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# Herbivory strains resilience in drought-prone aspen landscapes of the western United States

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10 **Herbivory strains resilience in drought-prone aspen landscapes of the western United States**  
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28

29 **Abstract**

30 **Aims:** Aspen forests around the northern hemisphere provide rich biodiversity compared to surrounding  
31 vegetation types. In both North America and Europe, however, aspen are threatened by a variety of  
32 human impacts: clear-felling, land development, water diversions, fire suppression, and both wild and  
33 domestic ungulate herbivory. We conducted a landscape assessment of quaking aspen (*Populus*  
34 *tremuloides*) for the purpose of identifying key components of resilience. Specifically, we strove to test  
35 novel measures linking plant-animal interactions, compare crucial functional differences in aspen types,  
36 and make appropriate restorative recommendations based on the outcome of these assessments.

37 **Location:** The Book Cliffs region of eastern Utah and western Colorado, USA.

38 **Methods:** Seventy-seven one hectare plots were sampled for forest structure, composition, regeneration  
39 and recruitment, landscape elements, browse level, and herbivore use. Use was determined by counting  
40 the number of pellet groups by ungulate species at each sample location. We tested the efficacy of a  
41 visual stand condition rating system when compared to objective metrics. A series of non-parametric  
42 analyses were used to compare functional aspen types and stand condition groups by key variables.  
43 Nonmetric multidimensional scaling (NMS) allowed us to explore all our data to find the most critical  
44 measures of aspen stand conditions for the purpose of better informing future aspen monitoring.

45 **Results:** Results indicate that plots differed significantly by seral or stable aspen functional types, stand  
46 condition rating, and browse species use. Ordination analysis revealed that regeneration level and  
47 herbivore use were the strongest objective indicators of aspen stand conditions, while the stand condition  
48 rating proved a valuable subjective index of forest status. While ungulate herbivory of aspen is  
49 problematic internationally, our results show acute impacts where moderate slopes, relatively low water  
50 availability, and intense browsing predominate.

51 **Conclusions:** Appropriate measures of aspen communities, informed by crucial functional divisions, have  
52 allowed us to gain a clear understanding of conditions across this large landscape. Overall, aspen in our  
53 study landscape is highly vulnerable to collapse due to narrow physiographic and climate limitations and

54 browse levels. Without herbivory reduction, future conservation in such areas will be strained and  
55 widespread system failure may occur.

56

57 **Keywords:** *Populus tremuloides*; ungulates; elk; deer; livestock; forest ecology; conservation;  
58 biodiversity; climate; ordination

59 **Nomenclature:** Plant species follow Welsh et al., (1987). Mammal taxonomy is derived from (Zaveloff  
60 & Collett, 1988).

61 **Abbreviations:** NMS = Nonmetric multidimensional scaling; NAIP = National Agriculture Imagery  
62 Program; SNOTEL = "snow telemetry" - a network of remote stations to gather and record snow water  
63 content, precipitation, and air temperature data.

64 **Running Head:** Aspen, ungulates, and forest resilience

## 65 **Introduction**

66 Aspen forests of the northern hemisphere provide unique resources where they are often the lone  
67 deciduous component of vast coniferous expanses. In both North America and Europe aspen are valued  
68 for their rich flora and fauna (Edenius & Ericsson 2007; Kuhn et al. 2011). These biodiverse  
69 communities, however, are regionally threatened by management practices, such as logging and fire  
70 suppression which favor conifers, and by overabundance of either domestic or wild herbivores (Kota &  
71 Bartos 2010; Edenius et al. 2011). While many of the underlying issues facing quaking aspen (*Populus*  
72 *tremuloides*) and European aspen (*P. tremula*) are similar, there are two notable differences: quaking  
73 aspen tend to form large contiguous stands and, particularly in western locales, they occur in relatively  
74 drier climates. Climate thus becomes a key component of future quaking aspen management where it is  
75 thought that these forests are at or near their moisture resource margins (Rehfeldt et al. 2009; Martin &  
76 Maron 2012). Stressors on aspen landscapes that augment climate impacts, therefore, are of high concern  
77 to those addressing forest system resilience.

78 In western North American there are numerous recent studies documenting both declines (Di  
79 Orio et al. 2005; Worrall et al. 2008) and expansions (Manier & Laven 2002; Kulakowski et al. 2004) of  
80 aspen forests. These works document cover change at a variety of spatial and temporal scales, therefore it  
81 is difficult to make direct comparisons between results. Moreover, recent authors have pointed out  
82 distinct aspen functional types (Shepperd et al. 2006; Rogers et al. 2013) which would be expected to  
83 respond differently to short- and long-term perturbations. Aspen cover change has been attributed to fire  
84 suppression and conifer encroachment, past logging, climate variability, settlement period burning, and  
85 browsing by wild and domestic ungulates (Kulakowski et al. 2004; Shepperd et al. 2006; Rogers et al.  
86 2011). Some results have indicated positive and negative cover change within the same landscape  
87 (Kulakowski et al. 2004; Sankey 2009), lending further support to the concept of varying aspen functional  
88 types (Rogers et al. 2013). Given that aspen forests have undergone modest-to-large change over the past  
89 150 years—often where human actions combine with stochastic disturbances—practitioners have become  
90 concerned about the future of these forests under current management regimes. Contemporary thinking

91 holds that “managing for resilience” will afford the best hopes for sustainable quaking aspen (as in most  
92 systems). Forest managers are therefore interested in sustaining or creating resilient aspen communities  
93 with a foundation of state-of-the-science knowledge and adaptive practices. Where plant-animal  
94 interactions are paramount, a barrier to such goals has been a lack of effective communication between  
95 federal forest and state wildlife practitioners in both scientific and applied realms.

96         While aspen is highly valued for its’ biodiversity, in some locales herbivores are having undue  
97 impact on the ability of these systems to maintain ecosystem functions. Aspen shoots and leaves provide  
98 valuable nutrition to several species, especially early and late in the growing season when diversity of  
99 browse is limited (Jones et al. 2005; Beck et al. 2006). In Scandinavia, moose (*Alces alces*) are the  
100 primary herbivore affecting aspen recruitment (Edenius & Ericsson 2007; Edenius et al. 2011). In the  
101 western United States browsing cattle (*Bos spp.*), sheep (*Ovis spp.*), North American elk (*Cervus*  
102 *elaphus*), and mule deer (*Odocoileus hemionus*) in many areas are severely inhibiting stand renewal via  
103 repeated aspen sprout consumption (DeByle 1985; Zeigenfuss et al. 2008; DeRose & Long 2010; Rogers  
104 et al. 2010). This phenomenon seems particularly acute where wild elk populations are thought to be  
105 beyond “historical range of variation” levels due to aggressive reintroduction programs (e.g., Bailey et al.  
106 2007; Stritar et al. 2010) and relatively low levels of predation (Beschta & Ripple 2009). Though reduced  
107 elk numbers from wolf predation may lead to successful aspen recruitment (Fortin et al. 2005), there is  
108 some dispute over whether commensurate alterations of browsing patterns wrought by fear of predation  
109 are further influencing regeneration success (Kauffman et al. 2010). In most of the western U.S.,  
110 however, significant predation of wild and domestic ungulates is absent as recent reintroductions of a  
111 critical carnivore, the gray wolf (*Canis lupus*), are limited to specific geographic zones. Cougar (*Felis*  
112 *concolor*) apparently do prey on younger or smaller elk, though their primary ungulate prey appear to be  
113 adult mule deer (Matson et al. 2007). Overall, the impact of large herbivores on aspen communities may  
114 be reduced to three key factors: nutrition, population, and frequency of movement. Browsers who require  
115 specific nutrient content of aspen leaves or bark (continuously or seasonally) and who are present in large

116 numbers for extended periods may reduce long-term system resilience (Beck et al. 2006; Martin & Maron  
117 2012). Presence of multiple aspen-browsing species will only amplify this phenomenon.

118         We undertook a landscape-level survey of aspen condition and resilience in a remote portion of  
119 the American West known as the Book Cliffs. As a relatively short-lived clonal species aspen is highly  
120 dependent on both continuous and episodic recruitment (Kurzel, et al. 2007). Accordingly, a large part of  
121 our monitoring effort would rely on cataloguing the status of this “next generation” component of these  
122 forests. With this in mind, the current study has three prime objectives: 1) to conduct a defensible  
123 landscape assessment of aspen status across the Book Cliffs, while testing new measures for linking  
124 animal impact to stand conditions; 2) to understand distinct aspen types and determine environmental  
125 conditions which differ among these groups; 3) to make appropriate restorative recommendations for  
126 aspen systems based on outcomes of the first two objectives. Findings from this work will have  
127 ramifications for large portions of western North America, and more broadly in northern Europe, where  
128 issues of large ungulate-aspen browsing are rife within conservation circles.

129

## 130 **Methods**

131

### 132 *Study Area*

133         The Book Cliffs is part of a larger 230-km long feature known as the Tavaputs Plateau, which is  
134 bisected by the Utah-Colorado border in the western United States (Figure 1). This arid plateau slopes  
135 gently northward to the Uintah Basin and drops abruptly to the south into Utah's Canyonlands region of  
136 the Colorado Plateau (Sexton et al. 2006). The area consists of plateau tops dissected by steep valleys.  
137 Soils are derived predominantly from sandstone and shale substrates, resulting in rocky-to-sandy loams in  
138 much of the range. The elevation zone where aspen occurs, between 2,075 to 2,611 m, is fairly narrow  
139 compared to other landscape-level assessments regionally (Kurzel et al. 2007; Rogers and Ryel 2008),  
140 suggesting that environmental conditions, particularly precipitation, are limiting to aspen occupancy  
141 (Mittanck 2012). A weather monitoring station located in the aspen zone of our study area (SNOTEL site

142 #461) recorded an average annual precipitation of 542 mm (SD  $\pm$  127) between 1987-2012. Aspen and  
143 conifer stands are bounded by sagebrush (*Artemisia spp.*) on adjacent dry sites and, as elevation  
144 decreases, pinyon (*Pinus edulis*) and juniper (*Juniperus osteosperma*, *J. scopulorum*) woodlands.

145 Our study area consists of 268 distinct aspen polygons scattered across ~18 000 ha of the Book  
146 Cliffs in Utah and Colorado. Polygons were identified using three bands, including near-infrared, of  
147 National Agriculture Imagery Program (NAIP) imagery. Images were enhanced to allow a linear stretch  
148 across three standard deviations of the spectral data. This process increases contrast between vegetation  
149 types allowing easier interpretation. An earlier aspen stand assessment in this same area yielded a photo  
150 interpretation accuracy level of 88% (Mittanck 2012). The primary criterion used to delineate aspen  
151 polygons was if the area was contiguously forested with an aspen component. Polygons greater than 50%  
152 aspen cover and more than 0.5 ha were randomly selected for sampling. The completed procedure  
153 resulted in an initial selection of 100 sample polygons, of which 77 were field sampled (Figure 1).  
154 (Sixteen polygons were inaccurately identified as meeting our species/cover criteria and seven were  
155 eliminated due to access and time constraints.) Average sampled polygon size equaled 3.5 ha (range 0.5-  
156 31 ha). In sum, we sampled 29% of the total polygon population (representing 34% of aspen area) within  
157 the study area, enabling us to make strong inferences about the overall Book Cliffs aspen landscape.

158

### 159 *Field Methods*

160 The prime sample unit for this study consists of a ha<sup>-1</sup> area, henceforth called the "plot," at the  
161 centroid of each polygon. Plots were sampled only if they were at least 50% aspen cover and entirely  
162 within a forested area. Certainly variation was encountered in aspen polygon conditions. However, with  
163 the above requirements—along with the random polygon selection and systematic centroid location—plot  
164 data are assumed to represent mean conditions for each polygon. At each plot, visual estimates of aspen  
165 and conifer cover were made for the entire polygon with the aid of aerial photos. A walk through the ha<sup>-1</sup>  
166 sample area was made to gain an overall rating of stand conditions using criteria defined in Table 1, an  
167 estimate of discrete vertical "layers" of aspen, and the dominant understory cover by plant group (i.e.,



168 shrub, trees, grasses, forbs). Each plot was assigned an aspen stand type, either seral or stable (Harniss &  
169 Harper 1982). We define seral aspen as containing more than 10% conifer cover or, if stand-replacing  
170 disturbance such as fire or logging occurred within the past three decades, the potential to exceed this  
171 cover. Stable aspen implies < 10% conifer cover and long-term "stability" in a single species state (i.e.,  $\geq$   
172 100 years). In most instances the distinction between seral and stable plots is immediately evident as  
173 there are either no conifers or many conifers within an aspen forest. Geographic coordinates were  
174 obtained and four plot photos were taken to document understorey composition and structure.

175 At each plot center, two perpendicular 30 x 2 m transects were established and the following  
176 field measures were taken: percent aspen, conifer, and sagebrush cover; regeneration (< 2 m height),  
177 recruitment ( $\geq$  2 m height, < 8 cm diameter breast height [dbh]), and mature tree ( $\geq$  8 cm dbh) counts by  
178 species; mature tree counts by three diameter classes (8-15 cm; 16-25 cm; >25 cm dbh); and fecal pellet  
179 counts by groups (deer and elk) and individual feces (cattle). Pellet groups were defined as any  
180 assemblage of feces consisting of three or more pellets from the same defecation (Bunnefeld et al, 2006).  
181 Pellet groups give relative frequency of species' visits (use) of aspen stands; they are not direct measures  
182 of browse intensity. Two mature representative, healthy, aspen and two conifer (if present) were aged at  
183 breast height to determine overall stand age. Finally, field personnel recorded recent disturbances, if  
184 applicable, across the sample  $\text{ha}^{-1}$ . All transect data were expanded to represent conditions on a  $\text{ha}^{-1}$  basis  
185 for analytical purposes.

186

### 187 *Analytical Methods*

188 Analytical efforts for this work were exploratory in nature, meaning our intent was to determine  
189 the most important measures among a suite of environmental variables. First, we wished to combine  
190 proven aspen landscape survey methods (Rogers et al. 2010) with experimental techniques designed to  
191 simplify monitoring methods for future work. Thus, we were in search of key metrics, or "indicators," of  
192 aspen conditions. Two non-parametric tests were used to address indicators individually. The two-sided  
193 Wilcoxon-Mann-Whitney U test was used to evaluate field variables for differences between seral and

194 stable aspen stands to establish whether such a delineation was ecologically meaningful. The Kruskal-  
195 Wallace test, a non-parametric equivalent to analysis of variance, was the primary means of assessing the  
196 usefulness of the stand condition ranking. Direct measures of aspen mortality, condition and amount of  
197 regeneration and recruitment, and level of browsing (Table 1) were not considered independent of stand  
198 condition, therefore they were removed from these tests of group differences. We evaluated the  
199 remaining field variables for group effects based on their overall rating of good, moderate, or poor stand  
200 condition. The Kruskal-Wallace test does not provide a between-groups test of significance, thus further  
201 evaluation of stand condition, as well as other field measures, would be addressed with a broader  
202 statistical approach using the entire data set in distance matrix analyses.

203 Nonmetric multidimensional scaling (NMS) is an ordination technique that provides a robust  
204 method of understanding salient structure within ecological data sets which are expected to be nonnormal  
205 and discontinuous in their nature (McCune et al. 2002). Our goal in using NMS was to seek out critical  
206 measures of aspen stand conditions within our data set to provide a basis for evaluating the entire Book  
207 Cliffs landscape. The wide variation in data types (e.g., counts, ratings, digitally generated location data,  
208 measures, cover estimates) required a flexible and defensible analytical approach such as NMS (Peck  
209 2010). Twenty-three plot-level variables (Table 2) found on the 77 sample plots within our study area  
210 formed the primary matrix in our NMS analysis. An initial outlier analysis was performed to check of  
211 data anomalies based on two standard deviations of the Sørensen distance measure (Peck 2010). No data  
212 transformations were required for this analysis. We used the PC-ORD software to conduct NMS and  
213 produce related graphic outputs (McCune & Mefford 2006). The ordination was initiated with a random  
214 start number upon 250 runs of the actual data set using Sørensen distance measure. We assessed final  
215 NMS solution dimensionality by plotting stress as a function of number of dimensions or axes. Where  
216 two consecutive dimensions were  $\leq 5$  points of stress apart the lower dimension was selected as our  
217 optimum solution (McCune et al. 2002). A Monte Carlo test was then run on the lowest stress solution  
218 using 250 randomized runs to evaluate the probability of our result being greater than chance occurrence.

219 For all analyses in this study results were considered significant when reaching the 95% confidence  
220 interval (i.e.,  $p$ -value  $\leq 0.05$ ).

221

## 222 **Results**

223

224 Two-thirds (66%) of our survey locations were considered stable aspen and the remaining one-  
225 third were seral to conifer species. No plots in our survey sampled stand-replacing disturbance, though  
226 significant “browsing” or “grazing” were noted on 16 % of stands. We found several significant  
227 differences in environmental variables by these two primary aspen stand types (Fig. 2). Overall, stable  
228 plots were at higher elevations ( $Z = -2.69$ ;  $p = 0.007$ ), with lower slope angles ( $Z = 3.78$ ;  $p < 0.001$ ), had  
229 greater regeneration ( $Z = -2.95$ ;  $p = 0.003$ ), and more trees  $\text{ha}^{-1}$  ( $Z = -2.21$ ;  $p = 0.027$ ). We found no  
230 statistical difference in recruitment levels between stand types. Seral aspen in the Book Cliffs were  
231 significantly older than stable aspen forests ( $Z = 2.09$ ;  $p = 0.039$ ). Stable stands are experiencing heavier  
232 levels of browse ( $Z = -2.21$ ;  $p = 0.038$ ; box plot not shown) which likely relates to higher scat counts  
233 among cattle ( $Z = -3.85$ ;  $p < 0.001$ ), elk ( $Z = -3.59$ ;  $p < 0.001$ ), and the total scat ( $Z = -4.41$ ;  $p < 0.001$ ).  
234 Deer pellet counts were not significantly different between stand types ( $Z = -1.13$ ;  $p = 0.257$ ). Elk feces  
235 accounted for 67% of the total scat count, with cattle and deer at 22% and 11%, respectively.

236 Recruitment levels were equally low in seral and stable aspen communities across our study area.  
237 Only three of 77 sampled plots contained greater than 500 recruitment stems  $\text{ha}^{-1}$ , a suggested minimum  
238 threshold for stand replacement (O'Brien et al. 2010). Given that many sample plots had fewer than 500  
239 mature trees  $\text{ha}^{-1}$  we took a closer look at aspen recruitment based on local conditions. Using a more site-  
240 driven approach, we calculated live recruitment as a percentage of total mature aspen trees  $\text{ha}^{-1}$  with the  
241 logic that 100% would support complete immediate aspen stand replacement and 50% ample recruitment  
242 for gradual (i.e., gap-phase) replacement. Even this conservative consideration yielded very poor  
243 recruitment across the Book Cliffs landscape (Fig. 3). Ninety-four percent of sample plots had a fewer

244 than 50% recruitment based on total mature aspen trees ha<sup>-1</sup>. Fifty-five of the total 77 aspen stands had  
245 zero recruitment.

246 In addition to a number of objective field-based metrics of aspen forest conditions, we tested the  
247 efficacy of a subjective stand condition rating system. We found several significant group trends along  
248 our stand condition continuum (Fig. 4). Aspen polygons in both poor and good condition were at higher  
249 elevations than those with moderate visual impacts; stands in the worst condition were found at the  
250 highest elevations ( $\chi^2 = 7.62$ ;  $p = 0.019$ ). As expected, as stands age their condition deteriorates ( $\chi^2 =$   
251  $9.60$ ;  $p = 0.007$ ). Basal area ( $\chi^2 = 10.58$ ;  $p = 0.004$ ) and trees ha<sup>-1</sup> ( $\chi^2 = 20.15$ ;  $p < 0.001$ ) decreased as  
252 stands condition declines. As an indirect measure of browsing impact, there were significant increases in  
253 elk scat ( $\chi^2 = 20.09$ ;  $p < 0.001$ ) and total scat ( $\chi^2 = 17.68$ ;  $p < 0.001$ ) as stand condition deteriorates.  
254 Both cattle ( $\chi^2 = 3.95$ ;  $p = 0.138$ ) and deer ( $\chi^2 = 4.59$ ;  $p = 0.106$ ) failed to show significant relationships to  
255 stand condition. Overall, these data provide significant and visually compelling trends, but do not specify  
256 differences between each group. To pursue this further, we explored overall dataset structure using more  
257 powerful analytical tools.

258 Nonmetric multidimensional scaling (NMS) provided a parsimonious method for exploring  
259 distance relationships by ordination of all variables in "sample plot space." No data or plots were  
260 eliminated in outlier analysis. NMS ordination produced a 2-dimensional (i.e., axes) solution with a final  
261 stress of 12.03 (instability < 0.000). We assessed stability by plotting a graph of stress versus number of  
262 iterations. Stability was reached at 54 iterations from a maximum of 500 runs of our "real" dataset. Monte  
263 Carlo test results indicate that the two-axis solution using real data was significant ( $p = 0.004$ ). Two axes  
264 explain nearly all of variability in the Book Cliffs aspen dataset (Axis 1:  $r^2 = 0.61$ ; Axis 2:  $r^2 = 0.31$ ; total  
265  $r^2 = 0.92$ , orthogonality = 97.3%). Cumulatively, the degree of stability, randomization results, and  
266 variability explained by the two-axis solution indicate a highly significant final NMS result (McCune et  
267 al. 2002). An ordination joint plot and the categorical variable "stand condition class" were overlaid on  
268 the results of the NMS (Fig. 5). Axis 1 strongly represents aspen regeneration ha<sup>-1</sup> and to a lesser degree

269 aspen recruitment. Axis 2 displays a robust alignment with overall scat ha<sup>-1</sup>, as well as to individual  
270 browsing species; dominantly elk. All environmental variables are presented here in terms of Pearson's  
271 coefficient (*r*) values as they relate to the primary axes identified in NMS (Table 2).

272

## 273 **Discussion**

274

### 275 *Key aspen indicators inform resilience*

276 We set out to conduct a landscape assessment of aspen communities in the Book Cliffs of eastern  
277 Utah. Our random sample of nearly one-third of all stands in the area showed an overall aspen population  
278 under moderate to high threat. Stable aspen make up two-thirds of the Book Cliffs aspen landscape, thus  
279 continuous recruitment is crucial to long-term forest vigor. Only 23% aspen polygons were rated as being  
280 in good condition based on visual assessments of stand mortality, regeneration and recruitment, and  
281 browse levels (Table 1). While 27% of sample sites contained minimum required regeneration levels, just  
282 three of 77 stands contained adequate levels of recruitment (O'Brien et al. 2010). Whether aspen  
283 produces many or few suckers over time is less important than survivorship above browse level. Once  
284 above this height, understory stems can eventually fill canopy gaps as the relatively short-lived canopy  
285 trees die. Resilience to insects and disease, particularly in stable aspen, depends on a diverse height and  
286 age profile (Worrall et al. 2010) and young stands (both seral and stable) dominated by aspen are less  
287 prone to fire (Shinneman et al. 2013) thereby providing a buffer against stand collapse. In an effort to  
288 gain appropriate measures of recruitment based on site-specific data, which include relatively low water  
289 resource availability (Mittanck 2012), we looked at recruitment as a proportion of actual live mature  
290 stems (Fig. 3). Even with this more conservative adjustment, landscape-level recruitment was very low  
291 indicating a great majority of aspen stands with little resilience to future drought or disturbance.  
292 Ordination of all physical, mensuration, browse, and scat data gives us a strong indication of what factors  
293 are responsible for this poor level of aspen recruitment.

294           Teasing apart causality among multiple domestic and wild herbivores continues to be a vexing  
295 problem for forest, range, and wildlife ecologists. Standard measures of animal and tree populations  
296 occur at widely varying scales and browsers may not exhibit predictable movement and feeding patterns  
297 from year to year. Moreover, in areas of limited predation and accessible aspen terrain the combined  
298 effects of herbivory are severely limiting to aspen recruitment (Beschta & Ripple 2010; Rogers et al.  
299 2010). In the current work, we sampled scat on the same scale (i.e., transects) as forest structure data. To  
300 our knowledge, this spatial symmetry has not been attempted elsewhere and may help overcome previous  
301 barriers in understanding effects of widely roaming herbivores at stand-levels. Browse levels to  
302 regeneration were moderate-to-high across most of the study area as reflected by a 51% average browse  
303 level combined with very low levels of recruitment. Olmstead (1979) suggests that more than 30% aspen  
304 sucker utilization by elk lead to declines in stand density. Others suggest a more conservative guideline  
305 where > 20% annual browse of aspen leaders will result in decreases in stand density (Jones et al. 2005).  
306 Further connections between elk use, browse level, and recruitment success are presented for the Book  
307 Cliffs landscape through ordination (Fig. 5; Table 2). In NMS analysis, Axis 1 positively represents  
308 aspen regeneration, as well as moderate correspondence to recruitment and trees ha<sup>-1</sup>. Axis 2 relates most  
309 strongly to elk scat counts, but also to deer and cattle scat. Additionally, axis 2 corresponds with percent  
310 aspen canopy cover (negative to conifer cover) and heightened browse levels (Table 2). This indicates  
311 greater impacts and use of stable aspen stands by all herbivores likely due to their generally moderate  
312 terrain (Fig. 2). We should emphasize that while overall strong correspondence to regeneration and scat  
313 counts in the ordination were exhibited, most physiographic indicators showed weak relationships to both  
314 objective and subjective indices (Table 2). This poor showing of environmental variables may be further  
315 indication that our landscape-level results from the NMS are not tied to specific locations, but rather to  
316 other causal factors.

317           Our study used scat counts to represent herbivore use of aspen habitat and indirectly level of  
318 aspen browse. Use of scat counts as surrogates for habitat use have been criticized by some (Smart et al.  
319 2004), but favored by others when compared to animal radio-telemetry data (Borkowski 2004; Bunnefeld

320 et al. 2006). The central advantage of the scat count method was a direct correspondence of site and scale  
321 of sampling. Studies using radio-telemetry cannot be easily calibrated to our stand-level sample units and  
322 thus would be very difficult to understand as we attempted to measure landscape conditions and habitat  
323 use based on these  $\text{ha}^{-1}$  measures. A disadvantage when comparing between species is that each feces  
324 occurrence cannot *a priori* be assumed to mean the same level of use. We feel, however, that nominal  
325 differences between elk—two-thirds of all scat; > 3x cattle and > 5x deer—and other herbivore scat  
326 counts provide proximate evidence for elk's primary role in limiting aspen recruitment on this landscape.  
327 Ordination results (Fig. 5; Table 2) confirm a dominant role of elk among all herbivores and only elk and  
328 total scat counts related significantly to our stand condition rating system (Fig. 4).

329 Our chief motivation for developing an aspen stand rating system was efficiency. Degraded  
330 aspen communities in our region are commonplace (Binkley 2008; Worrall et al. 2008; Rogers et al.,  
331 2010), therefore a quick and credible means for managers to assess conditions across very large  
332 landscapes is desirable. We pitted several objective measures of aspen systems against our subjective  
333 stand condition and confirmed the utility of this measure as a surrogate for overall condition, as well as  
334 aspen mortality, stand structure, regeneration/recruitment, browse, and (independently) animal use. We  
335 consider the high correspondence to scat  $\text{ha}^{-1}$  (Fig. 5) an independent estimate of herbivore use, as there  
336 are no direct elements of scat or animal visitation in our stand condition classes (Table 1). Where  
337 resources are low and there is need for widespread aspen monitoring we suggest use of stand condition  
338 ratings alongside key site measures, such as regeneration, recruitment, and browse counts, to glean  
339 meaningful information with minimum expenditure.

340

#### 341 *The role of functional aspen types in the Book Cliffs*

342 Before we can assess impacts on a particular system it is important to understand broad-scale  
343 ecological divisions. Our initial findings showed two distinct aspen types occupying different realms of  
344 key environmental variables (Fig. 2). This overall picture generally fits that of the Colorado Plateau  
345 stable and montane seral functional types described by Rogers et al. (2013), although the Book Cliffs

346 appear to be within the lowest elevation and precipitation niche for western aspen (Sexton et al. 2006;  
347 Mittanck 2012). Within our study area, a novel finding is that seral aspen occupy relatively lower  
348 elevations, unlike other locations where stable aspen is common on the Colorado Plateau (Rogers et al.  
349 2010). We do find, however, that pure aspen types often occur on lower slope angles which make them  
350 more vulnerable to herbivores (Harniss & Harper 1982; Binkley 2008; Zegler et al. 2012 ). Our results  
351 confirm use on lower angle slopes as heavier levels of elk and cattle occupancy occurred in stable aspen  
352 forests (Fig. 2). An alternative explanation for greater herbivory in stable aspen may simply be greater  
353 availability of young stems, as shown by the strong positive correlation of regeneration to stable aspen  
354 (Fig. 2). It appears that deer use both seral and stable habitat equally, though at lower overall levels.

355 In terms of stand structure measures, we also found evidence of distinct functional groupings  
356 between seral and stable aspen. Where aspen are seral to conifers, stands are generally older than pure  
357 sites (Fig. 2; Rogers et al. 2010), although clear indication of stand age is sometimes difficult in healthy  
358 uneven-aged stable aspen. Seral stands in the Book Cliffs contained less mature aspen trees ha<sup>-1</sup> than the  
359 upland stable type. Greater aspen regeneration on upland stable sites corresponds to overall tree counts.  
360 Although there is more regeneration in stable forests, it appears an insignificant number of stems in either  
361 functional category are surviving to a recruitment stage (Fig. 3). Thus, where healthy stable aspen  
362 (particularly) should exhibit multiple stand layers (Harniss & Harper 1982; Rogers et al., 2010; 2013), we  
363 found only about one-third (35%) of such vertically diverse locations in the Book Cliffs. The low overall  
364 tally of recruitment (Fig. 3) amplifies the lack of vertical diversity and high level of concern at the  
365 landscape-scale. Anecdotally, ungulate exclosures observed with the Book Cliffs demonstrate adequate  
366 recruitment, even where deer are allowed access (supplemental photos online).

367

### 368 *Resilience, restoration, and monitoring of herbivore impacted aspen*

369 Consumption beyond replacement level of understory plants, and in particular juvenile trees, by  
370 large herbivores is common globally (White et al. 1998; Gill 2006; Edenius & Ericsson 2007; Takatsuki  
371 2009; Tanentzap et al. 2009). In areas dominated by conifers (e.g., northern Europe, northern and western



372 North America), aspen provide unique habitat and high levels of biodiversity (Kouki et al. 2004; Kuhn et  
373 al. 2011). As a keystone species (Campbell & Bartos 2001; Edenius et al. 2011), loss or reduction of  
374 aspen communities has cascading effects on dependent biota (Bailey et al. 2007; Rogers & Ryel 2008;  
375 Kuhn et al. 2011) including target herbivores (Beck et al. 2006). In our study area in the arid western  
376 United States we consider aspen forests, particularly stable stands, to be of relatively low resilience to  
377 environmental changes due to low water availability and high accessibility provided by generally  
378 moderate- to low-angle slopes (Fig. 2; Zegler et al. 2012). Mittanck (2012) found that the Book Cliffs  
379 was the most arid of regions supporting an "aspen niche" among his four study sites spread across Utah.  
380 A basic definition of *ecological carrying capacity* (Beck et al. 2006, p.283) simply states "an equilibrium  
381 between populations of plants and herbivores in the absence of harvest." Evidence presented here  
382 suggests that browsers, particularly elk, are beyond carrying capacity for the Book Cliffs aspen landscape  
383 and are having long-term effects on this landscape. Potential for significant aspen cover loss is high with  
384 consequent effects on dependent species. With continued heavy browsing, we should expect to see stand  
385 decline and loss of entire age cohorts that coincide with noted increases in large herbivore populations  
386 (Binkley 2008; Beschta & Ripple 2010). Furthermore, sites at lower elevations in accessible terrain may  
387 be most vulnerable to predicted warming climates via reduced snow cover which carries the dual negative  
388 impacts of decreased water resources and increased winter access by browsers (Martin & Maron 2012).

389 We recommend restoration of aspen forests based on appropriate aspen functional type (Rogers et  
390 al. 2013). In the current work we have highlighted key environmental differences between seral and  
391 stable aspen. With a view toward restoration, we favor emulating ecological processes that have shaped  
392 these aspen systems for centuries. While seral aspen depends on irregular fire and other stand-replacing  
393 disturbance, stable communities are driven by small group- and tree-level mortality and continuous or  
394 episodic recruitment (Harniss & Harper 1982; Kurz et al. 2007). Thus, commonly prescribed burning or  
395 clear-felling are in many cases appropriate for seral aspen and inappropriate for stable types. Once  
396 browse pressure is removed, or reduced to a sustainable level, stable aspen often need little or no stimulus  
397 to rejuvenate their stand structure. If herbivory cannot be curtailed stable stands will eventually die-off

398 and seral stands may be overtopped by conifers. In fact, Edenius et al. (2007), working in European  
399 aspen (*P. tremula*), found that heavy browsing in the absence of disturbance—either human-caused or  
400 natural—will accelerate succession toward conifer dominance to the detriment of remaining mature  
401 aspen. In smaller stands, or specific environmental situations (e.g., riparian or recreational locations),  
402 aspen may be protected by temporary fencing from browsers. However, this protection strategy is not  
403 feasible for large landscapes where fencing is cost prohibitive. Finally, we encourage allowance for  
404 natural or prescribed burns to increase chances of genetic diversity through aspen seedling establishment  
405 (Long & Mock 2012). This strategy is more appropriate for seral types that burn more readily, than for  
406 stable aspen that are generally not susceptible to fire (Shinneman et al. 2013). While it is now accepted  
407 that aspen establishment by seed is more common than previously thought (Long & Mock 2012), we have  
408 little understanding of mechanisms of occurrence in stable types where evidence suggests high genetic  
409 diversity, too (Mock et al. 2008).

410 Both seral and stable aspen will require significantly reduced browsing, thus elk population  
411 reduction should be considered a core strategy where heavy browsing, such as in the Book Cliffs, can be  
412 credibly documented (Seager et al. 2013). Current elk and livestock management in this area encourages  
413 sustained or increased animal populations. We concur with Seager et al. (2013) that increased hunting  
414 can and should be implemented where reintroduction of apex predators, such as wolves (*Canis lupus*), are  
415 politically unfeasible. Secondly, seral types may require complementary conifer disturbance to create  
416 forest openings and facilitate both seedling and sucker regeneration (Long & Mock 2012; Rogers et al.  
417 2013).

418 Pre- and post-treatment monitoring using a scheme similar to the one tested here is required to  
419 further understand if actions are having desired restorative effects. For example, use of fenced exclosures,  
420 while appropriate for demonstrative purposes, raise concerns when prescribed as a landscape-level  
421 management option. Past exclosure studies have shown that aspen will respond heartily to complete  
422 protection (Kay & Bartos 2000; Kay 2001). Monitoring within and outside exclosures will give reliable  
423 measures of sprouting ability and no-browsing protection, respectively, but provide little useful

424 information regarding reduced herbivory in the context of stand- or landscape-level aspen restoration.  
425 For this reason, the current study area as well as locales with similar browse issues, will require  
426 documentation of active (stimulus) and passive (reduction or removal of browsers) management effects.  
427 While we fully expect confounding factors (i.e., climate, disturbance, human impacts), our overall  
428 objective with monitoring and adaptive management is to facilitate future aspen community resilience. In  
429 a setting such as the Book Cliffs that is predisposed to low resilience, restoration ecologists would do well  
430 to focus resources toward increasing the systems' capacity to rebound under expected stresses.

431

## 432 **Conclusions**

433

434 Findings from the present study have conservation applications in drought-prone, drought  
435 expectant, and chronically browsed forest systems. The Book Cliffs aspen landscape constitutes a  
436 relatively low elevation dry setting as compared to other locations around the region (Mueggler 1988;  
437 Mittanck 2012) and therefore may be viewed as a harbinger of future climate conditions in other settings.  
438 The narrow elevation and moisture band in which aspen exist here is thought to be vulnerable even in the  
439 absence of heavy browse (Rehfeldt et al. 2009). Though there is an abundance of seral aspen at generally  
440 lower elevations and on steeper slopes, the area is notable for its high presence of the single-species stable  
441 type. We recommend future conservation that emulates the dynamics within these distinct functional  
442 types. For example, while clear-felling or prescribed burning may fit seral types, they are inappropriate in  
443 stable aspen (Shinneman et al, 2013; Rogers et al. 2013). Given that mature aspen are short-lived  
444 compared to their conifer cohorts, aspen assessments must rely heavily on measures of regeneration and  
445 recruitment. Recruitment is a key measure of system resilience where stand-replacing disturbance,  
446 browsing pressure, and warming climates are expected to stress these systems. We suggest using 'natural  
447 range of variation' to guide adaptive actions (Landres et al. 1999). Based on results presented here, there  
448 is strong evidence of elk browsing being beyond sustainable levels for the aspen landscape in our study

449 area. Similar conditions may be found in a broader swath of the Colorado Plateau region where stable  
450 aspen prevails (Rogers et al. 2010; Rogers et al. 2013).

451         Where aspen forests are threatened by intense ungulate browsing, what conservation actions can  
452 be taken to increase community resilience? Aspen monitoring and management must include explicit  
453 documentation of all browsing pressures. Where domestic herbivores play an important role, actions to  
454 rest pastures and curtail stock numbers may be needed. Without significant predation on wild ungulates,  
455 greater human regulation of populations will be required to reduce herbivory and restore the structural  
456 diversity and functional capacity of these communities. Vegetation and wildlife managers, often favoring  
457 divergent priorities, will need to coordinate closely to restore aspen recruitment and overall landscape  
458 resilience. Failure to do so will result in declining aspen and loss of habitat for a wide range of species,  
459 including preferred game animals, which are dependent on these regionally biodiverse ecosystems.

460

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462

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470

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605

606

### Supplementary Materials

607

**Appendix S1:** Photos depicting an enclosure limiting ungulate browsing in the study area.

608

**S1a:** Ungulate enclosure depicts regular recruitment within fenced area, Book Cliffs, Utah, USA.

609

**S1b:** Alternate view of S1a showing opposite side of ungulate enclosure, Book Cliffs, Utah, USA.

610

**S1c:** Close-up of corner posts of ungulate enclosure depicting 0.5 m gap at base that allows mule deer

611

(*Odocoileus hemionus*) access, but not elk (*Cervus elaphus*) or cattle (*Bos* spp.), Book Cliffs, Utah, USA.

612

**Table 1:** Ranking of stand condition based on visual estimates of overstorey, regeneration/recruitment, and browse of young aspen suckers. A stand must meet all the criteria for either "Good" or "Poor" condition, otherwise it is rated as moderate. "Mortality" is defined as standing dead mature trees. Browse includes branch tips, buds, and leaves missing, as well as presence of multi-stemmed ("bushy") aspen regeneration.

<b>Code</b>	<b>Descriptor</b>	<b>Overstorey Mortality/disease</b>	<b>Vertical Stand Layers</b>	<b>Visible Browse Impacts</b>
1	Good	Minimal overstorey mortality and stem disease present (< 5%)	Several aspen layers ( $\geq 3$ )	Browsing impacts on regeneration uncommon (< 25%)
2	Moderate	Does not fit 1 or 3	Does not fit 1 or 3	Does not fit 1 or 3
3	Poor	Overstorey mortality and/or stem cankers common (> 25%)	layering absent or minimal ( $\leq 2$ )	Browsing impacts clearly evident (> 50%) on regeneration.

613

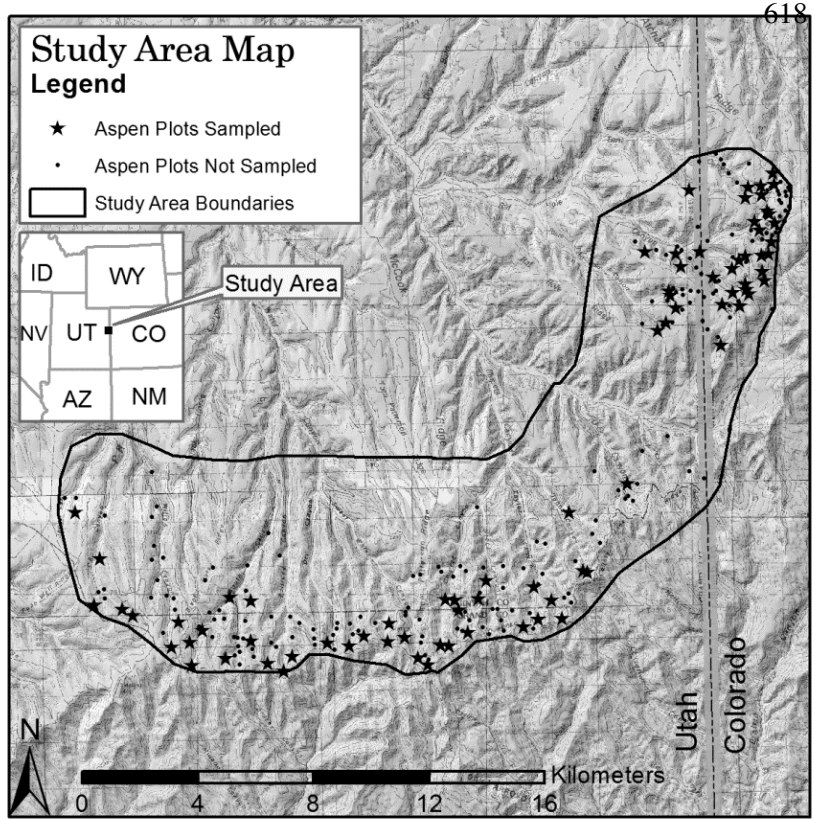
614



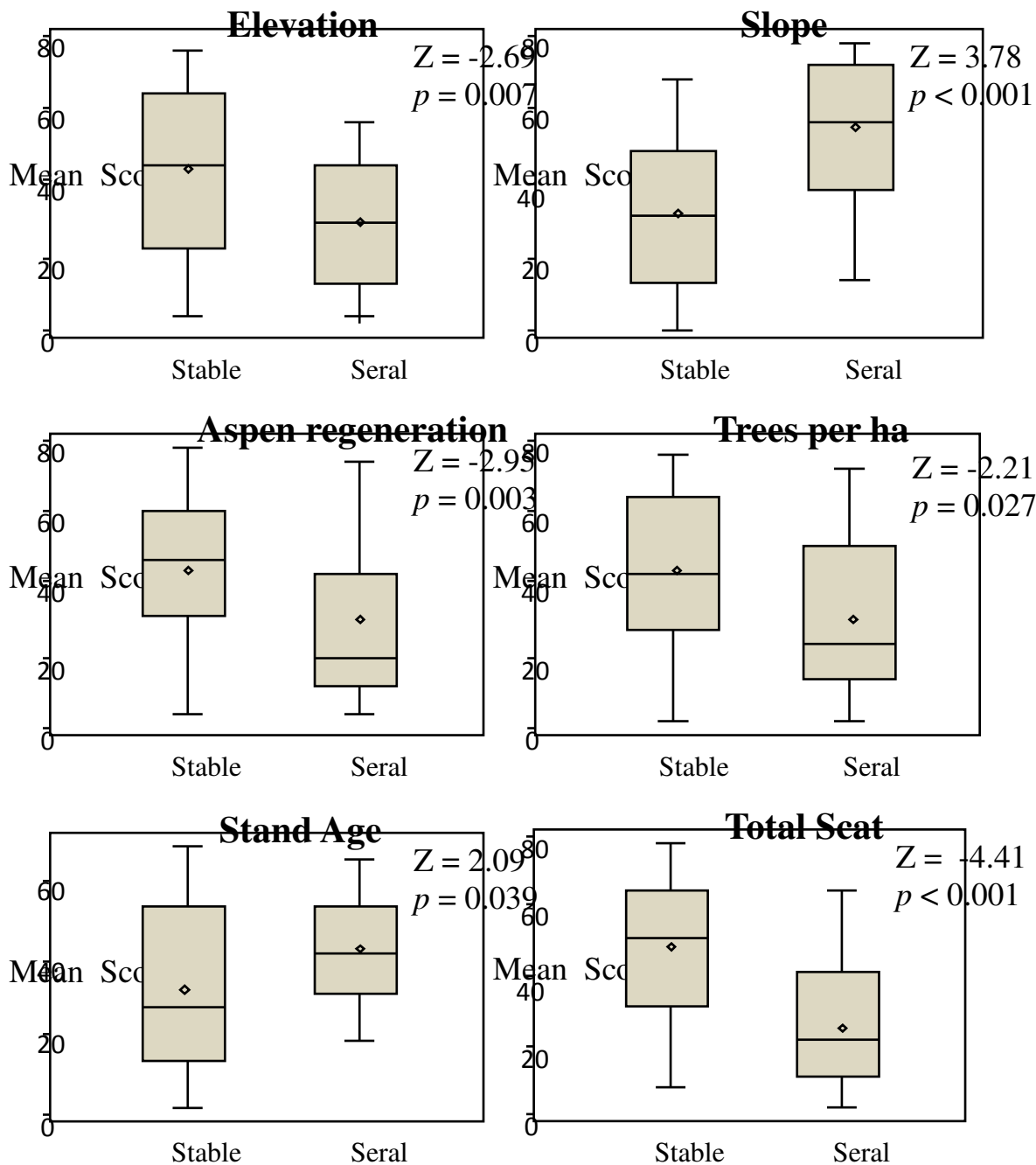
**Table 2:** Pearson's coefficients ( $r$ ) between environmental variables and primary ordination axes. The strongest response variables are in bold type where  $r > 0.5$  or  $< -0.5$ .

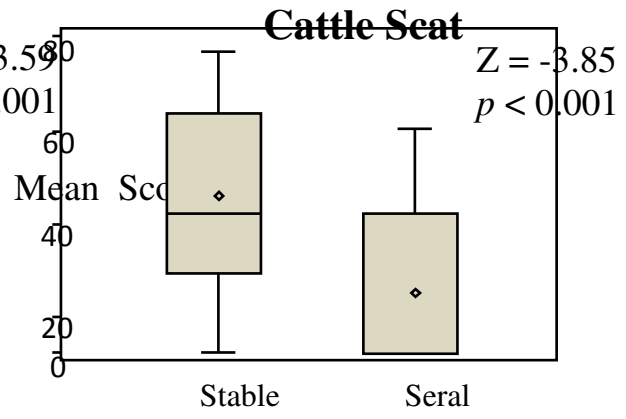
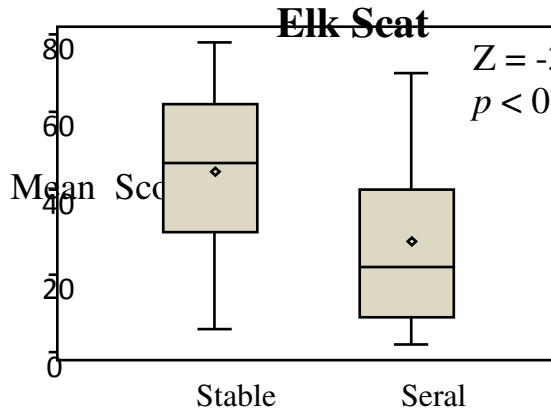
Variable name	$r$ - value	
	Axis 1	Axis 2
Elevation	0.361	0.225
Aspect	0.137	0.083
Slope	-0.169	-0.271
% Polygon aspen	0.334	<b>0.515</b>
% Polygon conifer	-0.244	-0.488
Aspen stand age	0.051	-0.112
<b>Total scat per ha</b>	0.206	<b>0.943</b>
<b>Cattle scat per ha</b>	0.011	<b>0.551</b>
<b>Elk scat per ha</b>	0.264	<b>0.839</b>
<b>Deer scat per ha</b>	0.043	<b>0.570</b>
Aspen cover ha	0.255	0.042
Conifer cover ha	-0.101	-0.282
Sagebrush cover ha	0.005	0.261
Total tree cover ha	0.165	-0.145
<b>Aspen regeneration</b>	<b>0.900</b>	0.046
% regeneration browsed	0.315	0.388
Live aspen recruitment	0.343	-0.233
Small tree BA	0.236	-0.147
Medium tree BA	0.213	0.033
Large tree BA	0.019	0.080
Total aspen BA	0.296	-0.023
Aspen trees per ha (TPH)	0.339	-0.091
Recruitment as % of TPH	0.328	-0.226

616 **Figure 1:** Map of the study area shows all aspen locations as identified with aerial imagery and aspen  
617 sample plot locations. Inset depicts the Book Cliffs study area within the Rocky Mountain region, USA.



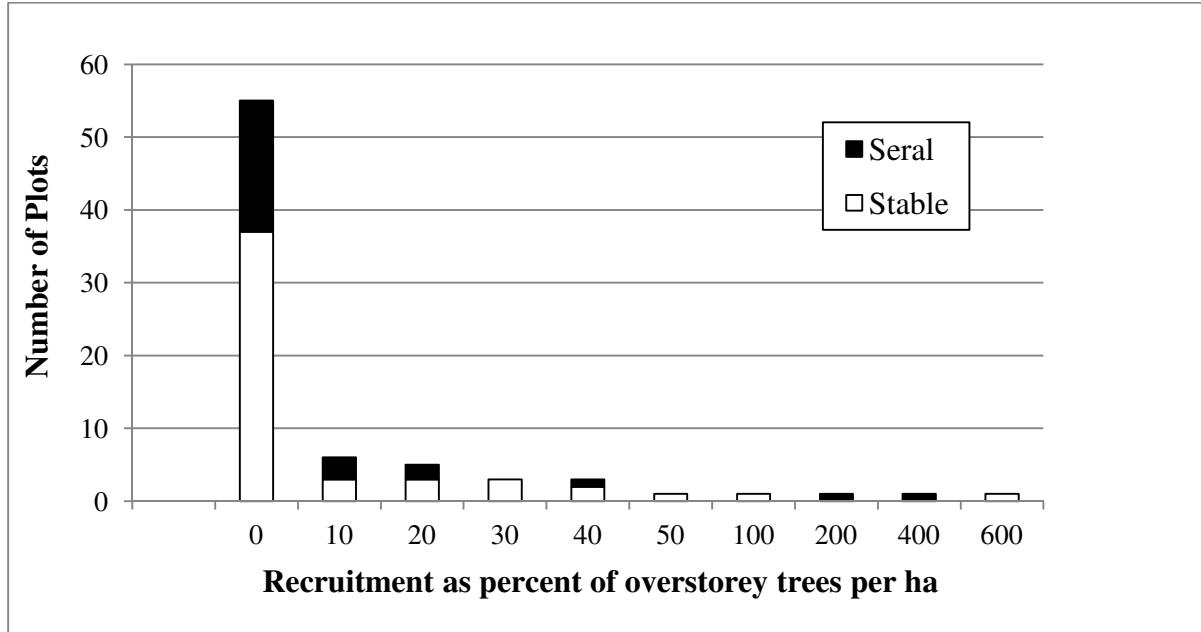
619 **Figure 2:** Wilcoxon-Mann-Whitney U test results displayed in box plots showing significant differences  
 620 between seral and stable aspen types by plot-level indicators across the study landscape. Wilcoxon mean  
 621 scores are shown on the Y-axis. Whiskers show minimum and maximum values, boxes represent 25-75%  
 622 data ranges, horizontal lines within boxes are medians, and diamond symbols are means. Only results  
 623 with > 95% confidence intervals are shown.  
 624





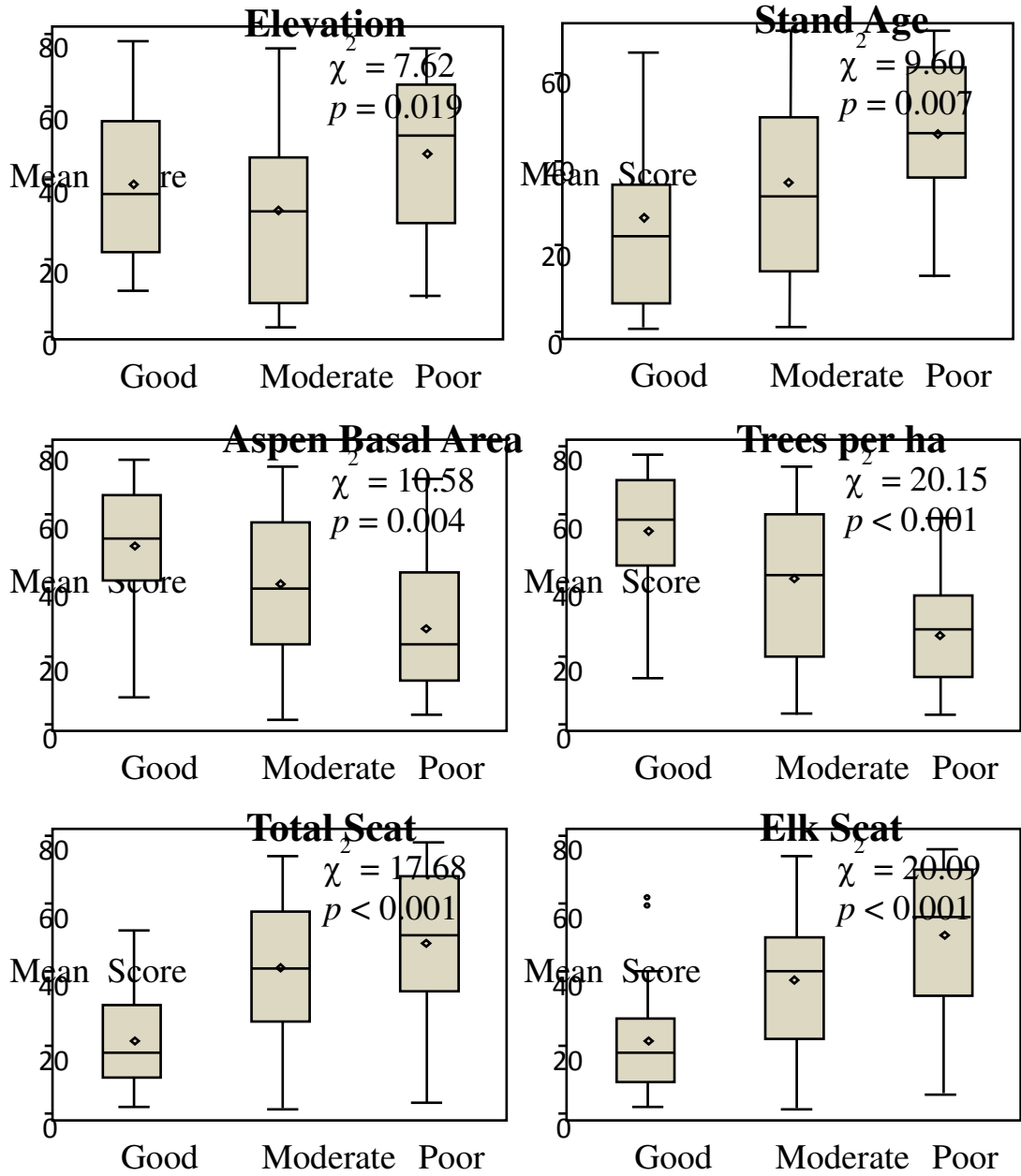
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629 **Figure 3:** Histogram depicting the number of stable and seral aspen sample plots (n = 77) by the ratio of  
630 recruitment stems (> 2 m height) to overstorey aspen trees ha<sup>-1</sup>. Ninety-four percent of sample plots in  
631 the study area had less than 50% of the overstorey stem count. The majority of aspen stands had zero  
632 recruitment.  
633



634

635 **Figure 4:** Kruskal-Wallis test results are displayed in box plots showing significant differences between  
 636 aspen condition classes across the study landscape. We intentionally did not test variables directly related  
 637 to condition class elements (Table 2) in an effort to independently assess the value of the rating system.  
 638 Wilcoxon mean scores are shown on the Y-axis. Whiskers show minimum and maximum values, boxes  
 639 represent 25-75% data ranges, horizontal lines within boxes are medians, and diamond symbols are  
 640 means. Box plots display general trends between three classes; test results apply only to an overall group  
 641 difference. Only results with > 95% confidence intervals are shown.  
 642

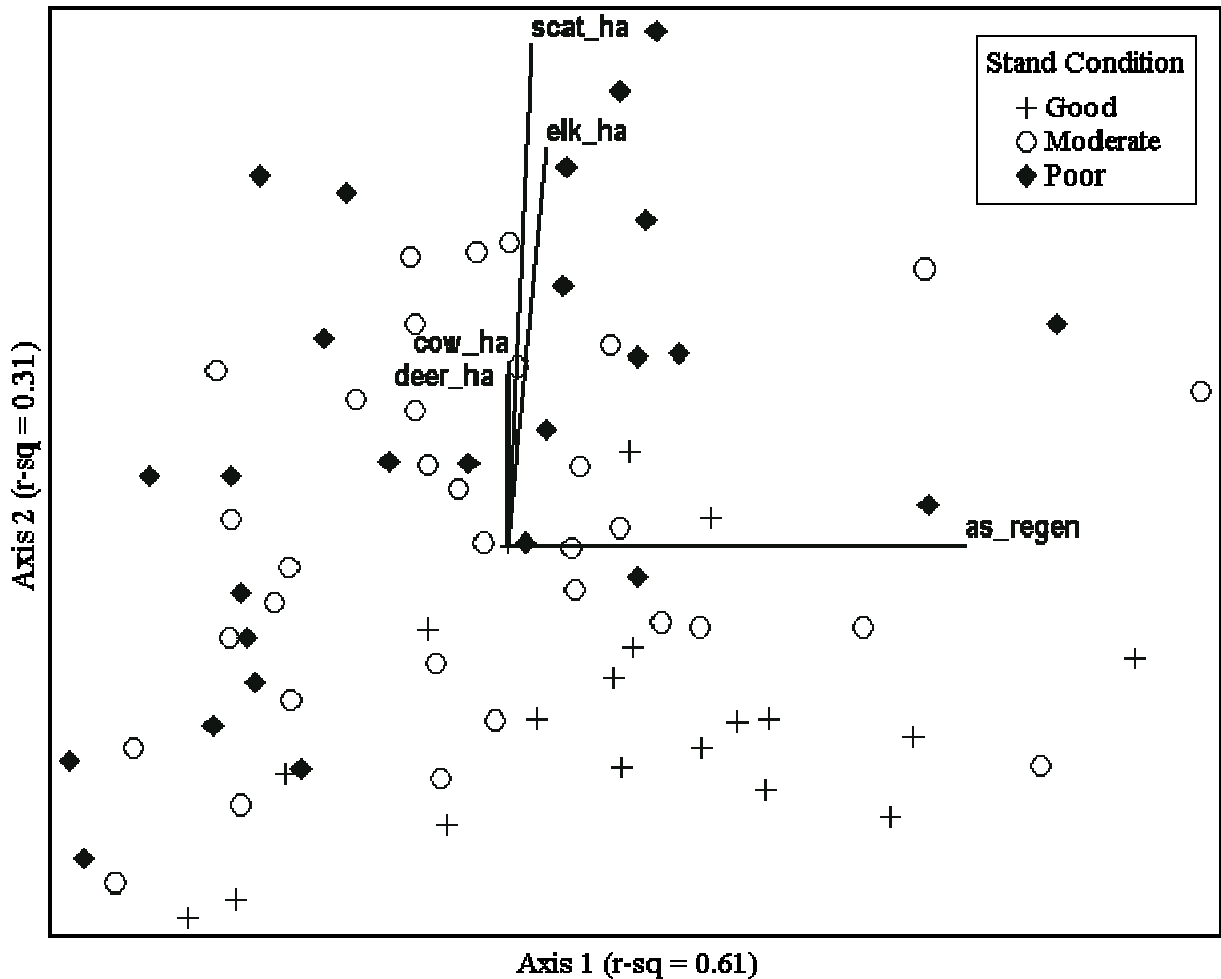


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647 **Figure 5:** Nonmetric multidimensional scaling (NMS) results are shown in a joint plot which highlights  
 648 prominent indicators within the total Book Cliffs data set. Vectors with  $> \pm 0.5$  Pearson's coefficient ( $r$ )  
 649 value (Table 2) are displayed in relation to "plot space". The length of vectors corresponds to their  $r$ -  
 650 value ("as\_regen" = aspen regeneration; scat\_ha = total scat; elk\_ha, cow\_ha, deer\_ha = animal scat  
 651 counts). Aspen stand condition ratings are superimposed within plot space to depict general relationships  
 652 to the primary axes. Axis 1 displays general trends in regeneration, recruitment, aspen basal area, and  
 653 aspen trees  $\text{ha}^{-1}$ . Axis 2 corresponds to animal presence, prominently elk, polygon-level aspen cover (+)  
 654 and conifer cover (-), and percent of regeneration browsed.  
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