

The emergence of heterogeneity in invasive-dominated grassland: a matter of the scale of detection

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Received: 28 May 2018 / Accepted: 9 October 2018
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Abstract

Context Plant invasions of native ecosystems are one of the main causes of declines in biodiversity via system-simplification. Restoring native biodiversity can be particularly challenging in landscapes where invasive species have become dominant and where a new set of feedbacks reinforce an invaded state and preclude restoration actions. We lack an understanding of the response of invaded systems to landscape-level manipulations to restore pattern and process relationships and how to identify these relationships when they do not appear at the expected scale.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10980-018-0725-x>) contains supplementary material, which is available to authorized users.

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Objectives To better understand how fire and grazing influence landscape-level heterogeneity in invaded landscapes, we assess the scale at which grazing pressure and seasonality mediate the success of re-introducing a historical disturbance regime, grazing driven by fire (termed pyric herbivory), to an invasive plant-dominated landscape.

Methods We manipulated grazing timing and intensity in exotic grass-dominated grasslands managed for landscape heterogeneity with spring fire and grazing. In pastures under patch-burn grazing management, we evaluated the spatial and temporal variability of plant functional groups and vegetation structure among and within patches managed with separate grazing systems: season-long stocking and intensive early stocking.

Results Warm- and cool-season grasses exhibited greater among-patch variability in invasive-plant dominated grassland under intensive early grazing than traditional season-long grazing, but landscape-level heterogeneity, as measured through vegetation structure was minimal and invariable under both levels of grazing pressure, which contrasts findings in native-dominated systems. Moreover, within-patch heterogeneity for these functional groups was detected; contrasting the prediction that among-patch heterogeneity, in mesic grasslands, manifests from within-patch homogeneity.

Conclusions In invaded grasslands, manipulation of grazing pressure as a process that drives heterogeneous vegetation patterns influences native and non-

native grass heterogeneity, but not heterogeneity of vegetation structure, within and among patches managed with fire. Fire and grazing-moderated heterogeneity patterns observed in native grass-dominated grasslands likely differ from invasive grass-dominated grasslands with implications for using pyric herbivory in invaded systems.

Keywords Biological invasion · Fire-grazer interaction · Information visualization · Non-stationarity · Patch-burn grazing · Semi-variance

Introduction

The simplification of complexity in nature has been a prominent feature of the Anthropocene and is one of the leading reasons for continued declines in native biodiversity within the world's remaining intact ecosystems (McGill et al. 2015). Plant invasions into native ecosystems are one of the main causes of declines in biodiversity via system-simplification (D'Antonio and Vitousek 1992; D'Antonio et al. 2000). Homogenization (increased uniformity) of landscapes has coincided with decreases in species diversity and changes in ecosystem function (D'Antonio and Vitousek 1992). Plant invasions are sources of system perturbation that substantially alter the hierarchical structure of a landscape (Seastedt et al. 2008; Twidwell et al. 2016). Examples are evident from every vegetated continent. They include notorious invaders such as Gamba grass (*Andropogon gayanus*) in northern Australia's savannas (Setterfield et al. 2010), Buffel grass (*Cenchrus ciliaris*) in tropical savannas, and cheatgrass (*Bromus tectorum*) and tall fescue (*Schedonorus arundinaceous*) in the western and central rangelands of North America (Brooks et al. 2004; Gaertner et al. 2012; McGranahan et al. 2013b; Twidwell et al. 2016). Invasions such as these disrupt the biotic and abiotic interactions and resulting spatial order that typically occur following disturbance. The complete loss or reduction of unique aspects or properties of terrestrial systems resulting from invasions underpins the collapse of complexity and resilience in many ecological systems (Allen and Holling 2010; Soranno et al. 2014; Oliver et al. 2015). For these reasons, recognition of the loss of ecosystem complexity through the reduction of microhabitat

abundance for ecosystem constituents has gained global attention and motivated efforts to restore structural heterogeneity in invaded landscapes (Loreau et al. 2001; Tews et al. 2004; Suding and Hobbs 2009).

Even with such recognition, restoring complexity in landscapes dominated by an invasive plant species has proven difficult. The effects of invasions are, for all practical purposes, irreversible, resulting in systematic changes in the feedbacks operating within the system that make it more challenging to restore heterogeneity at scales necessary for non-plant taxa to respond and increase in abundance (McGranahan et al. 2013a; Maresh Nelson et al. 2018). Novel methods have successfully reintroduced and manipulated historical disturbance regimes to increase landscape-level heterogeneity in the absence of exotic invasions (Fuhlendorf et al. 2012, 2017) and such approaches are being explored in landscapes dominated by exotic invasive species to mimic the feedbacks known to provide microhabitats for native species that evolved in complex and heterogeneous habitats (Davies et al. 2009; Delaney et al. 2016; Duchardt et al. 2016). In temperate grasslands, the occurrence of fire resulted in spatially discrete patches of vegetation that attracted moderate to large grazer densities and promoted spatial heterogeneity of vegetation on the grassland landscape (Fig. 1). This process is called the "fire-grazer interaction (or pyric herbivory)" (Fuhlendorf et al. 2009). When re-introduced to native grasslands previously managed for homogeneity, this process has been shown to restore the hierarchy of discrete spatial scales of vegetation pattern required by consumer guilds (Engle et al. 2008; Fuhlendorf et al. 2009; Ricketts and Sandercock 2016) but the effect has not been observed to the same degree in grasslands invaded by an exotic grass after introducing fire-grazer interactions (Fig. 1c; McGranahan et al. 2013a; Duchardt et al. 2016; Scasta et al. 2016).

In cases where systems exhibit strong threshold behavior that precludes overcoming newly entrenched feedbacks with a simple reinstatement of the original processes, alternative pathways that alter the intensity and duration of disturbance regimes can overcome thresholds in some cases and restore a semblance of the original structure and function (Twidwell et al. 2013). Disturbances generate heterogeneity of spatial patterns in vegetation that interacts with environmental conditions to shape ecosystem recovery (Franklin

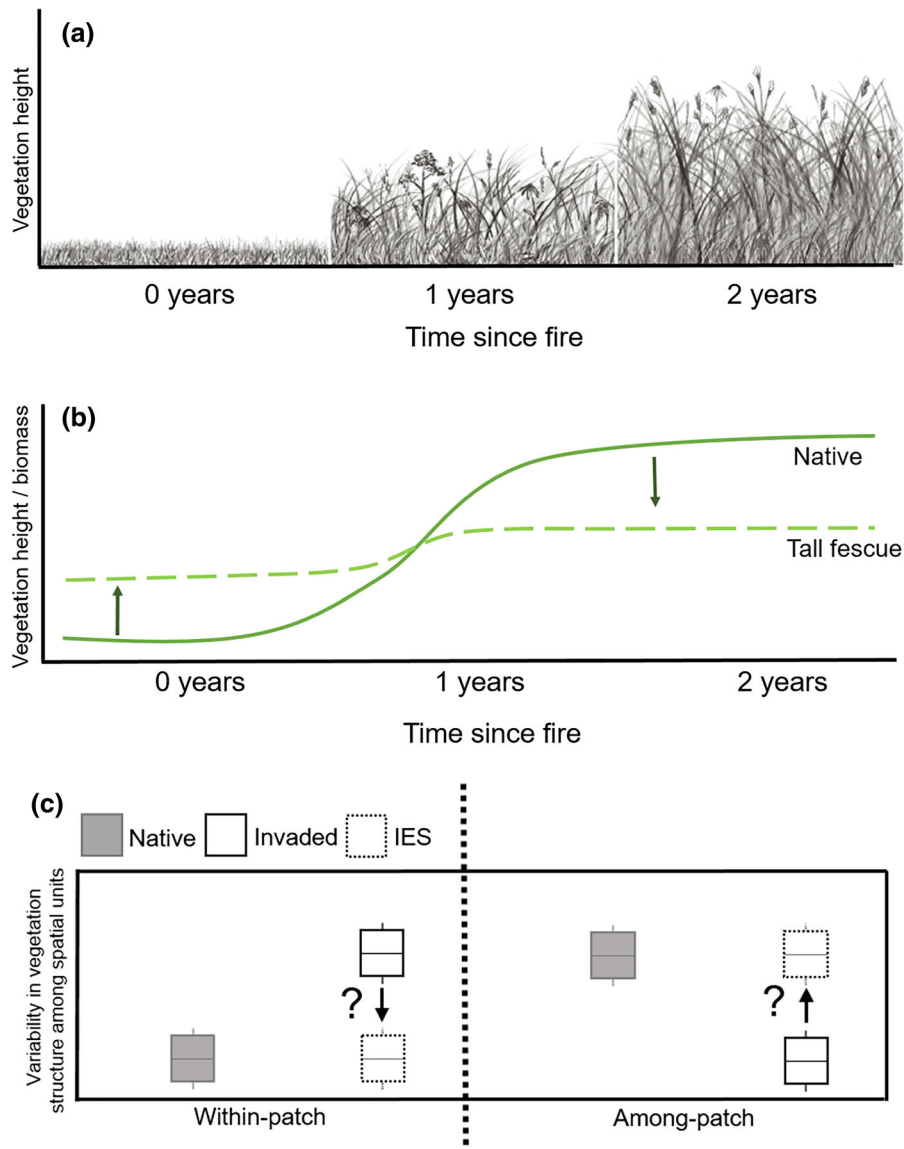


Fig. 1 Conceptual diagram of the expected vegetation response to fire and grazing in native versus invasive-dominated systems under different grazing systems. **a** Vegetation structure with the interaction of spatially and temporally discrete fires and grazing; in native-dominated landscapes with pyric herbivory managed with season-long stocking, moderate grazing pressure is most effective because it results in the lowest vegetative structure in the burn patch and the highest levels of variability among patches (modified from Scasta et al. 2016). **b** Tall fescue reduces the ability of fire and grazing (dark green arrows) to drive patch

contrast of vegetation structure (dashed green line) under season-long stocking, relative to native grasslands (solid green line). **c** Spatial variability expected in vegetation structure of native- and invasive-dominated landscapes managed with fire and grazing and season-long stocking. In native systems managed with fire and grazing, low within-patch variability begets high among-patch variability. In invaded grasslands, intensive early stocking (IES) is expected to lower within-patch variability relative to season-long stocking and increase among-patch variability. (Color figure online)

et al. 2000; Lindenmayer et al. 2008). Accordingly, manipulations of disturbance components (i.e., intensity or timing) that modify the contemporary environment and the persistent effects, or legacies, of past

events are likely tools for managing systems invaded by plants that alter feedback relationships (Davies et al. 2009; Gaertner et al. 2014; Bowman et al. 2015; Johnstone et al. 2016). Given that the range of

variability in fire and grazer relationships are tightly controlled in experiments today (Fuhlendorf et al. 2009; Twidwell et al. 2016), manipulation of the fire and grazer interaction beyond moderate stocking of cattle for an entire growing season may provide an alternative understanding of how structural heterogeneity manifests in a heavily invaded, uniform landscape.

Here, we conduct a multi-scale assessment to determine whether altering the intensity and duration of grazing following focal fire can promote landscape-level heterogeneity in grassland dominated by the invasive grass, tall fescue (Fig. 1). We manipulated the intensity and duration of grazing following focal fire by doubling the number of grazing animals and cutting the duration of the grazing period in half. This strategy aims to reduce non-native cool-season grass cover and increase native warm-season grasses in efforts to build potential fuel loads for subsequent prescribed fires.

First, we test for the emergence of heterogeneity among patches, which is defined by the extent of the fire treatment and where heterogeneity typically emerges at the landscape-level in native grassland following focal fire-grazer interactions (Fig. 1). However, spatial and temporal heterogeneity results from a variety of hierarchically organized forces (Allen and Starr 1982; O'Neill 1986; Holling 1992), so the scale at which heterogeneity emerges and the means by which a landscape acquires spatial order is often unknown before restoration actions (Allen et al. 2002). We, therefore, also test for the presence of homogeneity in vegetation structure within patches because it is at this scale where precursors to among-patch heterogeneity might first emerge (McGranahan et al. 2016; Bielski et al. 2018). Among-patch heterogeneity occurs when each patch with varying time since fire supports homogenous vegetation structure that is unique to each patch (Fig. 1b). This second test poses a 'big' data problem, where conventional approaches to detect variation in vegetation responses to management may not succeed. This invaded grassland is in a fundamentally different ecological state characterized by a new set of reinforcing feedbacks with deep hysteretic behavior (Fig. 1b, c) (McGranahan et al. 2012a, b). Scaling relationships between landscape structure and ecosystem processes also vary across scales of observation (Turner 1989; Peters et al. 2004; Wu 2004) and such pattern-process relationships are

not necessarily fixed or meet observer expectations (Bielski et al. 2018). In such instances, semivariance analysis has been used to detect scales of variability in ecological data (e.g., Koerner and Collins 2013), but this analysis is often based on data measured at a single point in space or time. Here, we use vegetation data on vegetation structure and plant functional groups collected at three periods in the growing season and a data visualization technique that borrows from applications used in ecoinformatics (Michener and Jones 2012) to detect the scale of spatial order, when it arises, and determine how long heterogeneity persists following the manipulation of the fire-grazer interaction.

Thus, our primary objectives are to (1) determine whether intensive early stocking in pastures under patch-burn grazing can create contrast in vegetation structure among management patches through recursive grazing within management patches, and (2) assess the temporal dynamics of spatial heterogeneity in these invasive-dominated pastures by quantifying the magnitude of spatial variability in vegetation structure within management patches over three periods after prescribed fire in a growing season. We hypothesize that in intensive early stocked (IES) pastures: (1) if recursive grazing reduces exotic cool-season grasses within a patch, the landscape-level uniformity in vegetation structure driven by the prevalence of exotic cool-season grasses will be diminished compared with pastures managed with traditional season-long stocking (SLS) (Fig. 1c), and (2) mid-growing season removal of grazers in IES pastures will promote end-of-summer prevalence of native warm-season grasses relative to SLS pastures; thereby providing an indication that IES can force invasive-dominated grassland in the desired direction for restoring native tallgrass prairie. Testing these hypotheses will allow us to understand both the spatiotemporal emergence of complexity in landscapes where controlled disturbance (i.e., fire and grazing) is employed to restore components of the disturbance regime, and what the effects of changing grazing intensity in invasive grass-dominated landscapes managed with prescribed fire might be on landscape-level heterogeneity.

Methods

Study area and experimental design

The study was conducted on invasive C_3 grass-dominated grasslands managed by the Iowa Department of Natural Resources in the Grand River Grasslands (GRG) region of southern Iowa, USA (40°42'N, 94°5'W; Fig. S1). Supplementary material contains further explanation of environmental characteristics. This study was implemented on four pastures ranging in size from 23 to 32 ha. To restore landscape-level structural heterogeneity expected in native tallgrass prairie, historic fire intervals for this region were implemented by burning a spatially-discrete patch composing a third of the area of the pasture once every 3 years. During any given year, one patch was burned in the early growing season (mid-March–early April) before cattle were released on the pasture for the growing season (April–September). As a result, each landscape replicate (i.e., a pasture) functioned as a shifting mosaic and consisted of the following management patches: burned in the spring of the current year (0 years since fire [hereafter, YSF]), last year (1 YSF), and 2 years ago (2 YSF). In this grassland management framework, where hierarchical patch structure resulting from the combined effects of fire and grazing was expected (Wu and Loucks 1995), a patch was an experimental unit within a pasture. Next, within the patch, a transect was established (described below) to measure the within-patch variability in plant measurements. Also, we detected functional group-specific swards and fine-scale variation in individual plant communities with semivariance analysis (described below). Hereafter, a sward refers to a spatially distinct grouping of a plant functional group detected along the transect (Roughgarden 1977; Forman and Godron 1981).

This fire/grazing regime was implemented in 2006 on four pastures that were stocked over the growing season at moderate rates and grazed for 5 months from early April to early September (Pillsbury et al. 2011). Past work in this study area indicated tall fescue modifies the fuel bed to the extent that its presence limits both fire spread and the concomitant creation of landscape-scale heterogeneity by grazers attracted to the recently burned patch in the study pastures managed with season-long stocking and patch-burning (Pillsbury et al. 2011; McGranahan et al.

2012b, 2013b; Scasta et al. 2016). In 2014, grazing intensity and timing of grazing were altered in two of the pastures with the knowledge that simple re-introduction of the fire regime coupled with moderate grazing intensity was less effective in restoring vegetation heterogeneity at the among-patch scale (McGranahan et al. 2012b) than what was reported in native-dominated tallgrass prairie in Oklahoma (McGranahan et al. 2013a), where recursive grazing in the recently-burned patch promoted variability in vegetation structure at the landscape-scale (Bielski et al. 2018). Each pasture was assigned randomly to one of two grazing treatments: (1) conventional season-long stocking (SLS) with cattle stocked from early April through early September (same grazing treatment established in 2006) and (2) intensive early stocking (IES) with cattle stocked from early April through early July. To maintain comparable grazing pressure among all pastures, stocking rates were set to arrive at similar end-of-season aboveground plant mass for all pastures. The target for end-of-season aboveground plant mass was 5000 kg/ha which was estimated to be the amount of fine fuel needed for spatially uniform prescribed fire in the subsequent year (H. Hillhouse unpublished data). One assumption of the patch-burn grazing framework is spatially uniform prescribed fire is required to create landscape-level heterogeneity (McGranahan et al. 2012b; Bielski et al. 2018). Each pasture was stocked with cross-bred Black Angus cows or heifers (*Bos taurus*) at rates based on forage availability, which were free to graze an entire pasture (i.e., no interior fencing).

Field methods

Plant community

To examine how grazing intensity affected spatial heterogeneity in the plant community, we established a permanent 300 m transect in each patch in each of the four pastures (2 SLS, 2 IES), summing to 12 transects. Transect locations spanned all topographic positions (hill top, slope, bottom) present within each individual patch. Vegetation measurements were taken within a 25 × 50-cm quadrat placed at 3-m intervals along each transect (100 quadrats/patch). To assess whether spatial heterogeneity was present throughout the growing season or if it manifested at

different times of the season within each patch, we collected data in June, August, and November of 2014 and 2015. These periods corresponded with the early, mid, and post-grazing season. In SLS pastures, vegetation measurements in June and August occurred while cattle were free to graze, while vegetation data for November corresponded to the post-grazing season when cattle had been removed. In IES pastures, June vegetation measurements pertain to when cattle were free to graze, while August and November measurements correspond to when cattle had been removed. In previous studies investigating fire-grazer interactions in mesic grasslands under patch-burn management, vegetation was measured in the mid-summer (June–July), when variability of vegetation structure among experimental patches is evident (McGranahan et al. 2012b).

Vegetation visual obstruction readings (VOR) were recorded at each quadrat, with a Robel pole placed at the center of the quadrat (Robel et al. 1970). Litter depth data were taken at three points within each quadrat. We visually estimated percentage cover of bare ground and litter cover, and canopy cover of plant functional groups (total live herbaceous, total grass, warm-season grasses, cool-season grasses, forbs, woody plants, and standing dead) in 0.5-m quadrats using a cover class index: 0–5, 5–25, 25–50, 50–75, 75–95, 95–100% (Daubenmire 1959).

Data analysis

Testing for landscape-level heterogeneity (among patches)

In native tallgrass pastures with patches of varying time since fire, spatial heterogeneity in vegetation structure is typically apparent at the landscape-scale, or at the among-patch scale (Fuhlendorf and Engle 2004). Among-patch spatial heterogeneity in vegetation structure (VOR and vegetation height) and canopy cover of functional plant groups were individually calculated as the standard deviation of patch-level means among experimentally burned patches with varying time since fire (0, 1, and 2 YSF; hereafter, management patches). At the among-patch scale, spatial variability in individual plant group measurements including VOR, vegetation height, and functional group cover was calculated as the mean standard deviation in individual plant group measurements

among experimentally burned patches. To test whether IES and SLS pastures varied in spatial variability in plant groups and if an interaction occurred with grazing treatments over our six sampling events, we compared means of among-patch spatial variability using permutational analysis of variance (perANOVA) in the R statistical environment (Anderson and Ter Braak 2003; R Development Core Team 2018). A significantly greater mean standard deviation for pastures managed with IES indicates that adjustment in grazing pressure created spatial variability among-patches for an individual plant group to a greater extent than SLS management. We report exact p values to allow readers to distinguish between significant effects ($p < 0.05$) and marginally significant effects that may still warrant attention ($0.05 < p < 0.1$).

To determine whether plant community measurements are the same across grazing treatment and a patch's fire history, we tested for variation of mean VOR, litter depth, bare ground and litter cover, and plant functional group cover among patches, grazing treatment, and their interaction using a permutational multivariate analysis of variance (PERMANOVA) (Oksanen et al. 2013). PERMANOVA is a useful tool when analyzing ecological data with low replications ($n = 2$ pastures for each grazing treatment). When the number of replications relative to the number of variables under scrutiny is low, PERMANOVA is a robust distance-based approach to test for dissimilarity in community structure between ecological communities unlike classical multivariate analysis of variance (MANOVA), which requires the total number of sample units to be large relative to the number of variables (Anderson and Walsh 2013). In this study, PERMANOVA was performed using a Bray–Curtis distance of $\ln(x + 1)$ transformation. Data were analyzed using grazing treatment (IES and SLS) and among management patches (0, 1, 2 YSF) as fixed factors. Next, principal component analysis (PCA) on VOR, litter depth and percentage cover of plant functional groups, standing dead, bare ground, and litter was used to investigate the relationship of plant community composition between grazing treatments and among management patches. PCA was conducted on plant community data pooled across sampling events and pastures.

Testing for homogeneity within patches

A precursor to landscape-level heterogeneity (i.e., spatial variability among patches in pastures) in patch-burned grazed grassland is the presence of homogeneity of vegetation structure within patches (Fig. 1a; Fuhlendorf and Engle 2001); thus we tested for the presence of homogeneity (or low heterogeneity) of vegetation measurements within patches. Spatial heterogeneity at the within-patch scale was calculated as the mean standard deviation in mean vegetation structure (i.e., VOR and vegetation height) and functional group cover within each patch's 300-m transect. To determine whether IES and SLS pastures varied in within-patch heterogeneity of vegetation structure and functional group cover, we tested for a difference in their mean standard deviation of transect measurements in our study pastures. We also tested for any potential interaction with grazing treatment comparisons over our six sampling periods. Grazing treatment and sampling period main effects and their interaction were evaluated using perANOVA (Anderson and Ter Braak 2003). A significantly lower within-patch mean standard deviation in pastures managed with IES would indicate that adjustment in grazing pressure created greater within-patch homogeneity for an individual plant group than SLS management (Fig. 1c), which is thought to be a precursor to among-patch variability (Fig. 1c; McGranahan et al. 2012b, 2016; Bielski et al. 2018).

Identifying patch-level structural heterogeneity

To quantify structural heterogeneity and sward size within management patches, we used semivariance analysis to create semivariograms on vegetation data collected along each patch's 300-m transect (Fig. 2) using the robust estimator in R package "geoR" (Ribeiro Jr et al. 2016). A semivariogram was created for each patch within each pasture for each sampling period to examine how grazing treatment affected within-patch variation in vegetation throughout the study. Semivariograms show the average spatial correlation in data measured at known locations of increasing distance. Of the four common semivariogram models used in the analysis of spatial structure—linear, exponential, spherical, and Gaussian—Gaussian had the best fit under restricted maximum likelihood for the majority of sampling occasions, so

we report our semivariance results with Gaussian covariance structure. Data collected along the permanently established transects and used in separate semivariance analyses included percentage cover of warm-season grasses, cool-season grasses, forbs, standing dead vegetation, bare ground, and litter cover, totaling six cover types. These functional groups were found to be highly variable across pastures and aided in determining contrasts in vegetation among grazing treatments and patches with varying time since fire (described in Results for PCA). Therefore, we focused on these groups while total live herbaceous, total grass, and litter depth were left out of further analysis. Woody plants made up less than 5% of total percentage cover and were also excluded from the analysis.

By calculating the sill, where semivariance increases with distance until reaching an asymptote (Fig. 2b), we were able to calculate the predominant scale of patchiness of each variable of interest in each grazing treatment (Fig. 2a). Size or mean diameter of a plant group's sward along each transect was identified by the distance beyond which pairs of observations no longer exhibit spatial autocorrelation (Fig. 2b). The transect data sets were all spatially continuous (i.e., no missing data), and transect data for each YSF patch within each landscape replicate (pasture) were averaged to provide information for overall within-patch heterogeneity. Sampling period-specific semivariograms were produced for each management patch and plant cover-type. Semivariograms ($n = 216$) were compiled into a polar coordinate plot by YSF patch-type and season (June, August, and November) to more easily illustrate the scale of patchiness of each plant measurement over the course of the study period (Fig. 3). Each polar coordinate figure depicts the difference in semivariance within a given patch between grazing treatments by illustrating the sill (variation within patch) and lag (sward size) at one point in time (Step 1), differences in semivariance structure between treatments within all patches at one point in time, ordered in terms of YSF (Step 2), differences in semivariance structure between treatments within all patches over three functional time steps within a year (Step 3), and shows differences between treatments in the range of semivariance within patches for each functional time step throughout the two-year study (Step 4, Fig. 3).

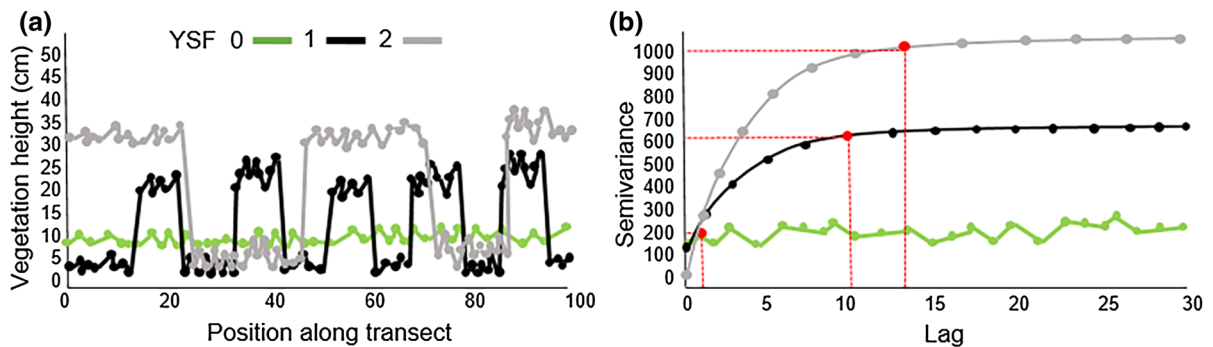


Fig. 2 Conceptual diagram of expected vegetation structure in response to fire-grazer interaction in pastures under patch-burn grazing management as observed in native-dominated grassland **a** Expected transect vegetation height and **b** semivariograms with different sill (within-patch heterogeneity) and range (within-patch sward size) values. Range is expected to increase progressively from the landscapes with different times since

focal disturbance: < 1 year since fire (YSF; green), 1 year since fire (black), and 2 years since fire (grey), reflecting the expected increasing size of the dominant vegetation swards with an increase in time since focal disturbances. The expected average distance between vegetation swards is revealed by repeated peaks in the semivariogram. (Color figure online)

Results

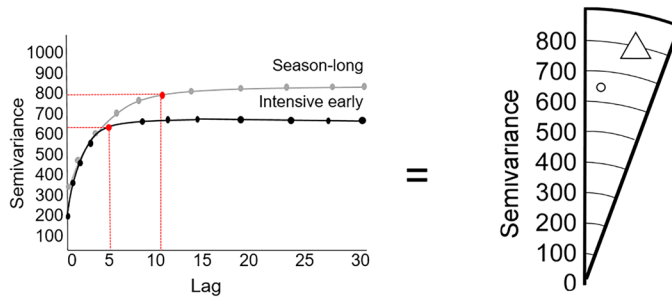
Testing for landscape-level heterogeneity (among patches)

When comparing vegetation structure (VOR and vegetation height) between grazing treatments, differences in among-patch heterogeneity were not apparent (Table 1). However, variation in among-patch heterogeneity in some constituents of these vegetation structure measurements was evident (Fig. 4). Graminoid (warm- and cool-season grasses) heterogeneity among patches in IES pastures was greater than in SLS pastures (Table 1). Analysis of among-patch heterogeneity of warm-season grasses revealed significant main effects of seasonal period ($F_{5,12} = 3.68$, $p = 0.02$) and grazing system ($F_{1,12} = 8.86$, $p = 0.02$) in addition to a significant sampling period-by-grazing system interaction ($F_{5,12} = 2.17$, $p = 0.01$). Warm-season grass heterogeneity was three times greater in IES pastures than SLS pastures across sampling periods; these differences were most evident in June and August (Fig. 4). The significant interaction term revealed warm-season grass among-patch heterogeneity (i.e., standard deviation of patch means) was greater in IES pastures in August of both years. Among-patch heterogeneity of cool-season grasses in IES pastures was two-fold higher than SLS pastures ($F_{1,12} = 11.79$, $p = 0.003$; Table 1); neither seasonal period or the interaction term was significant. Litter and bare ground exhibited the highest levels of among-

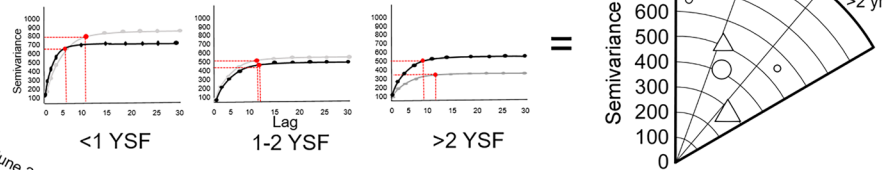
patch heterogeneity for any functional group over the study period (Fig. 4). Cover of forbs, standing dead, litter, and bare ground among patches did not differ across grazing treatments over the course of the study (grazing treatment main effect, $p > 0.10$; Fig. 4). Differences in seasonal among-patch heterogeneity were clear for these functional groups with June sampling events exhibiting the highest levels of spatial variability. However, in both years, forb cover among-patch heterogeneity was lowest in November but not significantly different between June and August (interaction term, $F_{5,12} = 3.54$, $p = 0.03$). Means (\pm SE) of plant functional groups for each management patch-type across the study period are presented in supplementary material (Fig. S4).

PERMANOVA showed that vegetation community structure differed as a result of grazing ($F_{1,68} = 4.89$, $p = 0.01$) and fire ($F_{1,68} = 16.77$, $p = 0.001$) treatments. However, a non-significant grazing system \times fire treatment interaction indicates plant communities in patches with varying years since fire in IES and SLS pastures did not respond differently to the fire-grazer interaction ($F_{1,68} = 1.11$, $p = 0.17$). This result bolsters the lack of variation in VOR and vegetation height between grazing treatments in our among-patch heterogeneity analysis above (Table 1). PCA ordination provided an additional indication of small differences in patches among grazing and fire treatments (Fig. 5). The first two axes of the PCA accounted for 56% of the variance in the data. The order of importance of plant structure and functional group

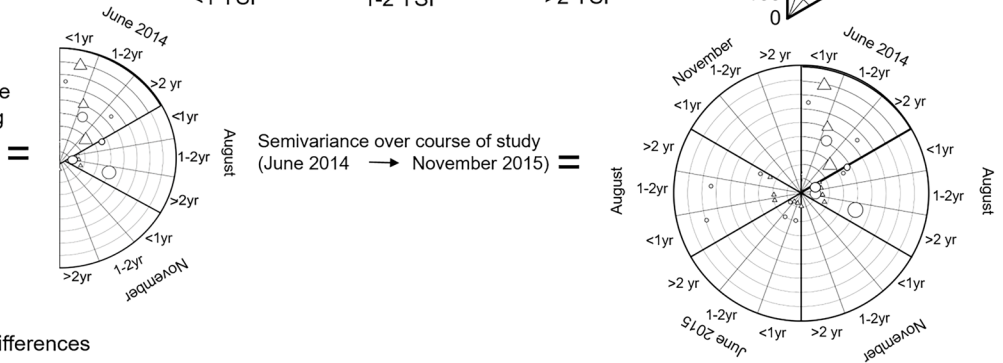
Step 1) Semivariogram results within a given patch at one point in time



Step 2) Differences in semivariance and lag between treatments within all patches at one point in time, ordered in terms of year since fire



Step 3) Semivariance and lag over growing Season (June - November)



Step 4) Treatment differences in range of semivariance within patches for each time step

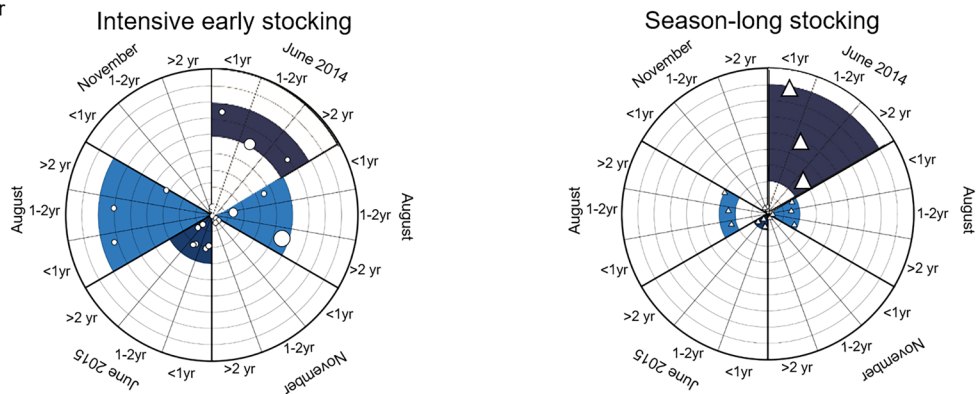


Fig. 3 Walk-through of visualization process using polar coordinate plots to illustrate semivariogram results in a clockwise direction for plant functional groups in experimental landscapes under intensive early stocking (IES) and season-long stocking (SLS) grazing treatments. Circles indicate patches in intensive early stocking pastures; triangles depict patches in

season-long stocking. Symbol size indicates range (lag) or patch size of detected functional group patch: smallest is a patch less than 10 m in diameter while largest symbol is a patch of 30 m or greater in diameter. Shading indicates seasonal variance: June (dark blue) and August (azure blue). (Color figure online)

measurements on PCA axis 1 was litter depth, warm-season grasses, standing dead, bare ground, litter cover, forbs and cool-season grasses (Fig. 5). Litter

depth, litter cover, and standing dead grasses had positive coefficients for PC axis-1, and bare ground, forbs, and warm-season grasses had negative to central

Table 1 Spatial variability (mean standard deviation among patches \pm SE) in vegetation components in pastures with pyric herbivory under intensive early stocking (IES) and season-long stocking (SLS) grazing treatments

Plant measurement	Within-patch		Among-patch	
	IES	SLS	IES	SLS
VOR (cm)	0.5 (0.02)	0.48 (0.02)	0.25 (0.03)	0.22 (0.04)
Vegetation height (cm)	4.88 (0.50)	4.8 (0.30)	1.66 (0.30)	1.59 (0.47)
Warm-season grass (%)	9.1 (1.40)	7.67 (0.97)	4.99 (1.64)	1.34 (0.32)*
Cool-season grass (%)	19.8 (0.54)	20.9 (0.43)	11.9 (1.68)	4.88 (0.68)*
Forb (%)	16.7 (0.83)	15.1 (0.71)	8.43 (1.98)	3.88 (0.63)
Litter (%)	18.0 (1.13)	17.5 (1.06)	17.4 (2.62)	21.1 (2.63)
Standing dead (%)	9.59 (1.06)	10.8 (1.11)	4.72 (1.30)	5.4 (0.89)
Bare ground (%)	18.50 (0.88)	16.8 (1.05)*	17.4 (2.64)	20.1 (2.37)

Asterisks represent results of the PerANOVA for differences in means of management groups: * $p < 0.05$

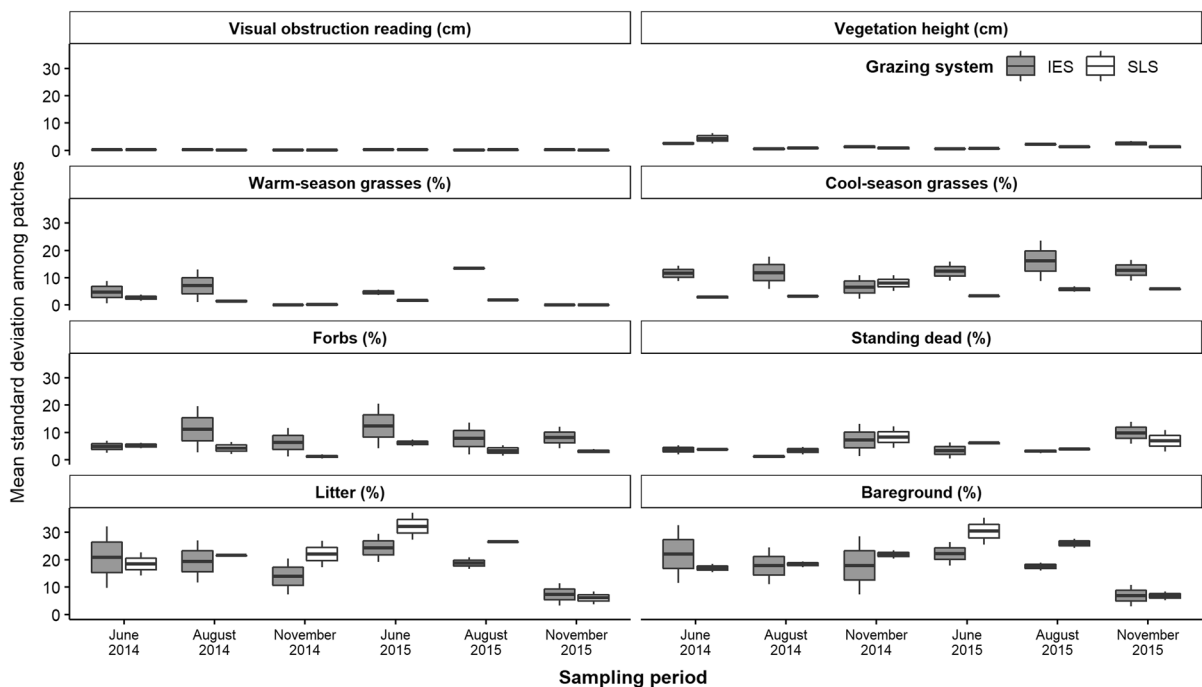


Fig. 4 Among-patch variability (standard deviation of measurements) in vegetation components in pastures managed with pyric herbivory under intensive early stocking (IES) and season-

long stocking (SLS) grazing treatments at Grand River Grasslands in southwest Iowa, USA

coefficients for PC axis-1. The order of importance of plant structure and functional group measurements on PCA axis-2 was warm-season grasses, litter depth, bare ground, litter cover, VOR, and cool-season grasses. Warm-season grasses, litter depth, and litter cover had positive coefficients for PC axis-2, while bare ground and cool-season grasses had negative coefficients for PC axis-2 (Fig. 5). Total live

herbaceous cover, VOR, and total grass cover appeared to contribute very little to differences in the plant community among grazing and fire treatments. A slight separation occurred orthogonally between grazing treatments and appeared to be driven by warm-season grasses and cool-season grasses (Fig. 5). Separation occurred among fire treatments

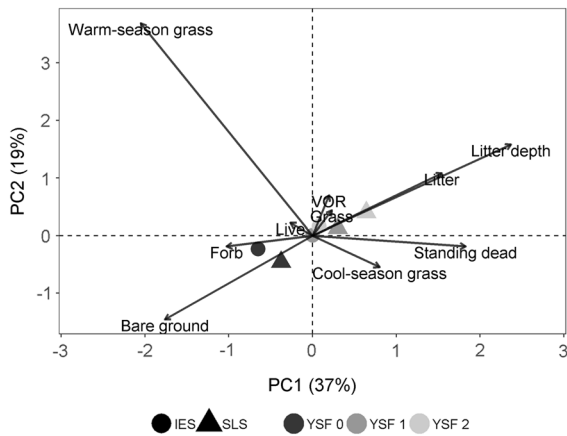


Fig. 5 Multivariate ordination of principal components on standardized vegetation measurements pooled across sampling events and pastures. Symbols are as follows: shapes represent grazing treatments of IES (circles), and SLS (triangles); colors represent years since fire of current year burn (black), previous year burn (gray), and 2 years post-fire (light gray)

along PC axis-1 and appeared to be driven by forbs, litter depth, litter cover, and standing dead.

Testing for spatial variability within patches

Within-patch variability of each plant measurement responded similarly among grazing treatments (grazing treatment main effect: $p > 0.10$, Table 1, Fig. S3), although variability in bare ground cover was greater in IES patches ($F_{1,12} = 11.46$, $p = 0.01$). Significant grazing treatment-by-sampling period interaction terms indicated within-patch variability was greater in SLS than IES pastures for visual obstruction in June 2015 ($F_{5,12} = 2.38$, $p = 0.03$) and standing dead vegetation cover in November 2015 ($F_{5,12} = 1.23$, $p = 0.001$). In contrast, within-patch variability of warm-season grass cover was significantly greater in IES during August 2015 ($F_{5,12} = 4.11$, $p = 0.001$; Fig. S3).

Analysis of fine-scale structural heterogeneity in patches with semivariance analysis showed few long-term patterns emerged in values of sill (patch variance) (Fig. 6, Table S1) and lag (sward size) (Fig. S2, Table S2). Figure 6 shows the range of variability in each functional plant group that existed within the pastures managed with IES and SLS at any given time for three periods of the growing season and for 2 years.

Spatial variation in the distribution (heterogeneity) within plant functional groups was evident in a nested manner that encompassed season and the level of grazing pressure (Fig. 6). Heterogeneity in the cover of warm-season and cool-season grasses and forbs within patches was especially pronounced in patches exposed to IES (Fig. 6), whereas cover of litter, standing dead, and bare ground was not variable across grazing system and season (Fig. 6, Table S1). YSF patch and season-specific semivariance and lag values presented in Fig. 6 and Fig. S2, respectively, are reported in Tables S1 and S2 in the supplementary material.

Discussion

Evaluating ecological processes at one spatial or temporal scale and their interactions with processes at another scale is a critical step in understanding multi-scaled problems, such as invasive species (Soranno et al. 2014). This approach allows identification of feedback mechanisms that can drive a system away from its original state or can have a dampening effect that counteracts change (Suding and Hobbs 2009). We tested the initial role of adaptive management through experimental manipulation with IES to return a system to a native grass-dominated state through adjusting grazing timing and pressure (Fig. 1c). By evaluating nested dynamics of plant functional group composition and vegetation structure across multiple spatiotemporal scales, we show that the detection of heterogeneity in exotic-dominated grassland depends on the scale under scrutiny. We detected heterogeneity in pastures managed with both moderate (SLS) and heavy grazing pressure (IES); however, by distilling information from numerous semivariograms, we demonstrate that maximal variance in vegetation emerges at a fine scale, the within-patch scale, in tall fescue-dominated pastures unlike native-dominated pastures where maximal variance occurs at the among-patch scale (e.g., Fuhlendorf and Engle 2004; Bielski et al. 2018). This finding occurred irrespective of the level of grazing pressure.

Among-patch heterogeneity

When evaluating spatial variability at the landscape-level, the multivariate ordination of the plant

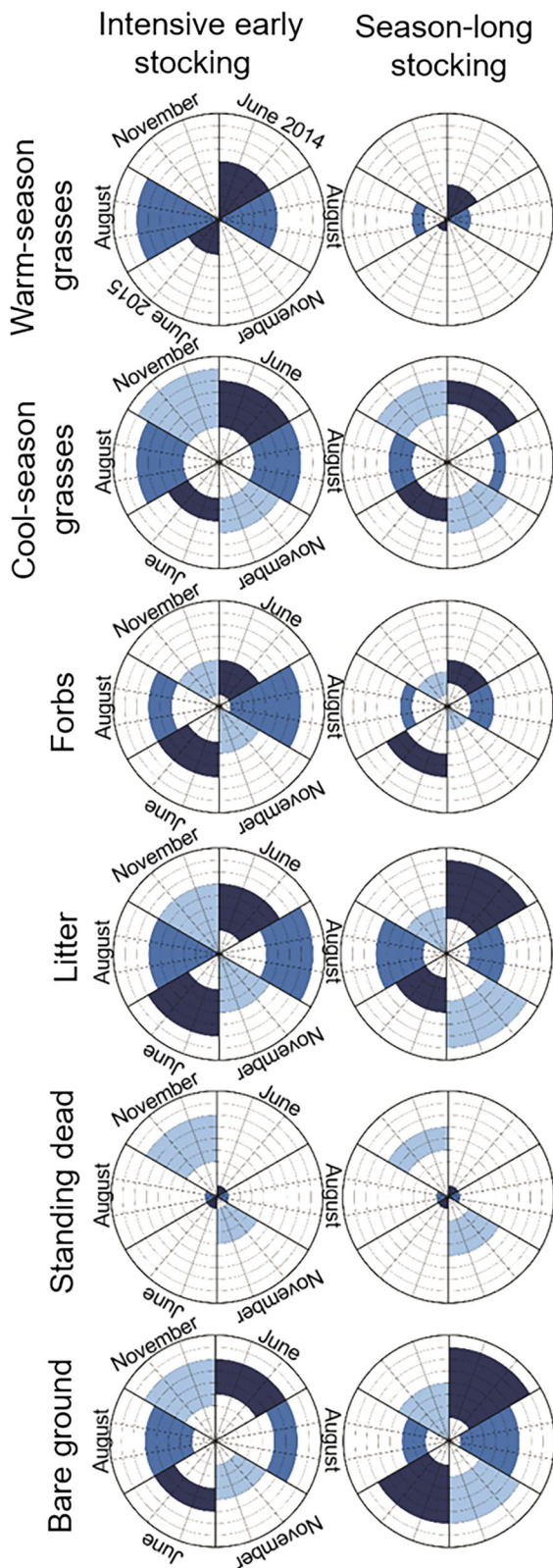


Fig. 6 Within-patch semivariogram results from six functional groups. Blue shading emphasizes the variability that exists within the landscape at any given time for three periods of the year and for 2 years. Shading indicates seasonal variance: June (dark blue), August (azure blue), and November (light blue). For ease of interpretation, these seasonal periods are denoted only in the first column of polar coordinate plots. The first half (clockwise) of the coordinate plot pertains to 2014 data while second-half pertains to 2015 data. See Fig. 3 for interpretation. (Color figure online)

community indicated pastures managed with SLS supported greater among-patch heterogeneity than intensive early stocked IES pastures. However, heterogeneity among patches in vegetation structural measurements (visual obstruction and vegetation height) did not differ by grazing system. Instead, two integral components of vegetation structure exhibited different levels of heterogeneity among patches managed with IES and SLS. In IES pasture, the cover of warm- and cool-season grasses, which composed $\sim 70\%$ of pasture cover, showed marked variability among patches when compared to SLS pastures. But, the mechanisms underlying these differences were unclear. Although some level of landscape-scale heterogeneity was observed through among patch variability for the graminoid components within both grazing treatments, visualization of semi-variance results revealed high heterogeneity in the distribution of grass cover at the within patch-level. The lack of an inverse relationship, in grass cover heterogeneity, between the within-and among-patch scales suggests tall fescue-dominated grasslands do not respond to the application of fire and grazing in the same way as native-dominated tallgrass prairie (Fuhlendorf and Engle 2004; Bielski et al. 2018). This was true for both moderate or high grazing intensity. This result demonstrates that the response of grasslands to the re-introduction of the fire-grazer interaction is not consistent across grasslands (McGranahan et al. 2013a) in meeting the conservation objective of restoring landscape-level heterogeneity of vegetation structure.

As observed by McGranahan et al. (2013a) in our study system, overall vegetation structure did not contrast among management patches and only litter and bare ground cover were consistently high in patch contrast (Fig. 4, S4), suggesting fire spread in the Grand River Grasslands was sufficient to remove litter and create bare ground in recently-burned patches.

Again, this result occurred for both IES and SLS grazing. Thus, we suggest that landscape-level heterogeneity in plant functional group composition and vegetation structure was limited less by grazing intensity and more by tall fescue invasion, which homogenizes the plant community (McGranahan et al. 2012b) and reduces vegetation height in the absence of taller native grass species. We surmise the paucity of taller native grasses in our study pastures inhibited either grazing system from exhibiting clear heterogeneity in overall vegetation structure at the landscape-level; however, an increase in tall warm-season grass cover has potential to alter this pattern.

Within-patch structural heterogeneity

Our semivariance analysis results demonstrate that assessing structural heterogeneity in exotic-dominated grasslands at a single spatiotemporal scale can be misleading. If we had focused on a single spatiotemporal scale, such as June, we would have potentially missed the emergence of heterogeneity and therefore abandoned a grazing-mediated resource that may be meaningful to some taxa (i.e., grassland birds and butterflies; Moranz et al. 2014; Delaney et al. 2016; Duchardt et al. 2016); or avoided exploring a change in the scale at which heterogeneity emerges. Past studies using semivariograms to detect spatial heterogeneity in plant communities based findings on a single sampling period at peak plant community production (i.e., mid-to-late summer) (e.g., Koerner and Collins 2013). In our study, we employed scaling and data visualization techniques to detect small-scale sward structure within distinct patches across two post-fire growing seasons and dormant seasons. We found clear seasonal-dependencies for the emergence of heterogeneity among dominant plant functional groups over two growing seasons, and visualization of our within-patch semivariance results illustrated the role of grazing pressure in mediating vegetation response to patch-burn grazing over the growing season.

Grasses with different reproductive periods showed divergent responses to grazing treatments. Unlike cool-season grasses under IES, within-patch variability of the warm-season grasses in IES pastures fluctuated widely across seasons from very low in the dormant season to pronounced patchiness during the growing season as revealed by our polar coordinate

plots. When grazed throughout the growing season under SLS, fine-scale sward structure of warm- and cool-season grasses remained low across seasons. In contrast, IES grazing altered seasonality and the degree of warm- and cool-season grass sward structure with pronounced variability in warm-season grass cover in August (post-removal of cattle in IES) and consistent patchiness of cool-season grass cover in June and August.

Like graminoids, within-patch spatial autocorrelation of forbs varied by season and grazing treatment. Under IES, forb patchiness was strongest at the end of the growing season (August), and sward size was approximately 15 m. On the other hand, across seasons, patchiness of forbs, as well as the presence of distinct sward structure, was minimal in SLS pastures. Large herbivores increase floristic diversity in grazed mesic grasslands by altering plant community structure (McNaughton 1983; Hartnett et al. 1996) through selective grazing and increased resource heterogeneity through soil disturbances (trampling) and nutrient deposition (Collins and Calabrese 2012; Limb et al. 2018). Distinct heterogeneity in forb cover occurred in August after cattle removal from IES pastures; whereas, forb patch structure remained low and stable in SLS pastures across all seasons. We surmise reduced resource competition between graminoids and forbs because heavy grass herbivory early in the season mediated season-specific forb heterogeneity in our tall fescue-dominated grassland.

Duration of grazing season

Furthermore, our experimental approach of adjusting timing and intensity of grazing pressure has revealed that manipulating a key driver of grassland structure and function, grazing pressure, can return a critical property, i.e., warm-season grasses, to landscapes that were historically dominated by warm-season grasses. Pooled mean warm-season grass cover was 47% greater in IES than in SLS pastures: 7% higher in IES for 2014, 54% higher in 2015. Removal of cattle in early July appeared to allow warm-season grasses to gain vigor and increase in spatial cover (Fig. S4). Moreover, the increased VOR and litter cover for all 1 and 2 YSF patches in IES pastures in November 2015 met the expectation that IES could improve fire potential. A potential explanation is that IES was successful in maintaining cattle use of the recently-

burned patch and drawing them away from non-burned patches (e.g., the magnet effect, Archibald et al. 2005). The magnet effect likely lowered the probability of 2 YSF patches being grazed due to accumulated dead plant material, thus increasing their burn potential for the following year. Further, the availability of forage in the 2 YSF patch may function as a spatial refuge, which facilitates adaptive foraging options and a more stable and productive environment for herbivores (Yoganand and Owen-Smith 2014; Sianga et al. 2017). For example, for wildebeest (*Connochaetes taurinus*) at Kruger National Park, South Africa, the ability to shift habitat use from grazing lawns and recently-burned areas to seepzone grasslands resulted in adequate nutrient intake throughout the year (Yoganand and Owen-Smith 2014). Such functional heterogeneity in vegetation resources may also act to sustain grassland herbivore populations during drought (Owen-Smith 2004; Fuhlendorf et al. 2017; Raynor et al. 2017).

An additional aim of introducing IES grazing to patch-burn grazed pastures was reducing cover of cool-season grasses which are dominated by tall fescue and other non-native C3 grasses in the GRG ecosystem (McGranahan et al. 2012a; Delaney et al. 2016). Compared to SLS pastures (Fig. S4), low cool-season grass cover in 0 YSF patches relative to 1 YSF and 2 YSF patches in IES pastures in August 2015 offers additional evidence of focal grazing in the 0 YSF patch under this adaptive management scheme. Focal grazing of the cool-season grasses early in the grazing season in the 0 YSF patch inhibits plant maturity, resulting in a high percentage of new vegetative tillers that attracts further grazing through the grazing season (Hobbs et al. 1991; Raynor et al. 2015, 2016).

Extant fire-grazer interactions

The potential to investigate the spatial extent of fire-grazer interactions is limited in today's highly fragmented and intensively managed landscapes. Following the introduction of fences and today's management-intensive grazing systems, herbivores no longer have opportunities to abandon expansive landscapes in search of new regions with better forage resources (Tucker et al. 2018). The potential to make decisions at broader geographical scales could lead to unexpected and alternative pattern-process

relationships than those observed in studies of confined grazers (this study; Raynor et al. 2017; Bielski et al. 2018). Outside of a few unfragmented grassland remnants (e.g., Greater Yellowstone Ecosystem), this opportunity has been removed in modern North American landscapes and represents a significant change in large herbivore behavior (Axelrod 1985). Assumptions based on past knowledge derived from studies at broader spatial scales with a greater range of disturbance regimes should not be used to understand drivers of current-day ecological structure and function (Twidwell et al. 2016). For instance, without removing cattle before the period of warm-season grass reproduction in IES, we would not have learned that this strategy can enhance native warm-season grass abundance on an invaded landscape while supporting landscape-level heterogeneity albeit at an initial cost of lower among-patch variability (Fig. 5). Before European settlement in this region, large herbivores were not confined and could search for alternative forage resources, thus releasing warm-season grasses from grazing pressure. In this study, we changed the timing and intensity of grazing in efforts to return native grassland constituents to this invasive grass-dominated landscape while simultaneously mediating some level of heterogeneity at the landscape-scale.

Conclusion

Altering grazing intensity in invasive-dominated grasslands managed with patch-burning could alter the core assumptions about how vegetation structure is distributed under patch-burn grazing management. By adopting a data visualization process that allowed us to detect when fine-scale heterogeneity emerged, we could illustrate where signals of heterogeneity manifest at the basal-level (i.e., within-patch) of the patch-burn grazing framework. Relative to SLS pastures, cover of warm- and cool-season grasses showed greater variability among patches under IES. This result depended on the time period under scrutiny with warm- and cool-season grass cover variability being highest in IES pastures in August after cattle removal. By assessing the vegetation community across among- and within-patch scales over the growing season, we found that timing of fire and grazing can be used in patch-burn grazing to reduce cool-season grass cover

while increasing native grass cover and forb heterogeneity. Because this multi-scale evaluation results in a new understanding of the role of grazing pressure in grasslands managed with spring fire and grazing, the spatiotemporal patterns we identified may also indicate that SLS is insufficient to create spatial heterogeneity of vegetation structure in invaded pastures. Adopting altered grazing practices under the patch-burn grazing framework may be essential to create temporal and spatial heterogeneity of vegetation structure in the commonly-occurring, simple grasslands dominated by invasive grasses.

Acknowledgements We would like to thank many individuals from the University of Nebraska-Lincoln, the Iowa Department of Natural Resources, U.S Fish & Wildlife Service, the Missouri Department of Conservation, the University of Illinois at Urbana-Champaign, and Iowa State University who helped with field data collection or funding for this study. Special thanks to Heidi Hillhouse, Kayla Tarr, Gunnar Malek-Madani, Jon Soper, Dee Ebbeka, Amanda Hefner, Aaron Shropshire, Jace Stott, Doug Tosoni, and Madison Hergenrader.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

- Allen C, Holling C (2010) Novelty, adaptive capacity, and resilience. *Ecol Soc* 15(3):24
- Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Stacey PB, Morgan P, Hoffman M, Klingel JT (2002) Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl* 12(5):1418–1433
- Allen TF, Starr TB (1982) *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago
- Anderson MJ, Ter Braak CJF (2003) Permutation tests for multifactorial analysis of variance. *J Stat Comput Simul* 73(2):85–113
- Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecol Monogr* 83(4):557–574
- Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire–grazer interactions in an african savanna. *Ecol Appl* 15(1):96–109
- Axelrod DI (1985) Rise of the Grassland Biome, Central North America. *Bot Rev* 51(2):163–201
- Bielski CH, Twidwell D, Fuhlendorf SD, Wonka CL, Allred BW, Ochsner TE, Krueger ES, Carlson JD, Engle DM (2018) Pyric herbivory, scales of heterogeneity and drought. *Funct Ecol* 32(6):1599–1608
- Bowman DMJS, Perry GLW, Marston JB (2015) Feedbacks and landscape-level vegetation dynamics. *Trends Ecol Evol* 30(5):255–260
- Brooks ML, D’Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54(7):677–688
- Collins SL, Calabrese LB (2012) Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *J Veg Sci* 23(3):563–575
- D’Antonio CM, Tunison JT, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecol* 25(5):507–522
- D’Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23(1):63–87
- Daubenmire RF (1959) A canopy-coverage method of vegetational analysis. *Northwest Sci* 33:43–64
- Davies KW, Svejcar TJ, Bates JD (2009) Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecol Appl* 19(6):1536–1545
- Delaney JT, Moranz RA, Debinski DM, Engle DM, Miller JR (2016) Exotic-dominated grasslands show signs of recovery with cattle grazing and fire. *PLoS ONE* 11(11):e0165758
- Development Core Team R (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Duchardt CJ, Miller JR, Debinski DM, Engle DM (2016) Adapting the fire-grazing interaction to small pastures in a fragmented landscape for grassland bird conservation. *Rangel Ecol Manag* 69(4):300–309
- Engle DM, Fuhlendorf SD, Roper A, Leslie DM (2008) Invertebrate community response to a shifting mosaic of habitat. *Rangel Ecol Manag* 61(1):55–62
- Forman RT, Godron M (1981) Patches and structural components for a landscape ecology. *Bioscience* 31(10):733–740
- Franklin JF, Lindenmayer D, MacMahon JA, McKee A, Magnuson J, Perry DA, Waide R, Foster D (2000) Threads of Continuity. *Conserv Pract* 1(1):8–17
- Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51(8):625–632
- Fuhlendorf S, Engle D (2004) Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. *J Appl Ecol* 41(4):604–614
- Fuhlendorf SD, Engle DM, Elmore RD, Limb RF, Bidwell TG (2012) Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangel Ecol Manag* 65(6):579–589
- Fuhlendorf SD, Engle DM, Kerby J, Hamilton R (2009) Pyric herbivory: rewinding landscapes through the recoupling of fire and grazing. *Conserv Biol* 23(3):588–598
- Fuhlendorf SD, Fynn RWS, McGranahan DA, Twidwell D (2017) Heterogeneity as the basis for rangeland management. In: Briske DD (ed) *Rangeland systems: processes, management and challenges*. Springer, Cham, pp 169–196
- Gaertner M, Biggs R, Te Beest M, Hui C, Molofsky J, Richardson DM (2014) Invasive plants as drivers of regime

- shifts: identifying high-priority invaders that alter feedback relationships. *Divers Distrib* 20(7):733–744
- Gaertner M, Holmes PM, Richardson DM (2012) biological invasions, resilience and restoration. In: Aniel JV, Aronson J (eds) *Restoration ecology*. Wiley, New York, pp 265–280
- Hartnett DC, Hickman KR, Walter LEF (1996) Effects of bison grazing, fire, and topography on floristic diversity in tall-grass prairie. *J Range Manag* 49:413–420
- Hobbs NT, Schimel DS, Owensby CE, Ojima DS (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72(4):1374–1382
- Holling CS (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol Monogr* 62(4):447–502
- Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Front Ecol Environ* 14(7):369–378
- Koerner SE, Collins SL (2013) Small-scale patch structure in North American and South African grasslands responds differently to fire and grazing. *Landscape Ecol* 28(7):1293–1306
- Limb RF, Hovick TJ, Norland JE, Volk JM (2018) Grassland plant community spatial patterns driven by herbivory intensity. *Agric Ecosyst Environ* 257:113–119
- Lindenmayer D, Hobbs RJ, Montague-Drake R et al (2008) A checklist for ecological management of landscapes for conservation. *Ecol Lett* 11(1):78–91
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294(5543):804–808
- Maresh Nelson SB, Coon JJ, Duchardt CJ, Miller JR, Debinski DM, Schacht WH (2018) Contrasting impacts of invasive plants and human-altered landscape context on nest survival and brood parasitism of a grassland bird. *Landscape Ecol*. <https://doi.org/10.1007/s10980-018-0703-3>
- McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol Evol* 30(2):104–113
- McGranahan DA, Engle DM, Fuhlendorf SD, Miller JR, Debinski DM (2012a) An invasive cool-season grass complicates prescribed fire management in a native warm-season grassland. *Nat Areas J* 32(2):208–214
- McGranahan DA, Engle DM, Fuhlendorf SD, Winter SJ, Miller JR, Debinski DM (2012b) Spatial heterogeneity across five rangelands managed with pyric-herbivory. *J Appl Ecol* 49(4):903–910
- McGranahan DA, Engle DM, Fuhlendorf SD, Winter SL, Miller JR, Debinski DM (2013a) Inconsistent outcomes of heterogeneity-based management underscore importance of matching evaluation to conservation objectives. *Environ Sci Policy* 31:53–60
- McGranahan DA, Engle DM, Miller JR, Debinski DM (2013b) An invasive grass increases live fuel proportion and reduces fire spread in a simulated grassland. *Ecosystems* 16(1):158–169
- McGranahan DA, Hovick TJ, Elmore RD, Engle DM, Fuhlendorf SD, Winter SL, Miller JR, Debinski DM (2016) Temporal variability in aboveground plant biomass decreases as spatial variability increases. *Ecology* 97(3):555–560
- McNaughton S (1983) Physiological and ecological implications of herbivory. *Physiological Plant Ecology III*. Springer, Cham, pp 657–677
- Michener WK, Jones MB (2012) Ecoinformatics: supporting ecology as a data-intensive science. *Trends Ecol Evol* 27(2):85–93
- Moranz RA, Fuhlendorf SD, Engle DM (2014) Making sense of a prairie butterfly paradox: the effects of grazing, time since fire, and sampling period on regal fritillary abundance. *Biol Conserv* 173:32–41
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) Package 'vegan'. *Community ecology package*, version 2(9)
- Oliver TH, Isaac NJB, August TA, Woodcock BA, Roy DB, Bullock JM (2015) Declining resilience of ecosystem functions under biodiversity loss. *Nat Commun* 6:10122
- O'Neill RV (1986) *A hierarchical concept of ecosystems*. Princeton University Press, Princeton
- Owen-Smith N (2004) Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecol* 19(7):761–771
- Peters DPC, Pielke RA, Bestelmeyer BT, Allen CD, Munson-McGee S, Havstad KM (2004) Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proc Natl Acad Sci USA* 101(42):15130
- Pillsbury FC, Miller JR, Debinski DM, Engle DM (2011) Another tool in the toolbox? Using fire and grazing to promote bird diversity in highly fragmented landscapes. *Ecosphere* 2(3):1–14
- Raynor EJ, Joern A, Briggs JM (2015) Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* 96(6):1586–1597
- Raynor EJ, Joern A, Nippert JB, Briggs JM (2016) Foraging decisions underlying restricted space use: effects of fire and forage maturation on large herbivore nutrient uptake. *Ecol Evol* 6(16):5843–5853
- Raynor EJ, Joern A, Skibbe A, Sowers M, Briggs JM, Laws AN, Goodin D (2017) Temporal variability in large grazer space use in an experimental landscape. *Ecosphere* 8(1):e01674
- Ribeiro Jr PJ, Diggle PJ, Ribeiro Jr MPJ (2016) Package 'geoR'
- Ricketts AM, Sandercock BK (2016) Patch-burn grazing increases habitat heterogeneity and biodiversity of small mammals in managed rangelands. *Ecosphere* 7(8):e01431
- Robel R, Briggs J, Dayton A, Hulbert L (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. *J Range Manag* 23:295–297
- Roughgarden JD (1977) Patchiness in the spatial distribution of a population caused by stochastic fluctuations in resources. *Oikos* 29(1):52–59
- Scasta JD, Duchardt C, Engle DM, Miller JR, Debinski DM, Harr RN (2016) Constraints to restoring fire and grazing ecological processes to optimize grassland vegetation structural diversity. *Ecol Eng* 95:865–875
- Seastedt TR, Hobbs RJ, Suding KN (2008) Management of novel ecosystems: are novel approaches required? *Front Ecol Environ* 6(10):547–553

- Setterfield SA, Rossiter-Rachor NA, Hutley LB, Douglas MM, Williams RJ (2010) BIODIVERSITY RESEARCH: turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. *Divers Distrib* 16(5):854–861
- Sianga K, van Telgen M, Vrooman J, Fynn RW, Langevelde F (2017) Spatial refuges buffer landscapes against homogenisation and degradation by large herbivore populations and facilitate vegetation heterogeneity. *Koedoe* 59(2):1–13
- Soranno PA, Cheruvilil KS, Bissell EG, Bremigan MT, Downing JA, Fergus CE, Filstrup CT, Henry EN, Lottig NR, Stanley EH, Stow CA, Tan P, Wagner T, Webster KE (2014) Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems. *Front Ecol Environ* 12(1):65–73
- Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* 24(5):271–279
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31(1):79–92
- Tucker MA, Böhning-Gaese K, Fagan WF et al (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359(6374):466
- Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst* 20(1):171–197
- Twidwell D, Fuhlendorf SD, Taylor CA, Rogers WE (2013) Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *J Appl Ecol* 50(3):603–613
- Twidwell D, West AS, Hiatt WB, Ramirez AL, Winter JT, Engle DM, Fuhlendorf SD, Carlson JD (2016) Plant invasions or fire policy: which has altered fire behavior more in tallgrass prairie? *Ecosystems* 19(2):356–368
- Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecol* 19(2):125–138
- Wu JG, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q Rev Biol* 70(4):439–466
- Yoganand K, Owen-Smith N (2014) Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography* 37(10):969–982