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

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

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Abstract

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

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

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

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

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

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

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

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

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

Running Head: Aspen, ungulates, and forest resilience

Introduction

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

In western North American there are numerous recent studies documenting both declines (Di Orio et al. 2005; Worrall et al. 2008) and expansions (Manier & Laven 2002; Kulakowski et al. 2004) of aspen forests. These works document cover change at a variety of spatial and temporal scales, therefore it is difficult to make direct comparisons between results. Moreover, recent authors have pointed out distinct aspen functional types (Shepperd et al. 2006; Rogers et al. 2013) which would be expected to respond differently to short- and long-term perturbations. Aspen cover change has been attributed to fire suppression and conifer encroachment, past logging, climate variability, settlement period burning, and browsing by wild and domestic ungulates (Kulakowski et al. 2004; Shepperd et al. 2006; Rogers et al. 2011). Some results have indicated positive and negative cover change within the same landscape (Kulakowski et al. 2004; Sankey 2009), lending further support to the concept of varying aspen functional types (Rogers et al. 2013). Given that aspen forests have undergone modest-to-large change over the past 150 years—often where human actions combine with stochastic disturbances—practitioners have become concerned about the future of these forests under current management regimes. Contemporary thinking holds that “managing for resilience” will afford the best hopes for sustainable quaking aspen (as in most systems). Forest managers are therefore interested in sustaining or creating resilient aspen communities with a foundation of state-of-the-science knowledge and adaptive practices. Where plant-animal interactions are paramount, a barrier to such goals has been a lack of effective communication between federal forest and state wildlife practitioners in both scientific and applied realms.

While aspen is highly valued for its’ biodiversity, in some locales herbivores are having undue impact on the ability of these systems to maintain ecosystem functions. Aspen shoots and leaves provide valuable nutrition to several species, especially early and late in the growing season when diversity of browse is limited (Jones et al. 2005; Beck et al. 2006). In Scandinavia, moose (*Alces alces*) are the primary herbivore affecting aspen recruitment (Edenius & Ericsson 2007; Edenius et al. 2011). In the western United States browsing cattle (*Bos* spp.), sheep (*Ovis* spp.), North American elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) in many areas are severely inhibiting stand renewal via repeated aspen sprout consumption (DeByle 1985; Zeigenfuss et al. 2008; DeRose & Long 2010; Rogers et al. 2010). This phenomenon seems particularly acute where wild elk populations are thought to be beyond “historical range of variation” levels due to aggressive reintroduction programs (e.g., Bailey et al. 2007; Stritar et al. 2010) and relatively low levels of predation (Beschta & Ripple 2009). Though reduced elk numbers from wolf predation may lead to successful aspen recruitment (Fortin et al. 2005), there is some dispute over whether commensurate alterations of browsing patterns wrought by fear of predation are further influencing regeneration success (Kauffman et al. 2010). In most of the western U.S., however, significant predation of wild and domestic ungulates is absent as recent reintroductions of a critical carnivore, the gray wolf (*Canis lupus*), are limited to specific geographic zones. Cougar (*Felis concolor*) apparently do prey on younger or smaller elk, though their primary ungulate prey appear to be adult mule deer (Matson et al. 2007). Overall, the impact of large herbivores on aspen communities may be reduced to three key factors: nutrition, population, and frequency of movement. Browsers who require specific nutrient content of aspen leaves or bark (continuously or seasonally) and who are present in large numbers for extended periods may reduce long-term system resilience (Beck et al. 2006; Martin & Maron 2012). Presence of multiple aspen-browsing species will only amplify this phenomenon.

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

Methods

Study Area

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

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

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

Field Methods

The prime sample unit for this study consists of a ha^{-1} area, henceforth called the "plot," at the centroid of each polygon. Plots were sampled only if they were at least 50% aspen cover and entirely within a forested area. Certainly variation was encountered in aspen polygon conditions. However, with the above requirements—along with the random polygon selection and systematic centroid location—plot data are assumed to represent mean conditions for each polygon. At each plot, visual estimates of aspen and conifer cover were made for the entire polygon with the aid of aerial photos. A walk through the ha^{-1} sample area was made to gain an overall rating of stand conditions using criteria defined in Table 1, an estimate of discrete vertical "layers" of aspen, and the dominant understory cover by plant group (i.e., shrub, trees, grasses, forbs). Each plot was assigned an aspen stand type, either seral or stable (Harniss & Harper 1982). We define seral aspen as containing more than 10% conifer cover or, if stand-replacing disturbance such as fire or logging occurred within the past three decades, the potential to exceed this cover. Stable aspen implies < 10% conifer cover and long-term "stability" in a single species state (i.e., $\geq$ 100 years). In most instances the distinction between seral and stable plots is immediately evident as there are either no conifers or many conifers within an aspen forest. Geographic coordinates were obtained and four plot photos were taken to document understorey composition and structure.

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

Analytical Methods

Analytical efforts for this work were exploratory in nature, meaning our intent was to determine the most important measures among a suite of environmental variables. First, we wished to combine proven aspen landscape survey methods (Rogers et al. 2010) with experimental techniques designed to simplify monitoring methods for future work. Thus, we were in search of key metrics, or "indicators," of aspen conditions. Two non-parametric tests were used to address indicators individually. The two-sided Wilcoxon-Mann-Whitney U test was used to evaluate field variables for differences between seral and stable aspen stands to establish whether such a delineation was ecologically meaningful. The Kruskal-Wallace test, a non-parametric equivalent to analysis of variance, was the primary means of assessing the usefulness of the stand condition ranking. Direct measures of aspen mortality, condition and amount of regeneration and recruitment, and level of browsing (Table 1) were not considered independent of stand condition, therefore they were removed from these tests of group differences. We evaluated the remaining field variables for group effects based on their overall rating of good, moderate, or poor stand condition. The Kruskal-Wallace test does not provide a between-groups test of significance, thus further evaluation of stand condition, as well as other field measures, would be addressed with a broader statistical approach using the entire data set in distance matrix analyses.

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

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

Results

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

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

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

Nonmetric multidimensional scaling (NMS) provided a parsimonious method for exploring distance relationships by ordination of all variables in "sample plot space." No data or plots were eliminated in outlier analysis. NMS ordination produced a 2-dimensional (i.e., axes) solution with a final stress of 12.03 (instability < 0.000). We assessed stability by plotting a graph of stress versus number of iterations. Stability was reached at 54 iterations from a maximum of 500 runs of our "real" dataset. Monte Carlo test results indicate that the two-axis solution using real data was significant ($p = 0.004$). Two axes explain nearly all of variability in the Book Cliffs aspen dataset (Axis 1: $r^2 = 0.61$; Axis 2: $r^2 = 0.31$; total $r^2 = 0.92$, orthogonality = 97.3%). Cumulatively, the degree of stability, randomization results, and variability explained by the two-axis solution indicate a highly significant final NMS result (McCune et al. 2002). An ordination joint plot and the categorical variable "stand condition class" were overlaid on the results of the NMS (Fig. 5). Axis 1 strongly represents aspen regeneration ha^{-1} and to a lesser degree aspen recruitment. Axis 2 displays a robust alignment with overall scat ha^{-1}, as well as to individual browsing species; dominantly elk. All environmental variables are presented here in terms of Pearson's coefficient (*r*) values as they relate to the primary axes identified in NMS (Table 2).

Discussion

Key aspen indicators inform resilience

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

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

Our study used scat counts to represent herbivore use of aspen habitat and indirectly level of aspen browse. Use of scat counts as surrogates for habitat use have been criticized by some (Smart et al. 2004), but favored by others when compared to animal radio-telemetry data (Borkowski 2004; Bunnefeld et al. 2006). The central advantage of the scat count method was a direct correspondence of site and scale of sampling. Studies using radio-telemetry cannot be easily calibrated to our stand-level sample units and thus would be very difficult to understand as we attempted to measure landscape conditions and habitat use based on these ha^{-1} measures. A disadvantage when comparing between species is that each feces occurrence cannot *a priori* be assumed to mean the same level of use. We feel, however, that nominal differences between elk—two-thirds of all scat; > 3x cattle and > 5x deer—and other herbivore scat counts provide proximate evidence for elk's primary role in limiting aspen recruitment on this landscape. Ordination results (Fig. 5; Table 2) confirm a dominant role of elk among all herbivores and only elk and total scat counts related significantly to our stand condition rating system (Fig. 4).

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

The role of functional aspen types in the Book Cliffs

Before we can assess impacts on a particular system it is important to understand broad-scale ecological divisions. Our initial findings showed two distinct aspen types occupying different realms of key environmental variables (Fig. 2). This overall picture generally fits that of the Colorado Plateau stable and montane seral functional types described by Rogers et al. (2013), although the Book Cliffs appear to be within the lowest elevation and precipitation niche for western aspen (Sexton et al. 2006; Mittanck 2012). Within our study area, a novel finding is that seral aspen occupy relatively lower elevations, unlike other locations where stable aspen is common on the Colorado Plateau (Rogers et al. 2010). We do find, however, that pure aspen types often occur on lower slope angles which make them more vulnerable to herbivores (Harniss & Harper 1982; Binkley 2008; Zegler et al. 2012). Our results confirm use on lower angle slopes as heavier levels of elk and cattle occupancy occurred in stable aspen forests (Fig. 2). An alternative explanation for greater herbivory in stable aspen may simply be greater availability of young stems, as shown by the strong positive correlation of regeneration to stable aspen (Fig. 2). It appears that deer use both seral and stable habitat equally, though at lower overall levels.

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

Resilience, restoration, and monitoring of herbivore impacted aspen

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

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

We recommend restoration of aspen forests based on appropriate aspen functional type (Rogers et al. 2013). In the current work we have highlighted key environmental differences between seral and stable aspen. With a view toward restoration, we favor emulating ecological processes that have shaped these aspen systems for centuries. While seral aspen depends on irregular fire and other stand-replacing disturbance, stable communities are driven by small group- and tree-level mortality and continuous or episodic recruitment (Harniss & Harper 1982; Kurzel et al. 2007). Thus, commonly prescribed burning or clear-felling are in many cases appropriate for seral aspen and inappropriate for stable types. Once browse pressure is removed, or reduced to a sustainable level, stable aspen often need little or no stimulus to rejuvenate their stand structure. If herbivory cannot be curtailed stable stands will eventually die-off and seral stands may be overtopped by conifers. In fact, Edenius et al. (2007), working in European aspen (*P. tremula*), found that heavy browsing in the absence of disturbance—either human-caused or natural—will accelerate succession toward conifer dominance to the detriment of remaining mature aspen. In smaller stands, or specific environmental situations (e.g., riparian or recreational locations), aspen may be protected by temporary fencing from browsers. However, this protection strategy is not feasible for large landscapes where fencing is cost prohibitive. Finally, we encourage allowance for natural or prescribed burns to increase chances of genetic diversity through aspen seedling establishment (Long & Mock 2012). This strategy is more appropriate for seral types that burn more readily, than for stable aspen that are generally not susceptible to fire (Shinneman et al. 2013). While it is now accepted that aspen establishment by seed is more common than previously thought (Long & Mock 2012), we have little understanding of mechanisms of occurrence in stable types where evidence suggests high genetic diversity, too (Mock et al. 2008).

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

Pre- and post-treatment monitoring using a scheme similar to the one tested here is required to further understand if actions are having desired restorative effects. For example, use of fenced exclosures, while appropriate for demonstrative purposes, raise concerns when prescribed as a landscape-level management option. Past exclosure studies have shown that aspen will respond heartily to complete protection (Kay & Bartos 2000; Kay 2001). Monitoring within and outside exclosures will give reliable measures of sprouting ability and no-browsing protection, respectively, but provide little useful information regarding reduced herbivory in the context of stand- or landscape-level aspen restoration. For this reason, the current study area as well as locales with similar browse issues, will require documentation of active (stimulus) and passive (reduction or removal of browsers) management effects. While we fully expect confounding factors (i.e., climate, disturbance, human impacts), our overall objective with monitoring and adaptive management is to facilitate future aspen community resilience. In a setting such as the Book Cliffs that is predisposed to low resilience, restoration ecologists would do well to focus resources toward increasing the systems' capacity to rebound under expected stresses.

Conclusions

Findings from the present study have conservation applications in drought-prone, drought expectant, and chronically browsed forest systems. The Book Cliffs aspen landscape constitutes a relatively low elevation dry setting as compared to other locations around the region (Mueggler 1988; Mittanck 2012) and therefore may be viewed as a harbinger of future climate conditions in other settings. The narrow elevation and moisture band in which aspen exist here is thought to be vulnerable even in the absence of heavy browse (Rehfeldt et al. 2009). Though there is an abundance of seral aspen at generally lower elevations and on steeper slopes, the area is notable for its high presence of the single-species stable type. We recommend future conservation that emulates the dynamics within these distinct functional types. For example, while clear-felling or prescribed burning may fit seral types, they are inappropriate in stable aspen (Shinneman et al, 2013; Rogers et al. 2013). Given that mature aspen are short-lived compared to their conifer cohorts, aspen assessments must rely heavily on measures of regeneration and recruitment. Recruitment is a key measure of system resilience where stand-replacing disturbance, browsing pressure, and warming climates are expected to stress these systems. We suggest using 'natural range of variation' to guide adaptive actions (Landres et al. 1999). Based on results presented here, there is strong evidence of elk browsing being beyond sustainable levels for the aspen landscape in our study area. Similar conditions may be found in a broader swath of the Colorado Plateau region where stable aspen prevails (Rogers et al. 2010; Rogers et al. 2013).

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

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Supplementary Materials

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

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

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

S1c: Close-up of corner posts of ungulate exclosure depicting 0.5 m gap at base that allows mule deer (*Odocoileus hemionus*) access, but not elk (*Cervus elaphus*) or cattle (*Bos* spp.), Book Cliffs, Utah, USA.

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.

Code	Descriptor	Overstory Mortality/disease	Vertical Stand Layers	Visible Browse Impacts
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.

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.

	***r* - value**	
Variable name	**Axis 1**	**Axis 2**
Elevation	0.361	0.225
Aspect	0.137	0.083
Slope	-0.169	-0.271
% Polygon aspen	0.334	**0.515**
% Polygon conifer	-0.244	-0.488
Aspen stand age	0.051	-0.112
Total scat per ha	0.206	**0.943**
Cattle scat per ha	0.011	**0.551**
Elk scat per ha	0.264	**0.839**
Deer scat per ha	0.043	**0.570**
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
Aspen regeneration	**0.900**	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

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

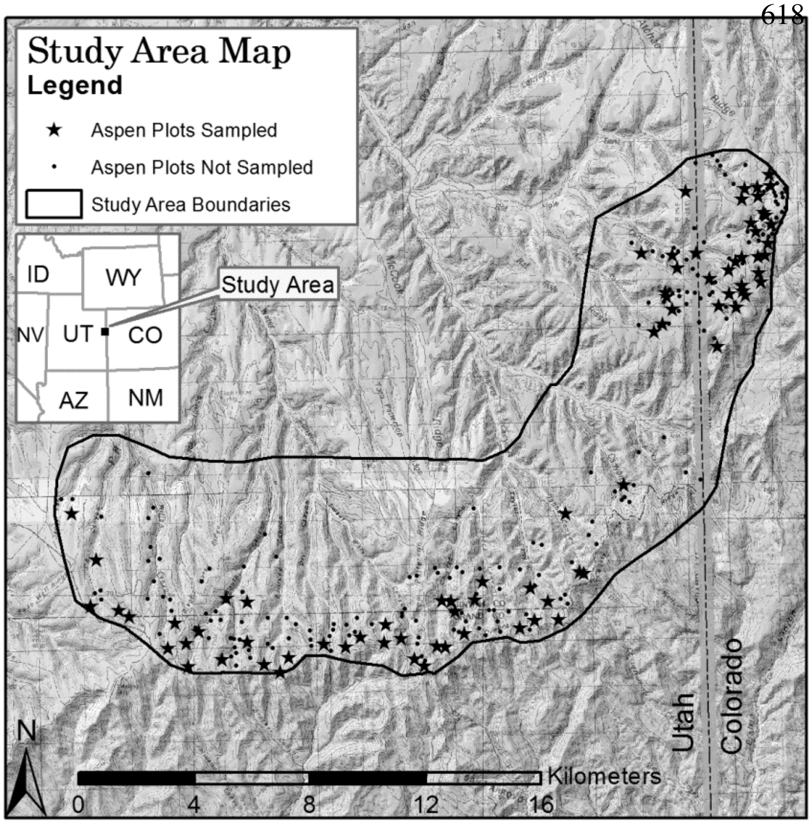
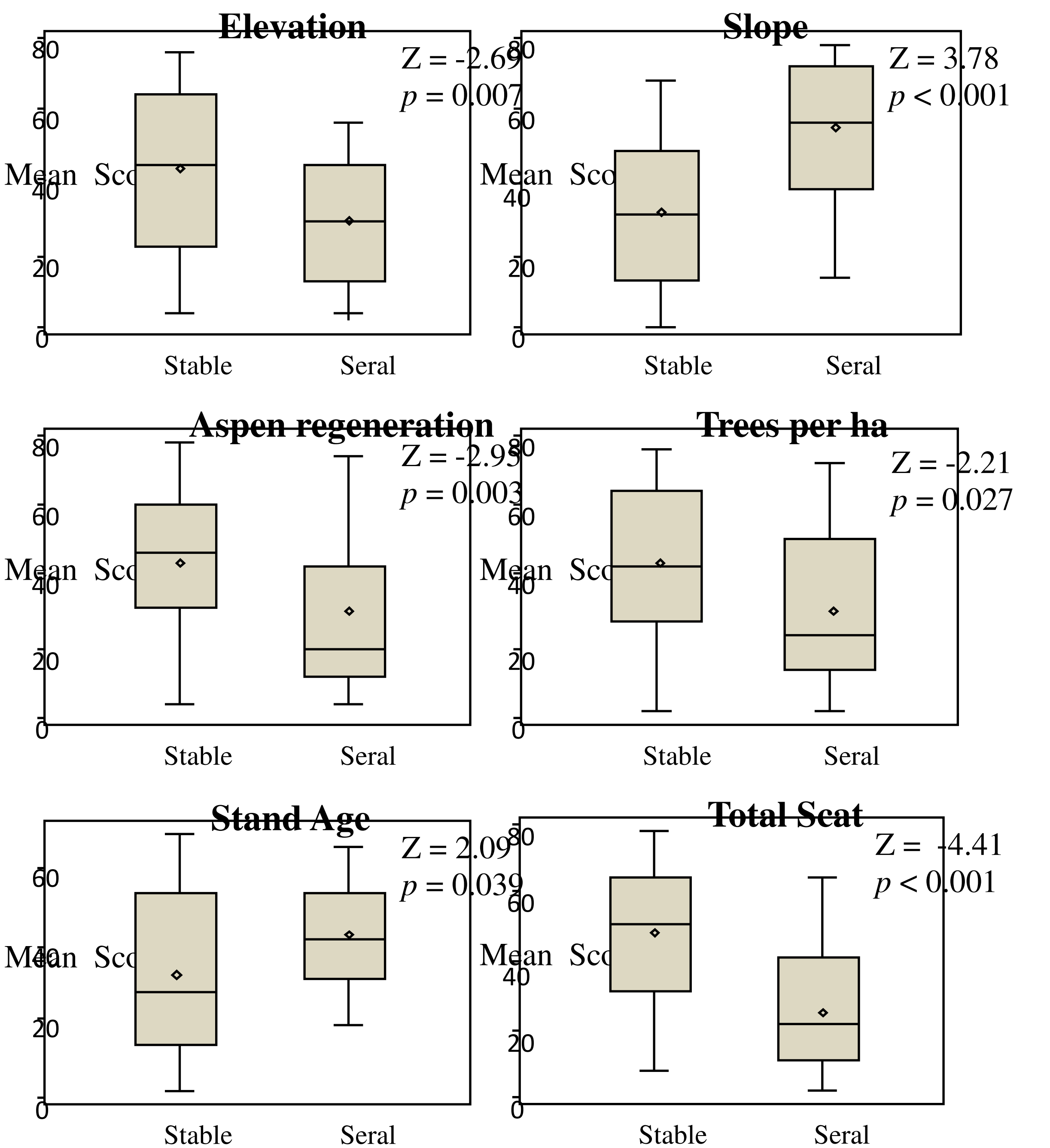


Figure 2: Wilcoxon-Mann-Whitney U test results displayed in box plots showing significant differences between seral and stable aspen types by plot-level indicators across the study landscape. Wilcoxon mean scores are shown on the Y-axis. Whiskers show minimum and maximum values, boxes represent 25-75%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



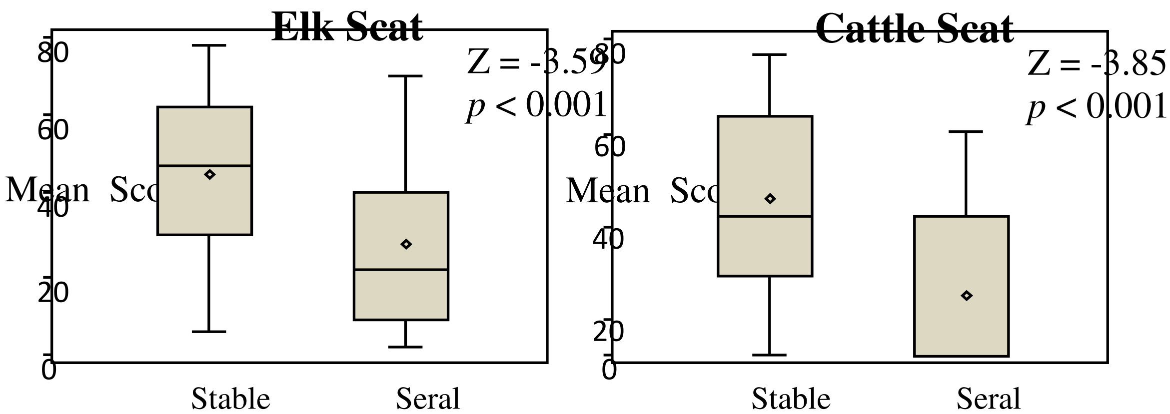

Elk Scat
Z = -3.59
p < 0.001
Mean Sco
80
60
40
20
0
Stable
Seral
Cattle Scat
Z = -3.85
p < 0.001
Mean Sco
80
60
40
20
0
Stable
Seral

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

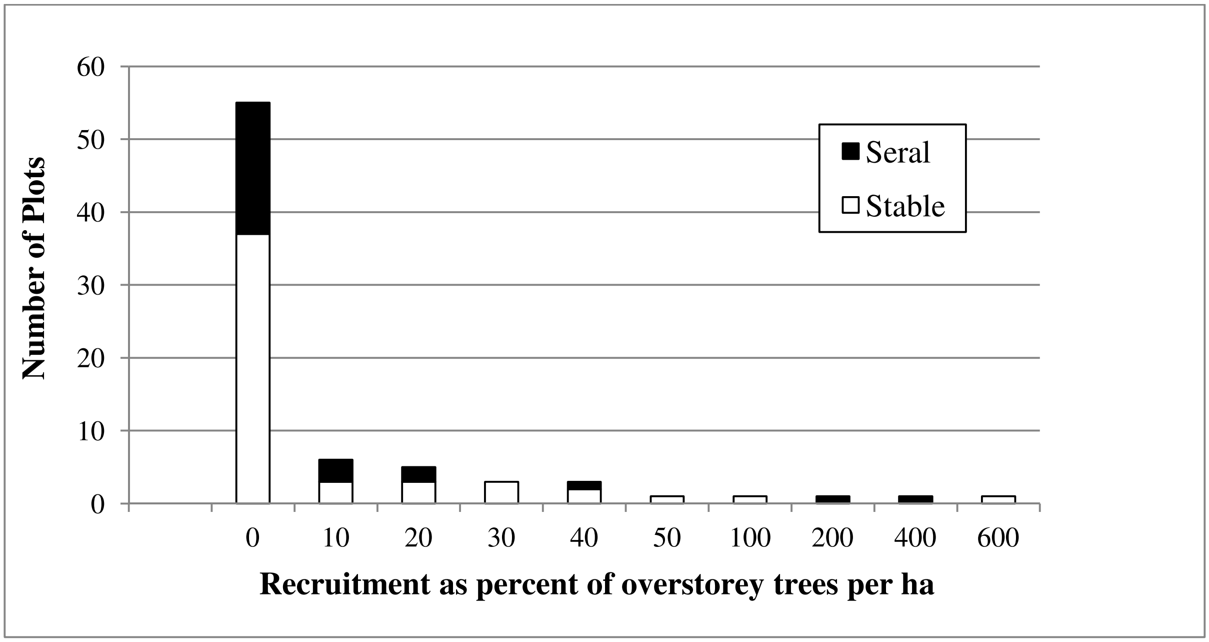


Figure 4: Kruskal-Wallace test results are displayed in box plots showing significant differences between aspen condition classes across the study landscape. We intentionally did not test variables directly related to condition class elements (Table 2) in an effort to independently assess the value of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

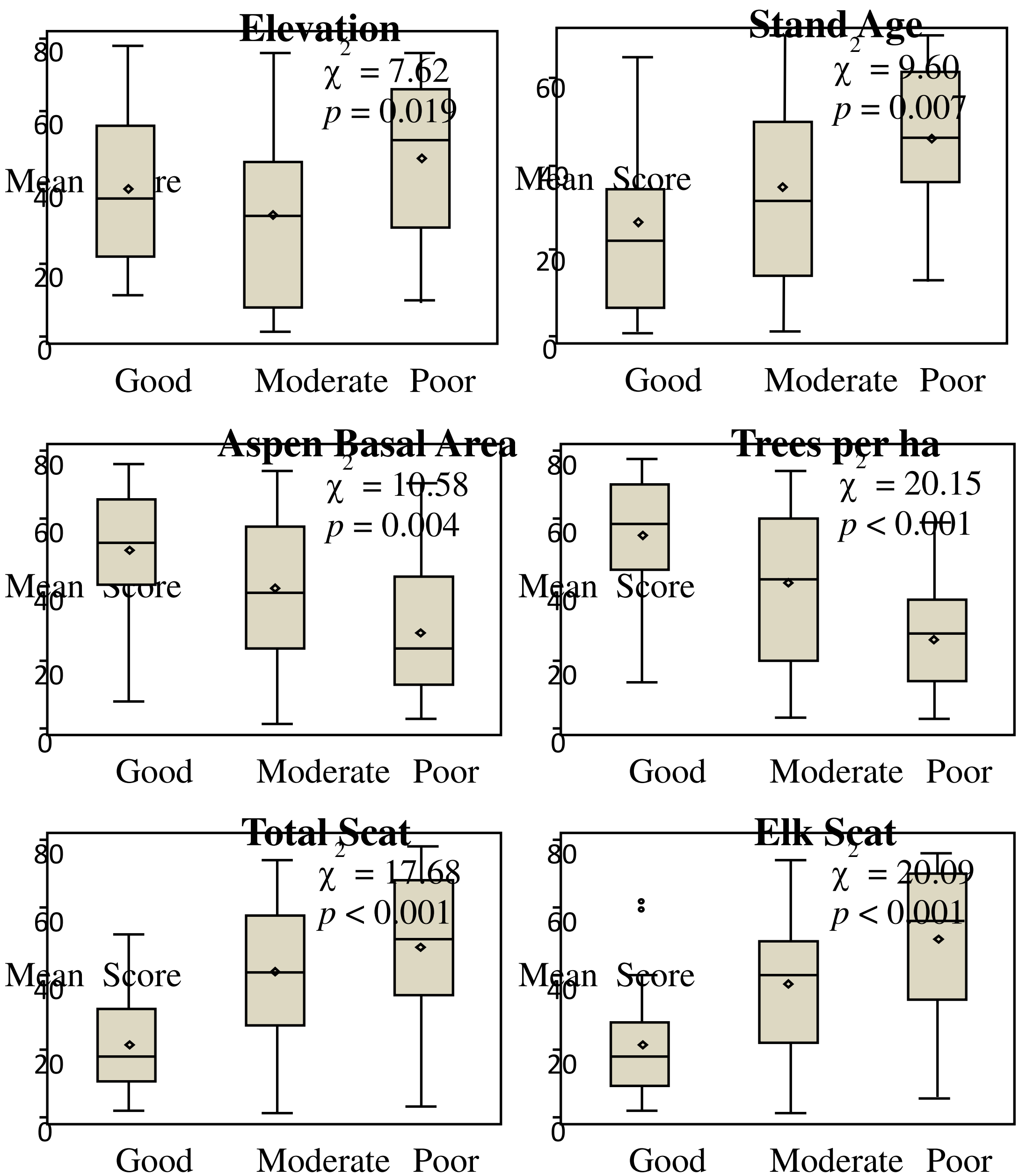


Figure 5: Nonmetric multidimensional scaling (NMS) results are shown in a joint plot which highlights prominent indicators within the total Book Cliffs data set. Vectors with > +/- 0.5 Pearson's coefficient (*r*) value (Table 2) are displayed in relation to "plot space". The length of vectors corresponds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