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Long-term livestock grazing alters aspen age structure in the northwestern Great Basin

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ABSTRACT

We determined the age structure of quaking aspen (*Populus tremuloides*) over the period 1850–2009 in Hart Mountain National Antelope Refuge riparian areas to evaluate potential influences of (a) livestock herbivory and (b) climate on aspen demography. We found a significant decline in aspen recruitment ($p < 0.05$) in the late 1800s, coincident with the onset of high levels of Euro-American livestock grazing. Although livestock use was regulated following establishment of the refuge in 1936, low levels of aspen recruitment continued. After termination of livestock grazing in 1990, aspen recruitment on the refuge increased ($p < 0.05$) by more than an order of magnitude in comparison to levels occurring during the previous half-century of regulated grazing. Climate variables (i.e., Palmer Drought Severity Index, annual precipitation, and annual temperature) appeared to have little influence on long-term patterns of aspen recruitment. Overall, results are consistent with top–down forcing by livestock herbivory as the major factor associated with a century of reduced aspen recruitment on HMNAR. Where long-term declines in aspen are currently underway on grazed lands in the western US, land managers need to carefully consider the potential effects of livestock and alter, as needed, management of these ungulates to ensure retention of aspen woodlands and their ecosystem services.

1. Introduction

Quaking aspen (*Populus tremuloides*) are widely distributed across the western United States (US) and are valued for landscape diversity, wildlife habitat, aesthetics, recreational sites, wood fiber, and livestock forage (Shepperd et al., 2001). Aspen normally occur on moist sites and their canopies transmit substantial light, contributing to a biologically diverse understory. Thus, changes in aspen stand dynamics often index alterations in the composition and structure of understory plant communities (DeByle and Winokur, 1985). The age structure of aspen stands (i.e., number of aspen/ha vs. date of establishment) provides an important approach for characterizing stand dynamics as well as assessing the effectiveness of factors influencing them (e.g., Olmsted, 1979; Binkley, 2008; Halofsky and Ripple, 2008).

Aspen extent in the western US greatly decreased over the last century with losses in seven western states ranging from 49% to 96% (Bartos, 2001). Possible causes of decline include altered fire regimes, conifer competition, direct and indirect effects of a changing climate, high levels of ungulate herbivory, and others (Kay, 1997; Hanna and Kulakowski, 2012; Seager et al., 2013). However, where aspen stands occur interspersed with coniferous forests, such as on the western slope of the Rocky Mountains in Colorado, their coverage has not declined (Manier and Laven, 2002; Zier and Baker, 2006). In western Canada, aspen have been undergoing upslope range expansion due to the combined effects of forest harvesting and a warming climate (Landhauser et al., 2010).

Early studies (e.g., Houston, 1954) reported that livestock herbivory could be a major factor reducing aspen recruitment (i.e., growth of sprouts/seedlings into tall saplings and trees) and altering the composition of understory plant communities. Not only are aspen sprouts/seedlings and many of the deciduous shrubs and forbs associated with aspen stands highly palatable to livestock (DeByle and Winokur, 1985), but livestock often spend a high proportion of time within riparian areas. Thus, plants growing in these areas frequently experience high levels of herbivory and trampling (Kauffman and Krueger, 1984). Livestock use has not only been found to affect soils, biological soil crusts, hydrologic processes, and habitat conditions for terrestrial and aquatic species

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(Fleischner, 1994; Belsky et al., 1999), but it is the most widespread use of public lands in the American West, occurring annually across nearly one million square kilometers (Beschta et al., 2013). Although aspen dynamics in the western US can be affected by a variety of factors, regional studies have recently identified climate change as a major driver of aspen woodland decline (e.g., Rehfeldt et al., 2009; Hanna and Kulakowski, 2012).

For at least several decades prior to 1990, aspen recruitment in gallery forests along perennial streams on the Hart Mountain National Antelope Refuge (HMNAR) was absent or occurring only at low levels, and mortality of overstory aspen trees was common (Fig. 1a). Although overstory mortality has continued in recent years, a major increase in aspen recruitment is currently underway in many stands (Fig. 1b; Earnst et al., 2012). Today, aspen stands on the refuge generally exhibit a "two-layered" canopy – an upper layer comprised of sparsely occurring overstory trees, many of which are dying, and a dense understory of sprouts, saplings, and medium-sized trees (Fig. 1c). We undertook this study to identify when major changes in the age structure of riparian aspen woodlands occurred and the factor(s) likely contributing to such changes. Because conifer competition, wildfires, and wild-ungulate herbivory are not having widespread effects on aspen stand dynamics within the refuge (Dobkin et al., 1995; Earnst et al., 2012), we were left with three competing hypotheses: shifts in aspen age structure have been primarily influenced by (1) livestock herbivory, (2) climate, or (3) a combination of these two major ecosystem drivers.

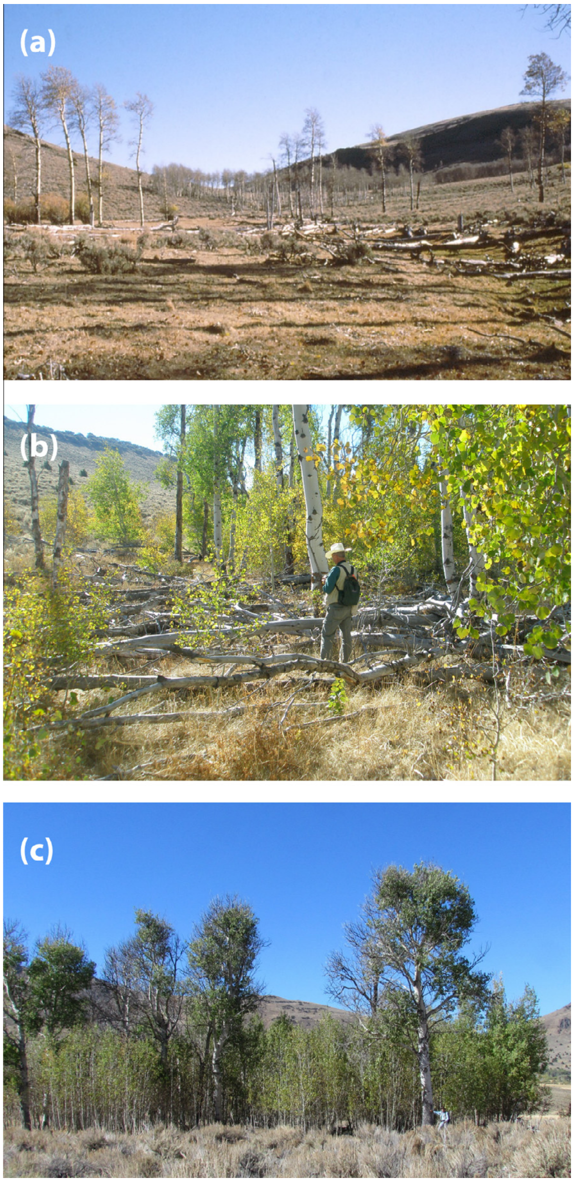

Fig. 1. Examples of aspen stands on Hart Mountain National Antelope Refuge showing (a) ongoing overstory mortality and a long-term lack of understory recruitment (1990 photo), (b) high levels of continuing overstory mortality with increased recruitment of understory aspen (2012 photo) and (c) remaining overstory trees with high levels of understory recruitment (2012 photo) resulting in a "two-layered canopy" indicative of a long-term recruitment gap.

1.1. Study area

HMNAR in southeastern Oregon (42°25′N, 119°40′W) is managed by the U.S. Fish and Wildlife Service and comprises 1125 km^2 in Lake County, with Harney County bordering the refuge's eastern edge. Hart Mountain is massive fault-block with a north–south trending axis and peaks up to 2444 m of elevation. A steep escarpment comprises the west side of the block whereas the east side descends in a series of rolling hills and low ridges to the sagebrush-shrub steppe typical of southeastern Oregon and the Great Basin. Rock, Guano, Deer, and Stockade Creeks are the primary perennial streams draining the eastern portion of Hart Mountain.

Upland vegetation on the eastern side of Hart Mountain consists primarily of sagebrush (*Artemisia* spp.) shrub steppe intermixed with smaller areas of bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), and western juniper (*Juniperus occidentalis*). Upland aspen (snow-pocket stands) occur on moist sites, often associated with seasonal snowpack accumulations (Dobkin et al., 1995; Earnst et al., 2012), and mostly comprised of dense stands of small trees. Nearly 90 ha of riparian habitat along intermittent and perennial streams on the refuge are dominated by aspen stands that were the focus of this study (FWS, 1994). In general, these stands persist in the absence of major disturbance (s) and represent a "stable" aspen type (Rogers et al., 2010; 2014).

Pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) reside on the refuge (HMNAR annual narrative reports). The refuge's summer pronghorn population of <500 animals in the 1970s increased to 1000–2000 animals by the 1990s. Over the past decade this population ranged from ca. 2000 to 3500 animals. Mule deer numbers during the last two decades have been estimated at well below 1000 animals (Oregon Department of Fish and Wildlife, unpublished data) and in 2003, a small herd of 15–20 elk (*Cervus elaphus*) began to use the refuge. However, neither pronghorn, deer, nor elk use the refuge as winter range at elevations supporting aspen.

After establishment in 1936, the refuge continued to be grazed each summer by domestic sheep, cattle, and horses. Except for small bands of feral horses, only cattle grazing occurred after 1946, with 30 fenced pastures eventually established for managing livestock distribution and forage utilization. Even with controlled livestock numbers and distributions, significant grazing impacts to upland and riparian plant communities, soils, and stream systems continued to accumulate (FWS, 1994). Livestock use on the refuge was eliminated following the 1990 grazing season (FWS, 1994).

2. Methods

In October 2012, we sampled riparian aspen along the four major perennial streams draining the eastern side of Hart Mountain's fault-block ridge, including Barnhardi Meadow which separates the upper and lower reaches of Rock Creek (Table 1 and

Fig. 2). A total of 17 plots (each 150-m long by 100-m wide) were established with the long axis of each plot centered on the stream corridor; adjacent plots were separated by at least 100 m and most were at least 250 m apart. These plots were distributed across six stream reaches and plot dimensions encompassed all riparian aspen along the channel. In nearly all cases aspen occurred continuously along a sampled reach. Thirteen of these plots were used in previous studies that evaluated changes to plant communities and bird populations after livestock removal (Dobkin et al., 1995, 1998; Earnst et al., 2012). The original plots were established in proportion to total aspen area within major drainages on the east side of the refuge (Dobkin et al., 1995). Four additional plots (one each along upper Rock Creek and Barnhardi Meadow and two more along lower Rock Creek) were included to provide a more balanced sampling within the six study reaches (Table 1).

We employed two approaches for characterizing the age structure of HMNAR's riparian aspen stands. The first focused on "overstory" aspen which consisted of trees mostly $\geqslant$19 cm in diameter at breast height (*DBH*). We subdivided each 150-m long plot into three subplots (i.e., 0–50, 50–100, and 100–150 m in length) and randomly selected one of them within which we measured the *DBH* of all overstory aspen trees. Overstory trees were readily identified by their relatively large diameters and bark along the lower portions of their boles that usually was furrowed or had moss, lichens, and fungal conks, thus contrasting with the relatively clear and unmarred bark of younger understory aspen. If overstory trees were absent or infrequent within a subplot, we inventoried all overstory trees in the remainder of the 150-m long plot.

Within each plot, we obtained increment cores from three to four aspen trees representing a range of diameters. We measured the *DBH* of each selected tree and obtained an increment core at breast height (1.5 m). We used a 12.5 mm diameter increment corer rather than the more commonly available 4–5 mm diameter corers to obtain a larger surface for identifying growth rings. Cores were glued onto grooved boards and removed to a laboratory where they were dried and sanded (400 grit). Tree age (*AGE*, year) was determined by a count of annual growth rings using a 10× binocular microscope. Regression analysis was used to establish a relationship between *AGE* and *DBH*. To determine the number of years needed for aspen to attain breast height, we counted the

Table 1
Characteristics of stream reaches, width of riparian aspen stands (based on length of 2-m belt transects), and aspen densities sampled in this study.

Stream reach	Number of plots	Elevation range (m)	Channels		Riparian width (m)	Aspen densities		
			Gradient (%)	Aspect		Overstory (N/ha)	Understory (N/ha)	Total (N/ha)
Deer Creek	3	1939–1975	5	E–NE	52	324	2510	2830
Guano Creek	3	1890–2024	6	SE	43	71	4520	4590
Stockade Creek	3	1969–1878	11	E	41	216	3740	3960
Upper Rock Creek	3	1987–2030	10	N	42	154	3240	3390
Lower Rock Creek	3	1828–1896	4	NE	47	127	4320	4450
Barnhardi Meadow	2	1954–1969	4	SE–NW	20	172	8140	8310
Average	2.8	1928–1962	6.7	–	41	177	4410	4590
±SE					±4.5	±35	±800	±790

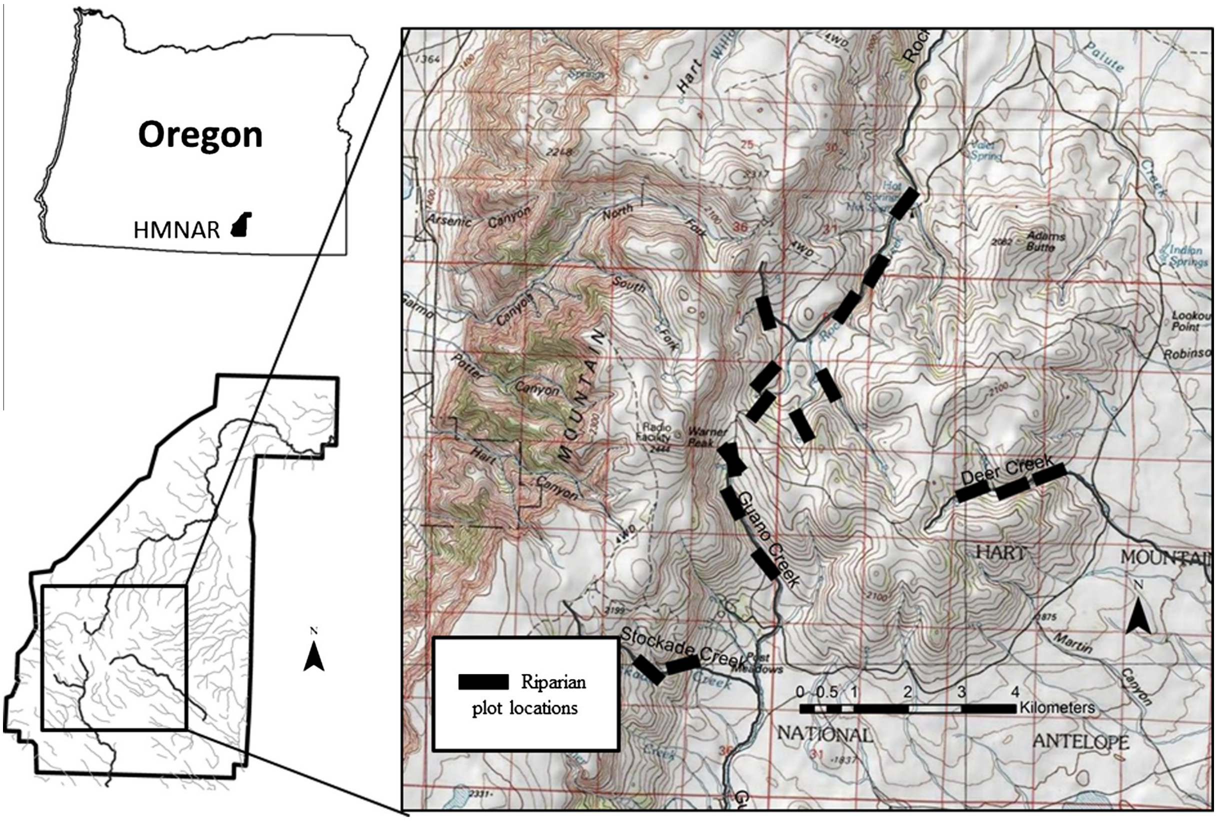

Fig. 2. Location map of Hart Mountain National Antelope Refuge (HMNAR) and the riparian aspen plots utilized in this study.

number of annual bud scars below 1.5 m on young aspen from across the study area.

Overstory aspen densities (#/ha) for each plot were "binned" into 5-year age-classes and then averaged across stream reaches to determine an overall age structure of these trees on HMNAR. We used linear regression to characterize the trend in aspen frequency over time from 1850 to 1879 (prior to significant livestock use). This regression provided a basis for comparing expected aspen frequency (regression line estimates) to those observed in subsequent years (1880–1939) when high levels of livestock use were common in southeastern Oregon. Observed aspen frequencies after 1879 were considered significantly different if they were outside the regression line's ±95% confidence limits (CL).

Our second method of characterizing age structure focused on understory aspen (Fig. 1c). Within each plot, we established a 2-m wide belt transect perpendicular to the channel at distances of 25, 75, and 125 m along the stream reach. Within each transect, we measured the *DBH* of all aspen $\geqslant$1.5 m in height. Each transect started at one edge of the aspen stand and crossed the channel to the stand's opposite edge; transect length was measured with a hand-held GPS unit. *DBH* measurements from these transects, in conjunction with the *AGE* vs. *DBH* relationship, were used to develop an age structure of riparian aspen from 1940 to the present. Aspen frequencies per hectare, by year of establishment, were again accumulated into 5-year age classes and averaged across stream reaches. We used linear regression to characterize the trend in aspen frequencies over time for the period 1940–1990, the period of managed livestock use on the HMNAR. Regression line estimates of aspen frequency were compared against observed frequencies after 1990 (following the cessation of livestock grazing) and were considered significantly different if they were outside the regression line's ±95% CLs.

We summarized the number of cattle, sheep, and horses in Harney and Lake Counties from US census records, by decade, to index general levels of livestock use in southeastern Oregon over the period 1850–1939. For this same 90-year period we compiled annual values of the Palmer Drought Severity Index (*PDSI*), a general indicator of climatic stress to plants (Alley, 1984), for 42.5°N latitude and 120.0°W longitude (grid point 45) from the NOAA National Climatic Data Center, http://www.ncdc.noaa.gov/paleo/newpdsi.html. We compared *PDSI* values for two 30-year periods (*t*-test): 1850–1879 (when livestock in southeast Oregon were absent or at low numbers) vs. 1880–1939 (when livestock numbers were at relatively high levels).

We compiled records of permitted livestock use in animal unit months (AUMs) annually from 1940 to 1990, representing the period of managed livestock use (HMNAR annual narrative reports). We also compiled monthly temperature and precipitation data from the HMNAR headquarters weather station for 1940–2009 and expressed annual values on a water-year basis (October 1–September 30). If five or more days of temperature or precipitation were missing from a given month, we estimated the monthly value based on correlations between refuge's weather station and the Lakeview weather station (located ~70 km to the southwest). We used linear regression to identify potential long-term trends in temperature and precipitation on Hart Mountain over the last seven decades (1940–2009). Using *t*-tests, we also compared annual temperature and precipitation data for two 20-year periods: 1971–1990 (when livestock grazing was ongoing) vs. 1991–2010 (after livestock grazing was eliminated). A *p*-value of $\leqslant$0.05 for any *t*-test was considered to represent a statistically significant result.

3. Results

Linear regression of *AGE* vs. *DBH* resulted in a significant relationship: $AGE = 3.59 \times DBH$ ($r^2 = 0.59$, $p < 0.001$, $n = 63$). Heart rot, decayed wood that is a common occurrence in aspen stands across many portions of the American West (DeByle and Winokur, 1985), was almost entirely absent in our cores. Inspection of young aspen within the study area indicated that five years was normally required for them to attain breast height. Thus, the estimated year of establishment (*EY*) for each sampled aspen was calculated as: $EY = 2012 - [(3.59 \times DBH) + 5]$.

Overstory aspen averaged 29.9 cm in *DBH* (SE ± 1.2; $n = 901$) and had an average density of 177 aspen/ha (SE ± 35; Table 1). Based on our *AGE* vs. *DBH* relationship, 94% of all overstory trees had established before 1940. Age structure results indicated an upward trend in aspen recruitment from 1850 through the 1870s (Fig. 3a). Based on a fitted regression line for this period, aspen densities after 1895 were significantly less than expected (i.e., outside the ±95% CL).

Grazing by domestic livestock in southeast Oregon began during the 1870s and their numbers rapidly increased in subsequent decades, peaking by the late 1800s (Fig. 3b). *PDSI* values were similar throughout most of 1850–1919 with relatively low values in the 1920s and 1930s, an indication of droughty conditions (Fig. 3c). Average *PDSI* values for 1850–1879 ($\bar{x} = +0.32$) and for 1880–1909 ($\bar{x} = +0.31$), the 30-year periods before and after livestock numbers peaked in southeast Oregon, respectively, were not significantly different ($p = 0.99$, *t*-test).

A total of 1760 aspen $\geqslant$1.5 m in height were measured within the 2-m wide belt transects, representing an average density of 4410 aspen/ha (SE ± 800; Table 1). Of these, 96% were <19 cm in *DBH* (i.e., established after 1940). Based on transect lengths, the average width of riparian aspen stands along the sampled streams was 41 m (SE ± 4.5; Table 1). Regression analysis indicated a small increase in understory aspen frequencies occurred from 1940 to 1989 ($r^2 = 0.96$, $p < 0.001$, Fig. 3a), the period when grazing was being regulated on the refuge. However, a relatively large increase in understory aspen frequencies began after livestock removal (Fig. 4a) and by 2005–2009 the rate of recruitment was nearly 14 times greater than what occurred during a half century of regulated grazing (i.e., 1940–1989) (Fig. 4a).

From 1940 to 1989, annual livestock use on the refuge averaged ~12,550 AUMs (~0.1 AUM/ha). Annual temperatures at Hart Mountain for 1940–2009, a period of seven decades, exhibited a significant ($p = 0.04$) upward trend of 0.1 °C/decade (Fig. 4b). Over this same period, annual precipitation also exhibited a significant ($p = 0.04$) upward trend of 1.0 cm/decade (Fig. 4c). However, because of the large variability in annual temperature and precipitation, each regression had a small coefficient of determination (i.e., $r^2 = 0.06$). Consistent with the upward trend in temperatures over time, the average annual temperature ($\bar{x} = 6.5$ °C) during 1971–1990 (livestock present) was significantly lower ($t_{38} = -2.46$, $p = 0.02$) than the average annual temperature ($\bar{x} = 7.0$ °C) during 1991–2010 (livestock absent). In contrast, the average annual precipitation ($\bar{x} = 31.4$ cm) during 1971–1990 (livestock present) was not significantly different ($t_{38} = -0.07$, $p = 0.94$) from the average annual precipitation ($\bar{x} =$ of 31.6 cm) during 1991–2010 (livestock absent).

4. Discussion

We used an *AGE* vs. *DBH* relationship based on tree ring counts, along with sampled *DBH*s across multiple stream reaches, to determine the general age structure of Hart Mountain aspen stands from 1850 to 2009. The resultant age structure provided a quantitative basis for identifying the timing and magnitude of major shifts in aspen recruitment over time. This general methodology has been used to assess the effects of native ungulates on aspen, cottonwood, and other woody browse species at various locations in

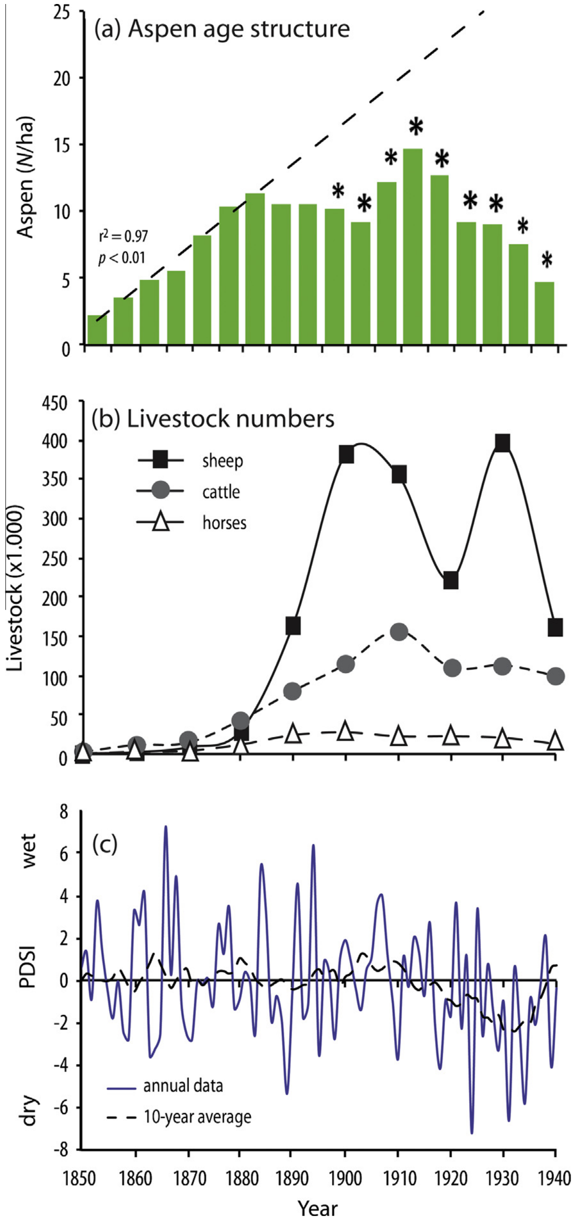

Fig. 3. (a) Aspen age structure (number of aspen per hectare by establishment year for 5-year periods) from 1850 to 1939 and linear regression (dashed line) of aspen frequency (*Y*) vs. establishment date (*X*) from1850 to1879, Hart Mountain National Antelope Refuge (HMNAR); an (∗) indicates observed aspen frequency exceed the lower 95% confidence level, (b) number of EuroAmerican cattle, sheep, and horses in Harney and Lake Counties, by decade, and (c) Palmer Drought Severity Index (*PDSI*) for HMNAR. Data sources: (b) US census records; (c) NOAA National Climatic Data Center.

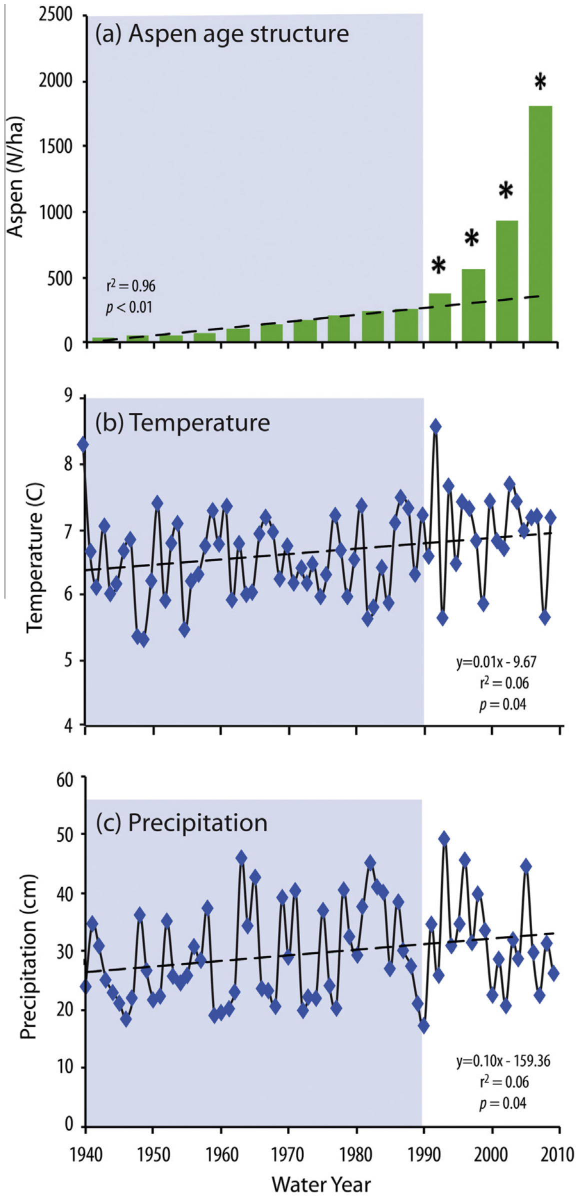

Fig. 4. (a) Aspen age structure (number of aspen per hectare by establishment year for 5-year periods) from 1940 to 2009 and linear regression (dashed line) of aspen frequency (*Y*) vs. establishment year (*X*) from 1940 to1989, Hart Mountain National Antelope Refuge (HMNAR); an (∗) indicates observed aspen frequency exceeds the upper 95% confidence level, (b) annual average temperature and (c) annual precipitation (both temperature and precipitation are on a water year basis; October 1–September 30). Shaded portions of (a–c) identify years when livestock grazing occurred on the refuge. Data sources: (b and c) HMNAR headquarters weather station.

the western US (Ripple and Larsen, 2000; Beschta, 2005; Binkley et al., 2006; Binkley, 2008; Beschta and Ripple, 2009, 2010). An age-structure approach has also been used to identify the timing of western juniper expansion in portions of southeastern Oregon, an invasion that began in the late 1800s coincident with the onset of Euro-American livestock grazing (Miller et al., 1994). Nevertheless, we are unaware of any study where age structure has been used to address the potential effects of Euro-American livestock introduction, and subsequent removal, on long-term aspen stand dynamics.

The age structure for an uneven-aged forest normally has relatively few old trees with increasing numbers of trees in younger age classes (Hunter, 1999). Consistent with that model, we found increasing numbers of riparian aspen trees over time for 1850–1879, the period prior to high levels of livestock use in southeastern Oregon. However, as introduced livestock numbers were peaking in the 1890s and remained high afterward, aspen recruitment began to significantly depart from the 1850 to 1879 regression equation, the magnitude of departure becoming greater over time. The relatively low rates of recruitment experienced in the 1930s could represent the additive effects of drought conditions experienced in the late 1920s and in the 1930s (low *PDSI*s). However, because average *PDSI* values for the 30 years before and after the introduction of livestock were not significantly different we conclude that the major reduction in aspen frequencies, which began in the late 1800s, was more likely to be associated with the effects of livestock herbivory than climate. We also note that *PDSI* values may over-represent fluctuations in climatic stress for riparian aspen growing along perennial streams, such as in this study.

After designation as a national wildlife refuge in 1936, refuge administrators began to manage livestock distribution and utilization (FWS, 1994). Our aspen age structure data for riparian stands indicate that such management allowed only a limited occurrence of aspen recruitment over time. The magnitude of browsing suppression becomes evident when comparing aspen frequencies during the period of managed grazing to those that occurred after cessation of grazing. Aspen frequencies, in the absence of livestock, have greatly increased over the last two decades and currently are more than an order of magnitude greater than what occurred during the period of managed livestock use.

With regard to the potential influence of climate upon aspen recruitment, statistically significant ($p < 0.05$) but weak ($r^2 = 0.06$) trends of increased annual average temperature and annual precipitation occurred at HMNAR over the period 1940–2009. While annual average temperatures for the 20 years before and after livestock removal (6.5 vs. 7.0 °C, respectively) were significantly different, annual precipitation amounts before and after livestock removal were not. Higher temperatures might contribute to longer growing seasons, but in arid environments such temperatures could also cause increased drought stress, possibly reducing the extent of suitable aspen habitat. Increases in temperature would likely exacerbate the generation of aspen sprouts (Worrall et al., 2013) and not contribute to the recent recruitment increases observed for riparian aspen stands on the HMNAR. Thus, the small but statistically significant increase in temperature during the last 20 years is not entirely consistent with the major increase in aspen frequencies observed during this same period. Instead, the dramatic increase in riparian aspen frequencies following the removal of livestock indicates that elimination of livestock herbivory has had a much greater influence, to date, than any fluctuations or trends in climate.

Although Kay (2003) and Rogers and Mittanck (2013) indicate that top-down forcing by ungulate herbivory can be a major driver of aspen decline in the western US, their results and those of this study are in contrast with regional studies that have instead identified climate as an important factor associated with aspen decline (e.g., Rehfeldt et al., 2009; Hanna and Kulakowski, 2012). Unfortunately, climate-based studies of aspen dynamics seldom include evaluations of the long-term effects of livestock grazing even though it is the most widespread use of public lands in the western US and has been shown to have wide ranging effects on riparian and upland plant communities, soils, and hydrologic processes (see reviews by Donahue, 1999; National Research Council, 2002; Belnap and Lange, 2003; Beschta et al., 2013).

A FWS (1994) assessment of environmental conditions on HMNAR indicated that long-term livestock grazing had altered riparian vegetation along many refuge streams, resulting in accelerated streambank erosion, channel downcutting, and lowered water tables. Loss of riparian vegetation and channel erosion normally contribute to degraded water quality (e.g., increased turbidity and stream temperatures) as well as adversely affecting riparian/aquatic habitat for fish, amphibians, and other species (Platts, 1991; Fleischner, 1994; Belsky et al., 1999). However, the increasing cover of understory vegetation (Earnst et al., 2012) and aspen now occurring along the refuge's stream systems, in spite of previous livestock impacts to streams and riparian systems, should assist in the long-term stabilization and narrowing of channels, improved water quality, and restoration of livestock-altered riparian and aquatic habitats (National Research Council, 2002).

In the western US, where aspen and other deciduous riparian woodlands support the region's greatest diversity and abundance of birds, ungulate herbivory can be a major stressor (Saab et al., 1995; Berger et al., 2001; Tewksbury et al., 2002). Birds that nest in the understory or on the ground are most affected by ungulates due to consumption and trampling of low-growing vegetation (Saab et al., 1995; Martin, 2007; Earnst et al., 2012), but effects throughout the avian community have been demonstrated where cattle have substantially altered vegetation (Tewksbury et al., 2002; Krueper et al., 2003). Within three years of removing cattle on the HMNAR, avian abundances (especially of ground and understory species) increased, along with increased cover of herbaceous plants and aspen shoots (Dobkin et al., 1998; Tewksbury et al., 2002). Within approximately a decade after cattle removal, total avian abundance in riparian aspen was 33% greater, with ground and understory nesters increasing by an astounding 133%. These increases occurred in conjunction with high densities of aspen shoots and stems <2 m in height and increased cover of native forbs and shrubs (Earnst et al., 2012). Similar responses of deciduous woody plants and ground- and shrub-nesting bird species in northern Arizona occurred within 6 years following complete exclusion of elk in deciduous woodlands of snowmelt drainages (Martin and Maron, 2012).

Aspen growth rates can be highly variable across sites and regions (DeByle and Winokur, 1985), thus we compared our results against estimates from the northern Rockies. The rate of diameter growth obtained from regression analysis of *AGE* vs. *DBH* in this study, 3.59 years per centimeter of diameter increase, was greater than the 2.89 and 3.13 years/cm obtained in Yellowstone by Kay (1990) and Ripple and Larson (2000), respectively. The 15–24% increased rate of diameter growth for Hart Mountain aspen could be due to: (a) our aspen stands occurred at ~1950 m of elevation whereas many of the aspen stands sampled by Kay (1990) and Ripple and Larson (2000) occurred at higher elevations and thus may have a more restricted growing season, (b) we sampled only riparian aspen stands whereas they sampled riparian and upland stands, (c) heart rot (often making cores unreadable) was essentially absent from our cores whereas its occurrence was common in Yellowstone's aspen, (d) or some other factor.

5. Conclusions

We utilized an age-structure approach to evaluate long-term aspen recruitment following the Euro-American introduction of domestic ungulates. Our results indicated that temporal patterns in aspen recruitment were primarily altered by two landscape-scale treatments: (a) the onset of livestock grazing in the late 1800s and (b) the removal of livestock grazing in 1990. Livestock introduction, over a century of grazing, and subsequent removal appears to represent the primary factor affecting long-term patterns of aspen recruitment in this Great Basin landscape. With regard to our climate hypothesis, *PDSI*, annual average temperature, and annual precipitation patterns appeared to have little, if any, association with temporal patterns of aspen recruitment. Given the potential for historical and contemporary grazing practices to significantly affect aspen plant communities and associated ecosystem services, future studies of climate on aspen stand dynamics need to concurrently address the relative importance of ungulate herbivory.

Because landscape-scale removal of livestock such as occurred on HMNAR is a rare occurrence in the American West, this situation provided a unique opportunity for evaluating the relative importance of top-down (livestock herbivory) and bottom-up (climate) factors on long-term aspen dynamics. The removal of livestock from the entire refuge provided an important test of passive restoration (i.e., the cessation of those anthropogenic activities causing degradation or preventing recovery; Kauffman et al., 1997), a test that resulted in greatly increased aspen recruitment and greater biotic diversity (Earnst et al., 2012). Our results indicate that for areas grazed by livestock and where aspen recruitment is either absent or occurring at low levels, implementing strategies that eliminate or minimize the effects of livestock herbivory may be needed. Given the vast amount of public land annually utilized by domestic ungulates (Beschta et al., 2013) and the large losses in aspen those lands have experienced to date (Bartos, 2001), reducing livestock grazing effects within and across ecoregions may be required for attaining ecological restoration of herbivore-altered plant communities. Such restoration is a pressing need in the face of climate change if the ecological integrity of these plant communities and their ecosystem services are to be conserved.

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References

Alley, W.M., 1984. The palmer drought severity index: limitations and assumptions. J. Appl. Meteorol. Climatol. 23, 1100–1109.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests. In: Shepperd, S.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), Sustaining Aspen in Western Landscapes: Symposium Proceedings, USDA Forest Service, RMRS-P-18, Fort Collins, Colorado, pp. 5–14.

Belnap, J., Lange O.L. (Eds.), 2003. Biological Soil Crusts: Structure, Function, and Management, Ecological Studies 150, Springer Publishing.

Belsky, A.J., Matzke, A., Uselman, S., 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. J. Soil Water Conserv. 54, 419–431.

Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P., 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecol. Appl. 11, 947–960.

Beschta, R.L., 2005. Reduced cottonwood recruitment following extirpation of wolves in yellowstone's northern range. Ecology 86, 391–403.

Beschta, R.L., Ripple, W.J., 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol. Conserv. 142, 2401–2414.

Beschta, R.L., Ripple, W.J., 2010. Mexican wolves, elk, and aspen in Arizona: is there a trophic cascade? For. Ecol. Manage. 260, 915–922.

Beschta, R.L., Donahue, D.L., DellaSala, D.A., Rhodes, J.J., Karr, J.R., O'Brien, M.H., Fleischner, T.L., Deacon Williams, C., 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. Environ. Manage. 51, 474–491.

Binkley, D., 2008. Age distribution of aspen in Rocky Mountain National Park, USA. For. Ecol. Manage. 255, 797–802.

Binkley, D., Moore, M.M., Romme, W.H., Brown, P.M., 2006. Was Aldo Leopold right about the Kaibab deer herd? Ecosystems 9, 227–241.

DeByle, N.V., Winokur, R.P. (Eds.), 1985. Aspen: Ecology and Management in the Western United States. USDA Forest Service, General Technical Report RM-119, Ft. Collins CO.

Dobkin, D.S., Rich, A.C., Pretare, J.A., Pyle, W.H., 1995. Nest site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97, 694–707.

Dobkin, D.S., Rich, A.C., Pyle, W.H., 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. Conserv. Biol. 12, 209–221.

Donahue, D.L., 1999. The Western Range Revisited: Removing Livestock from Public Lands to Conserve Native Biodiversity. University of Oklahoma Press, Norman.

Earnst, S.L., Dobkin, D.S., Ballard, J.A., 2012. Changes in avian and plant communities of aspen woodlands over 12 years after livestock removal in the northwestern Great Basin. Conserv. Biol. 26, 862–872.

Fleischner, T.L., 1994. Ecological costs of livestock grazing in western North America. Conserv. Biol. 8, 629–644.

FWS, 1994. Hart Mountain National Antelope Refuge, Comprehensive Management Plan. USDI, Fish and Wildlife Service, Final Environmental Impact Statement, Portland, OR.

Halofsky, J., Ripple, W., 2008. Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. Forest.: Int. J. For. Res. 81, 195–207.

Hanna, P., Kulakowski, D., 2012. The influences of climate on aspen dieback. For. Ecol. Manage. 274, 91–98.

Houston, W.R., 1954. A Condition Guide for Aspen Ranges of Utah, Nevada, Southern Idaho, and Western Wyoming. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper No. 32, Ogden, Utah.

Hunter, J.L., 1999. Managing Biodiversity in Forest Ecosystems. Cambridge University Press, UK, pp. 697.

Kauffman, J.B., Krueger, W.C., 1984. Livestock impacts on riparian ecosystems and streamside management implications—a review. J. Range Manage. 37, 430–438.

Kauffman, J.B., Beschta, R.L., Otting, N., Lytjen, D., 1997. An ecological perspective of riparian and stream restoration in the Western United States. Fisheries 22, 12–24.

Kay, C.E. 1990. Yellowstone's Northern elk Herd: A Critical Evaluation of the "Natural Regulation" Paradigm. PhD Dissertation, Utah State University, Logan, UT, pp. 490.

Kay, C.E., 1997. Is aspen doomed? J. Forest. 95, 4–11.

Kay, C.E., 2003. Aspen management guidelines for BLM lands in north-central Nevada. Wildlife Management Services, Providence, Utah.

Krueper, D., Bart, J., Rich, T.D., 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (USA). Conserv. Biol. 17, 607–615.

Landhäuser, S.L., Deshaies, D., Lieffers, V.J., 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. J. Biogeogr. 37, 68–76.

Manier, D.J., Laven, R.D., 2002. Changes in landscape patterns associated with the persistence of aspen (*Populus tremuloides* Michx.) on the western slope of the Rocky Mountains. Colorado. For. Ecol. Manage. 167, 263–284.

Martin, T.E., 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. Ecology 88, 367–380.

Martin, T.E., Maron, J.L., 2012. Climate impacts on bird and plant communities from altered animal–plant interactions. Nat. Clim. Change 2, 195–200.

Miller, R.F., Svejcar, T.J., West, N.E., 1994. Implications of livestock grazing in the intermountain sagebrush region: plant composition. In: Vavra, M., Laycock, W.A., Pieper, R.D. (Eds.), Ecological Implications of Livestock Herbivory in the West. Society for Range Management, Denver, CO, pp. 101–146.

National Research Council, 2002. Riparian Areas: Functions and Strategies for Management. National Academy Press, Washington, DC.

Olmsted, C.E., 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain National Park. In: Boyce, M.S., Hayden-Wing, L.D. (Eds.), North American Elk: Ecology, Behavior, and Management. University of Wyoming, Laramie, pp. 89–97.

Platts, W.S., 1991. Livestock grazing. In: Meehan, W.R. (Ed.). Influences of Forest and Rangeland Management on Salmonid Fisheries and their Habitats, American Fisheries Society, Special Publication 19, Bethesda, Maryland, pp. 389–423.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For. Ecol. Manage. 258, 2353–2364.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol. Conserv. 95, 361–370.

Rogers, P.C., Mittanck, C.M., 2013. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. J. Veg. Sci. 25, 457–469.

Rogers, P.C., Leffler, A.J., Ryel, R.J., 2010. Landscape assessment of a stable aspen community in southern Utah, USA. For. Ecol. Manage. 259, 487–495.

Rogers, P.C., Landhäuser, S.M., Pinno, D.B., Ryel, R.J., 2014. A functional framework for improved management of western North American aspen (*Populus tremuloides* Michx.). For. Sci. 60, 345–359.

Saab, V.A., Bock, C.E., Rich, T.D., Dobkin, D.S., 1995. Livestock grazing effects in western North America. In: Martin, T.E., Finch, D.M. (Eds.), Ecology and Management of Neotropical migratory birds. Oxford University Press, New York, pp. 311–353.

Seager, S.T., Eisenberg, C., St. Clair, S.B., 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. For. Ecol. Manage. 299, 81–90.

Shepperd, S.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), 2001. Sustaining Aspen in Western Landscapes: Symposium Proceedings, USDA Forest Service, RMRS-P-18, Fort Collins, Colorado.

Tewksbury, J.J., Black, A.E., Nur, N., Saab, V.A., Logan, B.D., Dobkin, D.S., 2002. Effects of anthropogenic fragmentation and livestock grazing on western riparian bird communities. Stud. Avian Biol. 25, 158–202.

Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Barchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. For. Ecol. Manage. 299, 35–51.

Zier, J.L., Baker, W.L., 2006. A century of vegetation change in the San Juan Mountains, Colorado: an analysis using repeat photography. For. Ecol. Manage. 228, 251–261.