. Landscapes comprised of spatially heterogeneous vegetation have less variability in aboveground plant biomass over time, due to a *portfolio effect* created by asynchrony in peak biomass of various plant functional groups along the time-since-fire gradient [18]. Basically, patchy landscapes always contain enough long-unburned, ungrazed vegetation to ensure at least some amount of aboveground biomass each year. The diversity of patches with respect to time-since-fire increases plant compositional diversity, as well, which can be expressed through conventional plant ecology concepts such as β diversity [19,20].

Landscape-level heterogeneity in vegetation structure driven by patchy fire and grazing supports livestock production in addition to biodiversity and conservation. In a commercial grazing system, stabilized aboveground plant biomass equates to greater predictability in the availability of forage for grazing, i.e., *standing crop* [18]; such reserves can buffer livestock performance and well-being against the potential negative impacts of drought [21–23]. However, if grazing livestock depend on the successful coupling of fire and herbivory, and the successful coupling of fire and herbivory depends on grazer density, it is essential to understand how stocking rate impacts the ecological patterns and processes behind the fire–grazing interaction in working rangeland landscapes. In the tallgrass prairie region, many semi-natural grasslands are grazed at high stocking rates [24] that minimize structural and compositional heterogeneity and disrupt spatial patterns of plant diversity [12,25,26]. When stocked heavily, forage demand of grazing animals can exceed primary production in the burned patch and the selection of grazing sites elsewhere in the landscape reduces patch contrast [7,27]. Conversely, light grazer densities also can reduce patch contrast when grazing pressure is too low to maintain the early maturity stage and low stature of forage plants that characterize grazing hotspots [27,28]. A better understanding of how management affects year-to-year variability in standing crop can increase the stability and subsequent predictability of livestock production [29,30].

While grazer density and fire have been studied individually, less is known about the relative contributions of grazer density and fire on temporal variability of standing crop when combined. Conducting such research is logistically challenging: Replicating multiple stocking rates across burned and unburned treatments at the landscape scale requires a vast amount of land, and must be maintained for several years to address questions about temporal variability. Here, we take a preliminary step by analyzing data from a long-term patch-burn grazing experiment that went through three multi-year stocking periods (heavy, light, and moderate). While such longitudinal data have limitations—principally, stocking rates are not synchronous and, therefore, not subject to the same environmental conditions—we found no evidence of variability in potentially confounding conditions that would preclude the value of this analysis in providing preliminary information on whether plant community processes associated with heterogeneity respond to differences in stocking rate.

The objectives of this study were to (1) Determine how stocking rate in pastures managed for either spatial heterogeneity (annual patch burns) or homogeneity (complete burns every third year) in tall fescue-invaded tallgrass prairie affect interannual variation of standing crop, and (2) Examine diversity–stability mechanisms underpinning temporal variability of standing crop under different grazer densities. Using non-destructively sampled data on standing crop and plant functional group composition, we test two hypotheses: (1) Patch-burned pastures to maximize responses in plant community metrics including temporal stability of aboveground plant biomass, demonstrate evidence for a portfolio effect, and have the greatest β diversity; (2) These responses will be greatest under moderate stocking rates.

2. Materials and Methods

2.1. Study Location & Design

This study was conducted in Ringgold County, Iowa, USA (40°42′ N, 94°5′ W). Mean annual precipitation totals 940 mm, 59% of which falls as rain [31]. Soils are Gara-Armstrong-Pershing [32]. Vegetation within the study area was tallgrass prairie invaded to varying degrees by non-native, C_3 grasses, especially tall fescue ($\bar{x}$ = 40% ± 11 s.d. cover, range = 18–62%) across study pastures [11,27]. The study ran from 2007–2013 on eight non-fertilized pastures (18–34 ha, $\bar{x}$ = 28 ha) grazed by cow–calf pairs (*Bos taurus*) stocked seasonally from May to October (~150 days) with no internal fences. Sites were therefore distributed among treatments nonrandomly, so that each treatment contained a range of land use histories. Land use histories are discussed in detail in McGranahan [33].

2.1.1. Fire Regime

Pastures were burned under one of two fire regimes that created a three-year fire return interval: four pastures managed for heterogeneity were under a patch-burn grazing treatment in which one-third of each pasture was burned each spring (mid-March to early April). Another four pastures were managed for homogeneity and treated with a three-year fire return interval by burning the entire pasture every third year. These experimental units represent control pastures in patch-burning studies as these sites are burned in their entirety and do not experience spatially discrete applications of prescribed fire. Each fire treatment comprised pastures with and without a recent history of grazing, as well as both remnant and reconstructed prairie communities.

2.1.2. Grazing Regime

The study was defined by three periods of different grazer densities (Table 1). In the first phase of the study, stocking rates were necessarily high ($\bar{x}$ = 3.2 ± 0.2) under continued requirements of long-term contracts between public land managers and landowners established prior to the initiation of our study. These stocking rates are considered severe relative to local recommendations from the USDA Natural Resource Conservation Service [11]. In 2010, contracts either expired or could be renegotiated, and a substantial reduction (~50%) in stocking rate was implemented across all pastures to prevent what was perceived to be excessive offtake of plant biomass that reduced fuel loads and prevented effective prescribed burning [27]. This reduced light stocking rate spanned 2010–2011 (Table 1). In 2012–2013, stocking rate was increased slightly to enhance grazer removal of vegetation in recently burned patches to ensure season-long contrast in vegetation structure in accordance with wildlife habitat management objectives.

Table 1. Order, duration, and mean (±s.d.) stocking rates of the three grazing densities compared in eight pastures in Ringgold County, Iowa, USA. † Stocking rate quantified as Animal Unit-Months · ha^{-1}, or the combined grazing pressure over time (months) of a number of animal units (455 kg of grazing animal) per hectare of grazed pasture.

Study Phase	Time Period	Stocking Rate (AUM †)
Heavy stocking	2007–2009	3.2 ± 0.2
Light stocking	2010–2011	1.5 ± 0.1
Moderate stocking	2012–2013	2.4 ± 0.2

2.2. Sampling Procedure

Vegetation data were collected with a nested hierarchical design in which pastures were each divided into three patches, with two sampling transects within each patch. Data for all pastures were collected during mid-July in each year from 30 sample points per patch, placed systematically along randomly located transects within each patch. In pastures burned entirely every third year (instead of the annual patch-burn treatment), we delineated similar patch boundaries for consistent hierarchical sampling. We used visual obstruction readings to non-destructively sample aboveground plant biomass, which incorporates both vegetation height and density [34] and correlates strongly with vegetation biomass determined by clipping irrespective of burn treatment in tallgrass prairie [35]. Used widely in grassland wildlife habitat monitoring, visual obstruction is also useful in estimating grassland standing crop for the purposes of modeling spatial heterogeneity [7,18,20].

Additional structure and plant community composition data was collected from each sample point using visual estimations of percent cover in 0.5 m^2 quadrats following the Daubenmire [36] canopy cover scale: percent cover was recorded as the midpoint of the following categories: 0, 1–5, 5–25, 25–50, 50–75, 75–95, 95–100. Vegetation structure included percent cover of bare ground and litter. Botanical composition was sampled as percent live cover by functional groups: C_4 grasses, tall fescue, all other C_3 grasses, non-leguminous forbs, herbaceous legumes, and shrubs. In total, 30 quadrats in each of three patches per eight pastures over seven years = 5040 total quadrats entered the study.

2.3. Data Analysis

We used the variance partitioning method of McGranahan et al. [7,18,20] to determine temporal variability in standing crop, measured as year-to-year variance in aboveground plant biomass. A random-effect generalized linear model was fit with a Gamma distribution using the `glmer` function in the *lme4* package for the R statistical environment [37,38], which allocated variance among years for each pasture during each grazer density period, using visual obstruction as the response variable. This random effects-only modeling approach has been applied several times previously to model variance structure across spatial and temporal components of vegetation sampling [7,18,20,39]. Although temporal variability is sometimes quantified as the coefficient of variation (CV), it is inappropriate to use CV for responses that include non-constant mean values because CV scales with the mean and is only appropriately applied when mean values remain constant [40]. Here, the tested effect—temporal variability of contrast between patch-level biomass—depends on variable means, therefore the pattern in CV would be overwhelmed by disproportionately small differences in the mean of low-biomass of the most recently burned patch.

To test temporal variability of standing crop against grazer densities and fire regimes, we fit a linear mixed-effect model with pasture as a random effect. Following this step, the fire regime term was removed from further analysis because its contribution did not improve fit (Table A1).

To explore how grazer density affects temporal variability in standing crop, we tested for statistical evidence of a *portfolio effect*, which refers to the fact that the risk in a portfolio of non-correlated resources is lower than the risk of a single resource. The portfolio outcomes tend to be less volatile than that of a single resource [41,42]. Here, the portfolio effect is represented by a slope greater than 1.0 in a linear model fitting the logarithm of variance in aboveground plant biomass against the logarithm of mean aboveground plant biomass [42,43].

To determine whether slopes of resulting regression equations were substantially different from 1.0, 95% confidence intervals (CIs) were simulated for regression coefficients in linear models. A slope is considered significantly different from 1.0 when 95% CIs do not overlap zero.

Beta diversity of plant functional group composition was calculated as beta dispersion—the breadth of groups in ordination space—with the `betadisper` function in the *vegan* package for R [44]. The function calculates mean distance of site scores to group centroids in an ordination based on the modified Gower distance matrix; tighter groups have less beta diversity [19]. The `permustats` function in the vegan package simulated pairwise comparisons (n = 999 permutations) among grazer density periods, which were then compared pairwise using a t-statistic.

3. Results

Fire regime did not significantly affect temporal variability of standing crop ($t_{1,22} = -0.03$, $p = 0.97$). A significant fire regime × grazer density interaction revealed temporal variability of forage under patch-burning and heavy grazer density was greater than patch-burned pastures with light and moderate grazer densities ($t = -4.44$, $p < 0.001$), and low-density pastures burned homogeneously ($t = -4.43$, $p < 0.001$; Figure 1). Grazer density did affect temporal variability in standing crop (Figure 1), which was significantly higher during heavy grazer density than under light ($t_{1,21} = -3.36$, $p < 0.003$) and moderate grazer density ($t_{1,21} = -4.63$, $p = 0.0001$), although light and moderate periods did not differ from each other ($t = -1.27$, $p = 0.41$).

We dropped the fire regime term before evaluating diversity–stability mechanisms because the model fitting temporal variability in forage availability against grazer density alone was more parsimonious than multiple regression models with grazer density and fire regime in AIC_c-based model comparison. In comparison to the grazer density-only model in log-likelihood ratio tests both additive and interactive model's χ-square p-value was greater than 0.15.

As evidence that the portfolio effect reduced temporal variability in standing crop, variance in standing crop increased with the mean standing crop under low and moderate grazer densities, with slopes significantly above 1.0 (Figure 2). We found no statistical evidence of the portfolio effect during the heavy grazer density period (Figure 2).

Beta diversity differences among grazer densities were marginal (Overall, $F = 2.10$, $p = 0.12$). Pairwise comparisons of beta diversity among plant functional groups indicated moderate grazer density had the greatest beta diversity (Figure 3); significantly greater than during heavy grazer density ($t = -2.32$, $p = 0.02$) and marginally greater than during light grazer density ($t = 1.49$, $p = 0.13$). Heavy and light grazer density periods were not statistically different from each other ($t = 0.15$, $p = 0.88$) (Figure 3).

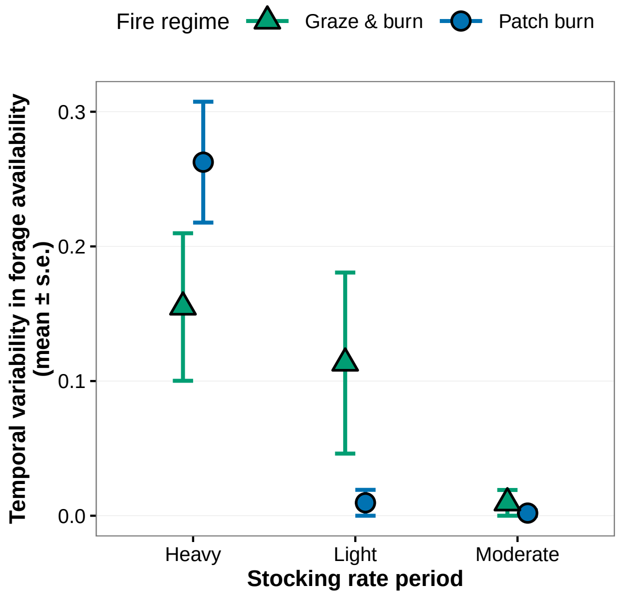

Figure 1. Temporal variability of forage availability—represented as non-destructive measurements of aboveground plant biomass, i.e., standing crop—during three periods of different grazer densities for tall fescue-dominated grassland plant communities under three grazer densities in Iowa, USA, presented as a time series in the order of grazer density treatments: heavy (2007–2009), light (2010–2011), and moderate (2012–2013). Under moderate grazer density, temporal variability of forage availability is lowest in both fire regimes.

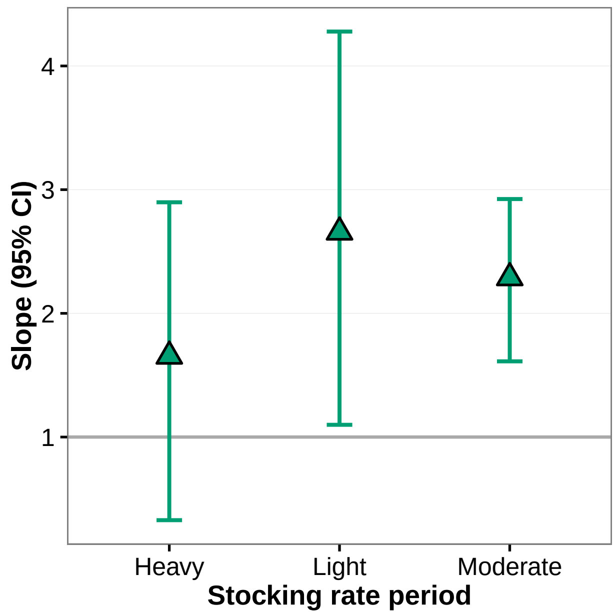

Figure 2. Slope coefficients and 95% confidence intervals for linear regression models fitting the logarithm of standing crop variance against the logarithm of mean standing crop for each grazer density. Data support the portfolio effect when the slope of the regression equation for log (variance) vs. log (mean) > 1.0 and 95% confidence intervals do not overlap 1.0. The portfolio effect mirrors temporal stability in standing crop as underpinned by functional group diversity.

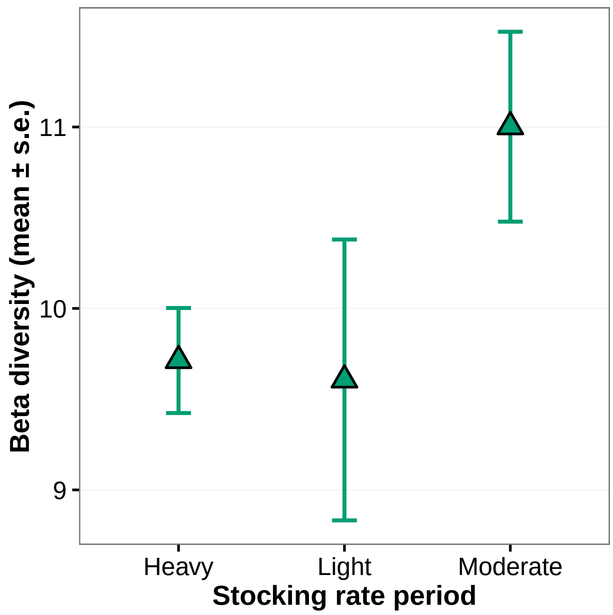

Figure 3. Mean beta diversity of plant functional groups, measured here as *multivariate dispersion*, or distance to group centroid in ordination space, across stocking rates. Beta diversity underlies temporal stability of a resource (i.e., standing crop or vegetation structure).

4. Discussion

In a seven-year experiment investigating fire and grazing interaction in a semi-natural tallgrass prairie dominated by tall fescue, a two-year period of moderate grazer density stabilized aboveground plant biomass (standing crop). These results complement indications that moderate grazer densities mediate spatial variability in forage structure [15,27] by showing that moderate grazer densities stabilize standing crop in southern Iowa pasturelands. Likewise, these results suggest moderate grazer density might reduce uncertainty in forage resource availability by stabilizing standing crop. Of course, we've arrived at these conclusions using non-destructive measures of vegetation height and density, which—as correlates with aboveground plant biomass—allow comparison of relative responses of standing crop across space and over time under categorical stocking rate levels. Estimates of primary production available as forage on a per-area basis, as is used in planning numerical stocking rates, are best informed by destructively harvesting samples of biomass.

Unexpected in our analysis was the lack of difference between the two burning regimes—annual patch burning vs. full burns every three years—with respect to stability and diversity responses. Previous work from elsewhere in the tallgrass prairie shows strong associations between patchy fire and all responses tested for here: low temporal variability in biomass, evidence for a portfolio effect among plant functional groups, and high beta diversity [18,20]. Contrary to these expectations, temporal variability in standing crop was similar under both heterogeneity-based and homogeneity-based fire regimes, which suggests there is no advantage of greater stability in standing crop from patch-burning continuously grazed pastures dominated by tall fescue.

We attribute the lack of difference among the two patterns of fire to the low stature of these tall fescue-invaded grasslands. Previous analyses showed patch-burning did not create substantial patch contrast in vegetation density or composition in these pastures [15]. Given that bare ground and litter cover did show contrast among patches in pastures managed for heterogeneity whereas plant biomass did not [12], prescribed fire was clearly effective in removing surface fuels in burned areas, which isolates the role of limited vegetation height in precluding structural contrast among patches.

Furthermore, an investigation of cattle feeding-site selection in these pastures found that, although tall fescue was grazed soon after prescribed burning, feeding sites dominated by tall fescue experienced less use as the growing season progressed [45]. This lack of repeated grazing of tall fescue likely inhibits clear structural contrast from developing in burn patches. Additionally, greater beta diversity in plant functional group composition during the moderate grazer density period suggests the dominance of tall fescue might decline; should the plant community diversify, subsequent burns might create greater patch contrast. Meanwhile, lacking structural contrast, a likely driver of spatial foraging patterns in all three grazer density periods could have been persistent grazed patches of palatable regrowth not attributable to the spatial pattern of fire [28], consistent with other tall fescue pastures [46].

We found support for our expectation that diversity–stability mechanisms underlie temporal stability in aboveground plant biomass at moderate grazer densities, where we found statistical evidence for the portfolio effect and high beta diversity of plant functional group composition. These results suggest that moderately stocked pastures had the least variability in standing crop from year to year when compensatory effects among plant functional groups could stabilize the availability of forage resources in invasive-dominated pastures, corroborating evidence first shown at a landscape level in native-dominated tallgrass prairie [18].

Although based on longitudinal data, this analysis is an important if preliminary step towards an understanding of how variability in stocking rate influences stand-level dynamics that drive landscape-level patterns in rangeland plant production and diversity. A review by Foster et al. [16] indicated disturbance-interaction studies using patch-burning design (i.e., patch-burn vs. graze-burn pastures) employed constant grazer density and did not evaluate effects of grazer density. In the current study, our dose-response framework allowed us to test temporal variability of standing crop against a range of grazer densities. Although we cannot control for error attributable to lag between years and periods due to a legacy effect of previous grazer densities, we have no evidence to suggest such effects are not consistent across transitions and thus have no reason to suspect any lag affects influenced the patterns described here. A fair justification for the potential lack of lag effects is that the eastern tallgrass prairie of North America is a high-rainfall, productive system [47] in which grassland pastures, such as the ones studied here exhibit little change in plant communities from management practices including a range of grazing intensity [48]. As simultaneously stocking replicate pastures of each grazer density is necessary to account for the potential role of temporal lag effects in affecting temporal stability of forage, the logistical constraints of such a study are enormous but probably worth committing resources to based on our preliminary results.

5. Conclusions

These results suggest that low temporal variability or relative stability in aboveground plant biomass is associated with diversity–stability mechanisms that underlie ecosystem function. Our results provide novel ecological evidence for a decades-old principle of grazing management: moderate grazing intensity enhanced diversity and stability, which might help mitigate shortfalls in primary productivity during periods of drought. We also demonstrated the challenges of restoring fire regimes in human-impacted ecosystems. Knowledge of how fire and grazing interact to control spatial and temporal variability in standing crop helps those who rely on working landscapes for their livelihood to buffer against climatic variability and uncertainty while integrating agricultural production and biodiversity conservation goals simultaneously.

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Appendix A. Additional Statistical Results

Table A1. Generalized linear models explaining the effects of fire regime and grazer density on temporal variability of standing crop, Grand River Grasslands, southern Iowa, USA. Table includes the number of parameters included in the model (K), Akaike's information criterion adjusted for small sample sizes (AIC_c), change in AIC_c from previous model (ΔAIC_c), and model weights (w_i).

Model	K	AIC_c	ΔAIC_c	w_i
Grazer density	5	−38.61	0.00	0.78
Grazer density + Fire regime	6	−35.00	3.61	0.12
Grazer density × Fire regime	8	34.10	4.47	0.08
Null	3	27.00	11.56	0.002
Fire regime	4	24.10	14.47	0.001

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