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Spatial Heterogeneity Across Five Rangelands Managed with Pyric-Herbivory

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Spatial Heterogeneity Across Five Rangelands Managed with Pyric-Herbivory

Abstract

1. Many rangelands evolved under an interactive disturbance regime in which grazers respond to the spatial pattern of fire and create a patchy, heterogeneous landscape. Spatially heterogeneous fire and grazing create heterogeneity in vegetation structure at the landscape level (patch contrast) and increase rangeland biodiversity. We analysed five experiments comparing spatially heterogeneous fire treatments to spatially homogeneous fire treatments on grazed rangeland along a precipitation gradient in the North American Great Plains. **2.** We predicted that, across the precipitation gradient, management for heterogeneity increases both patch contrast and variance in the composition of plant functional groups. Furthermore, we predicted that patch contrast is positively correlated with variance in plant functional group composition. Because fire spread is important to the fire–grazing interaction, we discuss factors that reduce fire spread and reduce patch contrast despite management for heterogeneity. **3.** We compared patch contrast across pastures managed for heterogeneity and pastures managed for homogeneity with a linear mixed effect (LME) regression model. We used the LME model to partition variation in vegetation structure to each sampled scale so that a higher proportion of variation at the patch scale among pastures managed for heterogeneity indicates patch contrast. To examine the relationship between vegetation structure and plant community composition, we used constrained ordination to measure variation in functional group composition along the vegetation structure gradient. We used the meta-analytical statistic, Cohen's *d*, to compare effect sizes for patch contrast and plant functional group composition. **4.** Management for heterogeneity increased patch contrast and increased the range of plant functional group composition at three of the five experimental locations. **5.** Plant functional group composition varied in proportion to the amount of spatial heterogeneity in vegetation structure on pastures managed for heterogeneity. **6. Synthesis and applications.** Pyric-herbivory management for heterogeneity created patch contrast in vegetation across a broad range of precipitation and plant community types, provided that fire was the primary driver of grazer site selection. Management for heterogeneity did not universally create patch contrast. Stocking rate and invasive plant species are key regulators of heterogeneity, as they determine the influence of fire on the spatial pattern of fuel, vegetation structure and herbivore patch selection, and therefore also require careful management.

Keywords

biodiversity conservation, fire–grazing interaction, grazing management, heterogeneity, patch contrast, pyric-herbivory, working landscapes

Disciplines

Biodiversity | Ecology and Evolutionary Biology | Natural Resources and Conservation | Plant Biology

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1 **Spatial heterogeneity across five rangelands managed with pyric-herbivory**

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25 **Summary**

26 1. Many rangelands evolved under an interactive disturbance regime in which grazers
27 respond to the spatial pattern of fire and create a patchy, heterogeneous landscape.

28 Spatially heterogeneous fire and grazing create heterogeneity in vegetation structure at
29 the landscape level (patch contrast) and increase rangeland biodiversity. We analysed five
30 experiments comparing spatially heterogeneous fire treatments to spatially homogeneous
31 fire treatments on grazed rangeland along a precipitation gradient in the North American
32 Great Plains.

33 2. We predicted that, across the precipitation gradient, management for heterogeneity
34 increases both patch contrast and variance in the composition of plant functional groups.
35 Furthermore, we predicted that patch contrast is positively correlated with variance in
36 plant functional group composition. Because fire spread is important to the fire–grazing
37 interaction, we discuss factors that reduce fire spread and reduce patch contrast despite
38 management for heterogeneity.

39 3. We compared patch contrast across pastures managed for heterogeneity and pastures
40 managed for homogeneity with a linear mixed-effect (LME) regression model. We used
41 the LME model to partition variation in vegetation structure to each sampled scale so that
42 a higher proportion of variation at the patch scale among pastures managed for
43 heterogeneity indicates patch contrast. To examine the relationship between vegetation
44 structure and plant community composition, we used constrained ordination to measure
45 variation in functional group composition along the vegetation structure gradient. We

46 used the meta-analytical statistic, Cohen's d , to compare effect sizes for patch contrast
47 and plant functional group composition.

48 4. Management for heterogeneity increased patch contrast and increased the range of plant
49 functional group composition at three of the five experimental locations.

50 5. Plant functional group composition varied in proportion to the amount of spatial
51 heterogeneity in vegetation structure on pastures managed for heterogeneity.

52 6. *Synthesis and applications.* Pyric-herbivory management for heterogeneity created patch
53 contrast in vegetation across a broad range of precipitation and plant community types,
54 provided that fire was the primary driver of grazer site selection. Management for
55 heterogeneity did not universally create patch contrast. Stocking rate and invasive plant
56 species are key regulators of heterogeneity, as they determine the influence of fire on the
57 spatial pattern of fuel, vegetation structure and herbivore patch selection, and therefore
58 also require careful management.

59

60 **Keywords:** Biodiversity conservation, Fire–grazing interaction, Grazing management,

61 Heterogeneity, Patch contrast, Pyric-herbivory, Working landscapes

62

63

64 **Introduction**

65 Many rangelands worldwide are working landscapes managed to meet economic goals as
66 well as biological goals (Polasky *et al.* 2005; Ellis & Ramankutty 2008). When economic
67 objectives take precedence, rangeland biodiversity is imperilled, such as when rangeland is
68 converted to cropland or overgrazed by livestock (Samson & Knopf 1994; Fuhlendorf & Engle
69 2001; O'Connor *et al.* 2010). Moreover, conventional rangeland management promotes
70 spatially-uniform, moderate grazing and the homogeneous removal of biomass by grazers at the
71 pasture scale (Holechek, Pieper, & Herbel 2003) even though uniform moderate grazing
72 degrades habitat quality and contributes to the decline of rangeland biodiversity (Fuhlendorf &
73 Engle 2001; Derner *et al.* 2009).

74 Many rangelands evolved under patchy disturbance regimes that vary in frequency and
75 intensity across multiple spatial scales (Fuhlendorf & Smeins 1999), therefore, reconciling
76 conservation and agricultural production in rangeland probably depends upon heterogeneity-
77 based management analogous to historical patterns of disturbance (Fuhlendorf & Engle 2001).
78 Heterogeneity is an important driver of biodiversity and an essential component of conservation
79 in ecosystems worldwide (Ostfeld *et al.* 1997). Although heterogeneity consists of many
80 ecosystem attributes, we apply the concept of patch contrast, which describes the degree of
81 difference between patches of otherwise similar properties (Kotliar & Wiens 1990). Patch
82 contrast is a useful concept for rangeland heterogeneity because many rangelands evolved under
83 a shifting mosaic of fire and grazing, in which grazing is concentrated on the most recently-
84 burned portions of the landscape in response to the high-quality forage that grows after fire and

85 focal grazing (Archibald & Bond 2004; Allred, Fuhlendorf, Engle, *et al.* 2011). Patch contrast is
86 created as grazers and vegetation respond to the pattern of fire in the landscape (Adler, Raff, &
87 Lauenroth 2001). This fire–grazing interaction – or pyric-herbivory – is an ecological
88 disturbance that differs from the effects of fire and grazing alone (Fuhlendorf *et al.* 2009).

89 When applied in a management context as patch burn–grazing, pyric-herbivory supports
90 rangeland biodiversity by increasing the diversity of habitat types, ranging from low stature
91 grazing lawns in recently-burned patches to tall, mature plants in patches unburned for several
92 years (Fuhlendorf & Engle 2004; Winter *et al.* 2012). Such differences in vegetation structure are
93 driven by the pattern of grazing as well as by differential plant responses to the fire–grazing
94 interaction among patches: the relative abundance of plant functional groups varies across
95 patches according to the length of time since a patch was burned (Fuhlendorf *et al.* 2006; Winter
96 *et al.* 2012). Again, patch contrast is a useful term to describe heterogeneity among patches
97 because habitat diversity reflects the degree of difference in vegetation structure among
98 rangeland patches (Fuhlendorf *et al.* 2006; Coppedge *et al.* 2008).

99 Heterogeneity clearly benefits biodiversity on rangeland, but universal efficacy of the
100 fire-grazing interaction is less clear. We use vegetation structure and plant functional group
101 composition data from five experiments that compare management for heterogeneity (pyric-
102 herbivory) with management for homogeneity (grazing with homogeneous fire regimes). The five
103 experimental locations span several gradients, including precipitation and plant community type
104 and land-use history. Given that evidence supporting an operative fire-grazing interaction has
105 been demonstrated in a breadth of ecosystems worldwide (Allred, Fuhlendorf, Engle, *et al.*
106 2011), we did not expect the strength of the fire–grazing interaction to vary across the ecological
107 gradient (plant community types and precipitation). However, because invasive species and

108 intense grazing both influence fuel load and continuity, which in turn affect fire spread (Davies
109 et al. 2010; McGranahan et al. 2012), we had reason to believe invasive species and intense
110 grazing might reduce the strength of the fire–grazing interaction.

111 In this study, we test the following hypotheses using comparable data from five
112 experiments: 1. Patch contrast is greater in rangeland managed for heterogeneity when compared
113 to rangeland managed for homogeneity; 2. Heterogeneity-based management increases variance
114 in the composition of plant functional groups; and 3. Patch contrast is positively correlated with
115 variance in plant functional group composition. We found that patch contrast was associated with
116 variance in plant functional group composition and that management for heterogeneity created
117 variation in vegetation structure. However, management for heterogeneity did not universally
118 create patch contrast across our five study locations. Stocking rate and invasive plant species
119 appear to regulate patch contrast more than primary productivity despite the precipitation
120 gradient and differences in plant communities across our study locations.

121

122

123 **Methods**124 *Study locations*

125 To compare the effect of spatially heterogeneous and spatially homogeneous fire regimes
126 on grazed rangeland, we combined vegetation structure and plant functional group composition
127 data from five experimental locations in central North America that span circa 650 km from
128 mixed prairie in the southwest to eastern tallgrass prairie in the northeast (Table 1). The five
129 locations include: Hal and Fern Cooper Wildlife Management Area, Woodward County,
130 Oklahoma; Marvin Klemme Range Research Station, Washita County, Oklahoma; Oklahoma
131 State University Range Research Station, Paine County, Oklahoma; Tallgrass Prairie Preserve,
132 Osage County, Oklahoma; and the Grand River Grasslands, Ringgold County, Iowa. While each
133 experiment was established independently, similarity of experimental design, treatment structure,
134 and data collected provide the opportunity to test for a connection between heterogeneity-based
135 management and actual heterogeneity in vegetation across a broad geographic area.

136 *Data*

137 We used vegetation structure and plant functional group composition data from each of
138 the five locations. Data were similar across all locations. Appendix S1 in Supporting Information
139 includes detailed accounts of the types of data and their specific collection methodologies. At
140 each location, cattle (*Bos taurus*) were stocked continuously during the grazing season on all
141 pastures and cattle were allowed unrestricted access to grazing and water within each pasture,
142 without interior fencing. Across all five locations, vegetation structure was quantified with visual
143 obstruction measurements, which combine vegetation height and vegetation density (Harrell &

144 Fuhlendorf 2002). Visual obstruction methods used in this study include visual obstruction
145 reading (Robel *et al.* 1970) and angle of obstruction (Kopp *et al.* 1998).

146 Plant functional group data were collected once each year at each location. Canopy cover
147 estimations follow the Daubenmire (1959) cover class index at all but the Cooper location, where
148 canopy cover was estimated to the nearest five per cent. While sampling periods varied slightly
149 across locations (see Appendix S1), the timing of the sampling periods was consistent from year
150 to year within each location. Sampling at each location followed a nested hierarchical design in
151 which pastures were divided into patches and patches were divided into transects. Sampling
152 points were randomly located along transects to measure visual obstruction and plant functional
153 group canopy cover (sampling points were located within avian point count areas rather than
154 along transects at the Tallgrass Prairie Preserve).

155 *Data analysis*

156 *Spatial heterogeneity in vegetation structure.*—To compare spatial heterogeneity in vegetation
157 structure (patch contrast) across heterogeneously-managed and homogeneously-managed
158 rangeland, we used a linear mixed-effect (LME) regression model to determine the proportion of
159 variance in vegetation structure attributable to each sampled spatial extent, and compared the
160 average proportion of variance in the patch term across treatments within each location (Winter
161 *et al.* 2012). We created an LME regression model with an intercept-only fixed-effect term (+1)
162 and a random-effect term that included the spatial extents that were sampled in common to each
163 location – sampling point, patch, and pasture – and a year factor to account for repeated
164 measures using the lmer function in the lme4 package for the R statistical environment (Bates &
165 Maechler 2010; R Development Core Team 2011). Because of the hierarchical and annually-
166 repeated design common to all five experiments, the random-effect term for each location was

167 fully crossed to account for statistical interactions between sampled spatial extents and time.
168 Variance estimates were returned for each factor in the random-effect term plus an additional
169 residual error factor (Baayen, Davidson, & Bates 2008). We calculated the proportion of
170 variance contributed by each factor by applying the sum of the variance estimations as a divisor
171 to each factor's original variance estimate. The LME model was applied to each pasture within
172 each location.

173 We tested for a difference in mean proportion variance in vegetation structure to compare
174 pastures managed for heterogeneity and homogeneity within each location using a Student's t
175 test in the R stats package. A significantly greater proportion of variance in the patch term for
176 pastures managed for heterogeneity within a location indicates that heterogeneity-based
177 management created patch contrast in vegetation structure within these pastures.

178 *Spatial heterogeneity in plant functional group composition.*—To test the hypothesis that
179 management for heterogeneity increases variance in plant functional group composition, we first
180 calculated the range of plant functional group composition in constrained ordination space. We
181 specified vegetation structure as the constrained axis in a redundancy analysis (RDA) of plant
182 functional group data for each location, and calculated the range of values, or site scores, along
183 the RDA constrained axis for each pasture. Redundancy analysis is a constrained ordination that
184 calculates variation in multivariate data with respect to *a priori* constraints (Ter Braak 1986;
185 Oksanen *et al.* 2011). This method allowed us to compare variation in plant functional group
186 composition with specific reference to the vegetation structure gradient, specified as RDA axis 1
187 (RDA1). We used the *rda* function in the *vegan* package for the R statistical environment
188 (Oksanen *et al.* 2011).

189 We scaled RDA1 output to allow the comparison of ordination results across all
190 locations. The overall range of possible variation in each ordination varied by location because a
191 separate ordination was performed for each location, and each ordination was based on the
192 specific plant functional groups measured at each location (see Appendix S1). Thus, prior to
193 further analysis, we combined RDA1 site scores into a single dataset and scaled the data to create
194 a standardized distribution that allows comparison across locations.

195 The range of site scores for a given pasture along RDA1 represents the variation in plant
196 functional group composition, as pastures with a greater range of functional group composition
197 span a larger range of site scores along RDA1. We tested for a difference in the mean range of
198 RDA1 scores to compare pastures managed for heterogeneity and homogeneity within each
199 location using a Student's t test in the R stats package. Again, a significantly greater range for
200 pastures managed for heterogeneity within a location indicates that heterogeneity-based
201 management created variance in plant functional group composition within these pastures.

202 *Calculating effect sizes.*—We used a meta-analytical statistic to compare the effect of
203 heterogeneity-based management on patch contrast and plant functional group composition
204 across all five locations. Effect size statistics use a single value to quantify the difference
205 between two replicated groups by comparing the mean and variance of each group (Harrison
206 2011). Effect size has been used elsewhere to compare the effect of ecological management
207 across studies testing common hypotheses (Côté & Sutherland 1997). Here, the greater the effect
208 size for a location, the more pronounced the difference between response variables among
209 pastures managed for heterogeneity compared to pastures managed for homogeneity. We
210 calculated the meta-analysis statistic Cohen's d (Cohen 1977) for each response variable,

211 proportion variance and range of RDA1 scores, to determine effect size with the following
212 formula:

$$213 \quad d = (\mu_{\text{het}} - \mu_{\text{hom}}) / \sqrt{(\sigma_{\text{mean}})},$$

214 In which μ_{het} and μ_{hom} represent the mean value of the response variables in pastures
215 managed for heterogeneity and homogeneity, respectively, and σ_{mean} represents the mean
216 standard deviation of each response variable. Using the R statistical environment, we estimated
217 95% confidence intervals with a two-part iterative re-sampling algorithm. First, a sampling
218 distribution for each Cohen's d was generated by 1000 simulations of each treatment groups'
219 mean and standard deviation. Second, the calculated Cohen's d was compared to the generated
220 sample distribution with 9999 iterations at alpha = 0.05 to generate the 95% confidence interval.

221 To test our third prediction that patch contrast is positively correlated with variance in
222 plant functional group composition, we plotted the patch contrast effect size against the plant
223 community composition effect size and calculated a correlation coefficient using Kendall's T, a
224 non-parametric test for association between two variables based on similarity of rank (Kendall
225 1938).

226

227

228 **Results**

229 Management for heterogeneity increased patch contrast at three of the five experimental
230 locations used in this study (Cooper, Stillwater, and the TGPP) (Fig. 1). At two locations,
231 Klemme and the GRG, management for heterogeneity did not increase spatial heterogeneity in
232 vegetation structure compared to management for homogeneity, and thus did not create patch
233 contrast.

234 At Klemme and the GRG, variance in vegetation structure among pastures managed for
235 heterogeneity was lower and variance in vegetation structure among pastures managed for
236 homogeneity was higher than at Cooper, Stillwater, and the TGPP. In other words patch-level
237 variation was neither as great as expected on pastures managed for heterogeneity at Klemme and
238 the GRG, nor was patch-level variation as low as expected on pastures managed for homogeneity
239 at these two locations.

240 Management for heterogeneity increased the variance in plant functional group
241 composition at two of the five locations (Cooper and the TGPP) (Fig. 2). An outlier among
242 pastures managed for homogeneity at Stillwater increased the variation around the mean such
243 that, despite generally higher variance in plant functional group composition among pastures
244 managed with heterogeneity, the difference was not significant ($P = 0.08$). As above, there was
245 no difference between pastures managed for heterogeneity and those managed for homogeneity
246 at Klemme and the GRG.

247 Calculated effect sizes for patch contrast and variance in plant functional group
248 composition were positive for both measures at all five locations, but at only three locations
249 (Cooper, Stillwater, and the TGPP) was Cohen's d significantly non-zero based on estimated
250 95% confidence intervals (Fig. 3). This trend was consistent for both patch contrast and variance
251 in plant functional group composition. In no instance did management for heterogeneity produce
252 a negative effect size in relation to management for homogeneity. The positive association
253 between patch contrast and variance in plant functional group composition ($T = 0.40$) indicated
254 that the amount of spatial heterogeneity in vegetation structure on pastures managed for
255 heterogeneity generally varied in proportion with plant functional group composition.

256 Notably, differences in patch contrast and plant functional group composition were
257 associated with neither environmental factors along the geographic gradient, nor with differences
258 in management, including pasture size, number of patches, or fire regime (Table 1). For example,
259 pastures managed for heterogeneity at the most arid location in the mixed-grass prairie (Cooper),
260 and in two of the three mesic, tallgrass prairie locations (Stillwater and TGPP) had significant
261 patch contrast compared to pastures managed for homogeneity. Thus, whether patch contrast
262 followed management for heterogeneity was independent of climate and vegetation type.
263 Likewise, pasture area did not appear to affect whether patch contrast followed management for
264 heterogeneity, as the area of pastures at Stillwater was similar to the area of pastures at Klemme
265 and the GRG. Historical stocking rate, however, was associated with differences in patch
266 contrast: only Klemme and the GRG were stocked heavily prior to the beginning of the
267 experiments (Table 1), and management for heterogeneity at these locations did not create patch
268 contrast compared to management for homogeneity.

269

270

271 **Discussion**

272 We found that management for heterogeneity applied through patch-burn grazing
273 increased patch contrast and increased the variance in plant functional group composition at
274 three of the five locations. Overall, patch contrast increased with variance in plant functional
275 group composition. Whether management for heterogeneity created patch contrast was
276 unaffected by precipitation, vegetation type, primary productivity, pasture area, patch area or
277 number of patches per pasture (Table 1), which is congruous with previous work noting the
278 range of ecosystems in which the fire–grazing interaction has been reported (Allred, Fuhlendorf,
279 Engle, *et al.* 2011). At the same time, the fact that heterogeneity-based management did not
280 universally create patch contrast underscores the fundamental link between fire and grazing in
281 pyric-herbivory.

282 Pyric-herbivory – the unique ecological disturbance created by the fire–grazing
283 interaction – depends upon fire to influence grazing behaviour such that both grazing and
284 vegetation respond to the spatial pattern of fire (Fuhlendorf *et al.* 2009). However, our results
285 clearly indicate that the influence of fire on the pattern of grazing and vegetation in the landscape
286 is weak unless fire and grazing function as an interacting disturbance. A universal response to
287 pyric-herbivory requires the pattern of fire in the landscape to influence vegetation structure and
288 grazing behaviour and create a contrast between patches that attract grazing (magnet patches)
289 and patches that deter grazing (deterrent patches). However, the influence of fire is weak if it
290 fails to override other environmental factors that contribute to grazer selectivity at the landscape
291 level (Adler, Raff, & Lauenroth 2001; Allred, Fuhlendorf, & Hamilton 2011).

292 Grazing followed the spatial pattern of fire and created patch contrast at three of our five
293 locations, but heterogeneity-based management failed to couple fire and grazing into an
294 interacting disturbance at two locations. We attribute the lack of a fire–grazing interaction at
295 Klemme and the GRG to poor fire spread in the burned patches created by a history of
296 overgrazing at each location and invasive plant species that modified the fuelbed in the GRG.
297 Severe grazing in years preceding fire reduces fire spread by reducing the fuel load and creating
298 gaps in the fuelbed (Kerby, Fuhlendorf, & Engle 2007; Davies, Svejcar, & Bates 2009; Leonard,
299 Kirkpatrick, & Marsden-Smedley 2010; Davies *et al.* 2010). At Klemme and the GRG, stocking
300 rates prior to experimental treatment were much greater than pre-treatment stocking rates at
301 Cooper, Stillwater and the TGPP (Table 1). Heavy grazing reduced fuel loading, which reduced
302 fire spread. As such, subsequent grazing preference was not determined by pyric-herbivory but
303 rather by environmental variability at spatial scales other than the burned patches– e.g., areas
304 close to water, shade, or patches of preferred forage species (Senft *et al.* 1987; Bailey *et al.*
305 1996).

306 Overstocking contributed to reduced fuel load in the GRG, but discontinuity in the
307 fuelbed appears to have been caused not by gaps of bare ground but by an abundance of invasive
308 tall fescue (*Schedonorus phoenix* (Scop.) Holub). Tall fescue creates a barrier to fire spread:
309 during the conventional prescribed burning period, live fuel moisture content in tall fescue
310 exceeds that required to sustain fire spread (McGranahan *et al.* 2012). In the GRG, grazing
311 reduced accumulated dead fuel and increased proportion of live tall fescue in the fuelbed, which
312 thereby reduced fire spread (McGranahan 2011).

313 Our multivariate method for determining variance in plant functional groups
314 accommodated functional group classifications for each location. This approach is both flexible

315 in combining data from individual experiments into a comparative analysis and allowed for
316 insight into the role specific plant functional groups play in the fire–grazing interaction. For
317 example, Cooper had the greatest shrub component in the vegetation, and patch contrast at this
318 location is likely due to the adaptation of the dominant shrub, sand sagebrush (*Artemisia filifolia*
319 Torr.), to quickly resprout after fire (Winter *et al.* 2011). At the other end of the productivity
320 gradient, management for heterogeneity failed to create patch contrast in the GRG, which had a
321 much lower abundance of native plant species (Pillsbury *et al.* 2011) than the other tallgrass
322 prairie locations, which were not only relatively free of invasive plant species but were
323 dominated by native plants (Fuhlendorf & Engle 2004; Fuhlendorf *et al.* 2006). Given that patch
324 contrast increases with variance in plant functional group composition (Fig. 3), native plant
325 species with an evolutionary history of pyric-herbivory are likely important in ensuring that
326 management for heterogeneity achieves the desired outcomes.

327 The long-term legacy effect of historical management as regulators of pyric-herbivory are
328 not known, although recent data from Klemme suggest that when stocking rate is moderated,
329 plant productivity recovers, fuel load and fuel continuity increase, and fire drives spatial pattern
330 of grazing (Limb *et al.* 2011). For the period examined in this study, Klemme had a diverse
331 composition of plant functional groups despite low patch contrast, which is probably due to
332 spatially-heterogeneous grazing driven by environmental factors other than fire, because the
333 influence of fire was small (Adler *et al.* 2001). In the GRG, however, both patch contrast and the
334 range of plant functional group composition were slight, probably due to the great abundance of
335 tall fescue on historically severely stocked pastures (McGranahan 2011). Thus, restoration of
336 pyric-herbivory at Klemme probably depends primarily on the recovery of plant productivity, but

337 recovery for overstocking and invasive species control may be required before pyric-herbivory
338 can be fully restored to the GRG.

339 The five rangeland locations included here used domestic cattle *Bos taurus* as grazers,
340 reflecting the fact that native herbivores have largely been extirpated from central North
341 American rangelands and cattle ranching is the predominant use of many rangelands worldwide.
342 Even in ecosystems where native herbivores persist, the natural fire regimes of many rangelands
343 have been substantially altered. However, domestic livestock and prescribed fire can re-create
344 the pre-historic mosaic: evidence from the North American tallgrass prairie suggests the
345 conservation value of cattle might be analogous to that of bison *Bison bison*, the dominant native
346 herbivore, in heterogeneous landscapes managed with fire (Towne, Hartnett, & Cochran 2005;
347 Allred, Fuhlendorf, & Hamilton 2011). Management for heterogeneity has been shown to
348 increase the diversity of invertebrates, small mammals, large ungulates and birds in several
349 ecosystems worldwide (Archibald & Bond 2004; Fuhlendorf *et al.* 2006; Bouwman & Hoffman
350 2007; Coppedge *et al.* 2008; Engle *et al.* 2008; Fuhlendorf *et al.* 2009; Doxon *et al.* 2011).
351 Moreover, patch burn-grazing is an agriculturally-productive management practice in working
352 rangeland grazed by cattle (Limb *et al.* 2011).

353

354

355 **Conclusion**

356 Our results demonstrate that management for heterogeneity using patch burn-grazing
357 does not universally create patch contrast in rangelands. Rather, patch burn-grazing creates patch
358 contrast only if fire is the primary driver of grazer site selection across the landscape. The level
359 of patch contrast appears to correspond to the level of variance in plant functional group
360 composition. Management for heterogeneity using patch burn-grazing can increase heterogeneity
361 in vegetation structure, and therefore increase rangeland biodiversity compared to management
362 for homogeneity, but only when fire behaviour influences grazing behaviour.

363 Three important themes that apply to management for heterogeneity emerged from our
364 findings. First, managers choosing to apply patch burn-grazing should stock livestock at a
365 moderate stocking rate. Each location in our study that did not show patch contrast was
366 excessively stocked before being managed with patch burn-grazing, which suggests that
367 excessive stocking reduces fire spread and decreases the influence of fire on the spatial pattern of
368 grazing. The second theme is that invasive species that reduce fire spread render fire ineffective
369 to drive spatial pattern of grazing. Finally, by moderating stocking rate on overgrazed
370 rangelands, plant productivity and fuel load will recover and fire will again influence spatial
371 pattern of grazing (Limb *et al.* 2011). However, the extent to which invasive species persist as a
372 barrier to effective patch burn-grazing remains unknown.

373

374

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520 **Supporting information**

521 Additional supporting information may be found in the online version of this article:

522 **Appendix S1.** Description of data included in rangeland heterogeneity analysis

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Table 1: Precipitation, vegetation, and grazing information for five experimental locations comparing heterogeneously-applied fire management with homogeneous fire regimes. Refer to Methods and Appendix S1 for information about experimental design, data collected, and years included. Locations are listed geographically from west to east

Study location	Stillwater				
	Cooper ^a	Klemme ^b	^c	TGPP ^d	GRG ^e
Annual precipitation (cm)					
Long-term mean	57	78	83	88	91
Study period range	41-77	51-82	61-99	59-109	97-147
Vegetation type	Artemisia shrubland- mixed prairie	Midgrass prairie	Tallgrass prairie	Tallgrass prairie	Tallgrass prairie
Stocking rate ^f					

Prior to study period	Moderate	Heavy	Moderate	Moderate	Severe
				-light	
Study period	0.8	1.6	4.3	3.2	3.1
(Animal-Unit-Months ha ⁻¹)	(Moderate)	(Moderate)	(Moderate)	(Moderate)	(Heavy)
			e)	e-light)	
Grazing season	1 April - 15 Sept.	15 Mar. - 15 Sept.	1 Dec. - 1 Sept.	15 Apr. - 20 Jul.	1 May - 1 Oct.
Pasture area (ha)	406-848	ca. 50	45-65	400-900	15 - 31
Annual primary productivity ^g (kg ha ⁻¹)	1500	2000	5600	6000	6700

^aHal and Fern Cooper Wildlife Management Area. (Gillen & Sims 2004; Winter *et al.* 2012)

^bMarvin Klemme Experimental Research Range. (Gillen, Eckroat, & McCollum 2000; Limb *et al.* 2011)

^cStillwater Research Range. (Gillen, Rollins, & Stritzke 1987; Fuhlendorf & Engle 2004; Limb *et al.* 2011; OK Mesonet

2011)

^d Tallgrass Prairie Preserve. (Hamilton 2007; Coppedge *et al.* 2008; OK Mesonet 2011)

^e Grand River Grasslands. (IEM 2011; Pillsbury *et al.* 2011)

^f Stocking rate categories expressed in relation to local recommendations from the USDA Natural Resource Conservation Service.

^g Estimated annual primary productivity of native vegetation not recently disturbed by grazing or fertilization. Published data were used for Cooper (Gillen & Sims 2004), Klemme (Gillen, Eckroat, & McCollum 2000), and Stillwater (Gillen, Rollins, & Stritzke 1987). Unpublished data on end-of-season biomass one year after fire from at least one year within the study period included here were used to estimate annual primary productivity at the TGPP and the GRG.

Figure 1: Proportion of total variance in vegetation structure contributed by the patch term in nested, spatially hierarchical sampling measures patch contrast at five experiments comparing management for heterogeneity (blue triangles) to management for homogeneity (orange circles). Data are plotted for each pasture replicate within each of the five locations. Locations are arranged along a general west-to-east geographical gradient (western Oklahoma – south-central Iowa), which corresponds to a precipitation gradient. Asterisks represent results of Student's t tests for differences in means of management groups: “ ** ” $P < 0.01$; “ * ” $P \leq 0.05$.

Figure 2: Range of RDA1 scores measures variance in plant functional group composition at five experiments comparing management for heterogeneity (blue triangles) to management for homogeneity (orange circles). Data are plotted for each pasture replicate within each of the five locations. Locations are arranged along a general west-to-east geographical gradient (western Oklahoma – south-central Iowa), which corresponds to a precipitation gradient. Asterisks represent results of Student's t tests for differences in means of management groups: “ * ” $P \leq 0.05$.

Figure 3: Effect size of patch contrast (Y axis) plotted against effect size of variance in plant functional group composition (X axis), with corresponding 95% confidence intervals, for five rangeland experiments comparing management for heterogeneity against management for homogeneity. Effect sizes are calculated with the meta-analysis statistic Cohen's d (see Methods for equation) and are plotted on a log scale.

Fig. 1

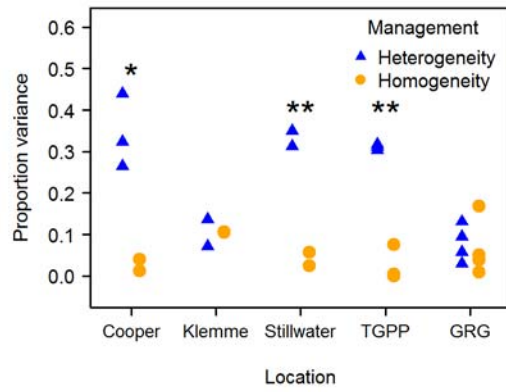


Fig. 2

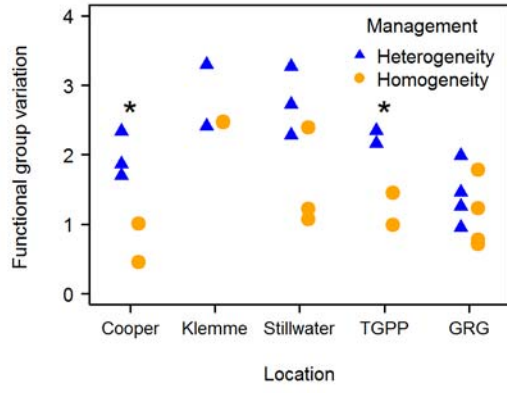


Fig. 3

