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Mexican wolves, elk, and aspen in Arizona: Is there a trophic cascade?

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ABSTRACT

In 1998, Mexican gray wolves (*Canis lupus baileyi*) were introduced into the Blue Range Wolf Recovery Area (BRWRA) that spans adjacent portions of Arizona and New Mexico. In 2009 we selected three mixed-conifer sites on the Apache National Forest, within the BRWRA of east-central Arizona, to characterize long-term age structure of aspen (*Populus tremuloides*) and to check for the possible occurrence of a tri-trophic cascade involving Mexican wolves, Rocky Mountain elk (*Cervus elaphus nelsoni*), and aspen. These mixed-conifer sites included (a) a refugium site, (b) an old-growth site, and (c) a site thinned in 1991–1992. The refugium site was inaccessible to elk and cattle whereas the old-growth and thinned sites were accessible to elk, but not cattle. Age structure results indicated that aspen recruitment (i.e., the growth of sprouts/seedlings into tall saplings, poles, and eventually trees) at the refugium site had been ongoing over a period of many decades. In contrast, aspen recruitment at the old-growth and thinned sites decreased significantly ($p < 0.05$) during the two most recent decades when elk populations, as indexed by annual harvest levels, were relatively “high”. From 2000 to 2008, only 2.9 Mexican wolves per 1000 elk were present on the Apache National Forest compared to 9.3 western gray wolves (*Canis lupus occidentalis*) per 1000 elk in Yellowstone National Park where tri-trophic cascades involving wolves, elk, and aspen have been reported. The low number of Mexican wolves relative to their primary prey (elk) suggests that an ecologically effective density of wolves has not become established in east-central Arizona. Furthermore, the lack of recent aspen recruitment in stands accessible to elk indicates an absence, to date, of a tri-trophic cascade.

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1. Introduction

Aspen (*Populus tremuloides*), also known as quaking aspen or trembling aspen, is the most widely distributed deciduous tree species in North America and unusual in reproducing primarily by sprouts (ramets) from a parent root system (Fowells, 1965; Perala, 1990). Areas that support aspen in the western United States (US) commonly contain a variety of woody and herbaceous plants that provide critical habitat and food-web support to many wildlife species (DeByle and Winokur, 1985). Historically, aspen forests occupied nearly 3.9 million hectares in eight western states (Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming) but had declined 60% by the end of the 20th century (Bartos, 2001). At the southern end of aspen's range in the western US losses have been particularly severe with aspen declines of 96% and 88% in Arizona and New Mexico, respectively. Various factors can contribute to the loss of aspen including reduced fire frequency, conifer invasion, disease, a changing climate, intensive browsing by large herbivores, and others (DeByle and Winokur, 1985; Worrall et al., 2007).

The browsing of aspen stands by native large herbivores, such as elk (*Cervus elaphus*) and deer (*Odocoileus* spp.), has likely occurred over many thousands of years in the American West since the leaves and stems of young aspen plants are highly palatable to ungulates. Yet the capability of these stands to persist over long periods of time and to cover large areas indicates that ungulate herbivory may not have seriously limited aspen recruitment (growth of sprouts/seedlings into tall saplings, poles, and eventually trees). However, with the introduction of domestic livestock and reduced populations of large predators across large areas of the West during the late 1800s and early 1900s, followed by enlarged populations of wild ungulates during the latter half of the 20th century, browsing of aspen sprouts/seedlings had become an increasingly important factor affecting recruitment (Mueggler and Bartos, 1977; DeByle and Winokur, 1985; Kay, 1997; Kay and Bartos, 2000).

Recent studies in Yellowstone National Park, an area where domestic livestock grazing has not occurred, point to an additional factor that may contribute to the long-term demise of aspen—the collapse of a tri-trophic cascade involving wolves, elk, and aspen. Following the extirpation of western gray wolves (*Canis lupus occidentalis*) from Yellowstone nearly a century ago, increased browsing by Rocky Mountain elk (*Cervus elaphus nelsoni*) not only suppressed the recruitment of aspen in the park's northern winter ranges but also that of willows (*Salix* spp.), cottonwoods (*Popu-*

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lus spp.), and various species of shrubs (Ripple and Larsen, 2000; Kay, 2001a; Barmore, 2003; Ripple and Beschta, 2004a,b; Beschta, 2005). Increased elk herbivory and decreased aspen recruitment similarly occurred in the Canadian Rockies when wolf populations in Jasper, Yoho, and Kootenay National Parks of Alberta were suppressed during the mid-1900s (White et al., 1998; Beschta and Ripple, 2006). In Rocky Mountain National Park, where elk were reintroduced in the absence of wolves, intensive browsing by elk reduced aspen and willow recruitment (Hess, 1993; Zeigenfuss et al., 2002; Binkley, 2008). Unimpeded browsing by native large herbivores in the absence of apex predators is increasingly recognized as an important factor affecting the biodiversity and ecosystem services of native plant communities that comprise temperate and boreal ecosystems (Ripple et al., 2010).

During the winters of 1995–1996, gray wolves were reintroduced into Yellowstone National Park, thus completing the park's historical predator guild. Soon thereafter studies began observing behavioral responses of elk (e.g., vigilance, use of habitat) due to the presence of wolves (Laundré et al., 2001; Mao et al., 2005; Halofsky and Ripple, 2008a). Altered patterns of browsing and reduced elk densities following wolf reintroduction (White and Garrott, 2005) also appeared to explain the spatially patchy release (increased heights of young woody plants in various locations) currently underway for willow, aspen, and cottonwood in Yellowstone's northern winter ranges (Beyer et al., 2007; Ripple and Beschta, 2007; Halofsky and Ripple, 2008b; Beschta and Ripple, 2010). Similarly, aspen recruitment improved following recovery of wolf populations in Jasper National Park (Beschta and Ripple, 2006).

Like much of the American West, wolves in Arizona and New Mexico were heavily persecuted in the late 1800s and early 1900s. For example, in 1920 alone over 100 wolves were removed from these two states (Brown, 1983). Removals dropped to ~15 wolves/year in the 1930s and by the mid-1940s, or soon thereafter, wolves in Arizona and New Mexico had become functionally extirpated. However, in 1998 Mexican gray wolves (*C. lupus baileyi*) from a captive breeding program were introduced into east-central Arizona and west-central New Mexico, an area designated as the Blue Range Wolf Recovery Area (BRWRA). While these introductions occurred approximately 200 km north of the historical range of Mexican wolves (see Brown, 1983), the BRWRA was thought to have suitable habitat and sufficient prey for maintaining a population of Mexican wolves (USFWS, 1996).



Fig. 1. Location map of Apache National Forest in east-central Arizona. This national forest along with the Gila National Forest in west-central New Mexico comprise the Blue Range Wolf Recovery Area (BRWRA) for the Mexican wolf.

We undertook this study on the Apache National Forest (Fig. 1) where introduced Mexican wolves have been present for a decade. This national forest comprises the portion of the BRWRA that extends into east-central Arizona. It is also adjacent to the White Mountain Apache Reservation where wolves have become protected in recent years. Field reconnaissance of the Apache National Forest in the summer of 2008 indicated that aspen recruitment in recent decades has been generally absent across major portions of the Springerville and Alpine districts. Thus, our overall objective was to assess temporal patterns of aspen recruitment in mixed-conifer stands accessible to elk where we hypothesized that a tri-trophic cascade involving wolves–elk–aspen might again be occurring following the introduction of Mexican wolves, potentially contributing to improved aspen recruitment. The occurrence of such a trophic cascade would suggest recovery of an ecologically effective density of wolves (Soulé et al., 2003).

2. Study area

Our study area was located along the southern portion of the Springerville District, Apache National Forest, approximately 20 km west of Alpine, Arizona. Here, mixed-conifer forests contained varying proportions of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), blue spruce (*P. pungens*), white fir (*Abies concolor*), subalpine fir (*A. lasiocarpa*), limber pine (*Pinus flexilis*), and ponderosa pine (*P. ponderosa*). Aspen, a desired browse species for elk and deer, commonly occurs within these mixed-conifer stands.

Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougar (*Puma concolor*), gray wolves, Merriam elk (*C. elaphus merriami*), mule deer (*O. hemionus*), and Coues white-tailed deer (*O. virginianus couesi*) originally inhabited portions of the Mogollon Rim and White Mountains of east-central Arizona (Hoffmeister, 1986). However, the influx of Euro-Americans into this area eventually resulted in the regional extirpation of grizzly bears and wolves as well as extinction of Merriam elk. Rocky Mountain elk from Yellowstone were introduced into east-central Arizona in 1913 and, as previously indicated, Mexican wolves in 1998. The Mexican wolf is the southernmost and smallest subspecies of gray wolf in North America (Mech and Boitani, 2003).

Three aspen sites, at an elevation of ~2700 m, were chosen to represent different treatments to forest stands (Fig. 2). They included (a) a “refugium site” that was inaccessible to wild and domestic ungulates because of topographic barriers (i.e., broken rock, cliff faces), (b) an “old-growth site” that had not experienced logging, and (c) a “thinned site” at which a partial overstory removal of conifers, along with the piling and burning of slash, occurred in 1991–1992. While both the old-growth and thinned sites were easily accessible to wild ungulates, neither had been grazed by domestic livestock. The old-growth site had been fenced to exclude cattle and the thinned site was sufficiently far from the nearest meadow that cattle did not forage at this site.

3. Methods

To help assess potential environmental or land-use factors within the general vicinity of our study sites that might affect aspen recruitment, we assembled annual records of snowpack accumulation, grazing use, timber harvest, and big game harvest within the Apache National Forest for the period 1970–2008. To characterize annual snowpack amounts, we calculated the average January 15 through April 1 snowpack water equivalent for the Beaver Head, Coronado Trail, Hannagan Meadow, Maverick Fork, and Nutrioso snow courses. Domestic livestock grazing was summarized in animal unit months (AUMs, where one AUM represents the foraging

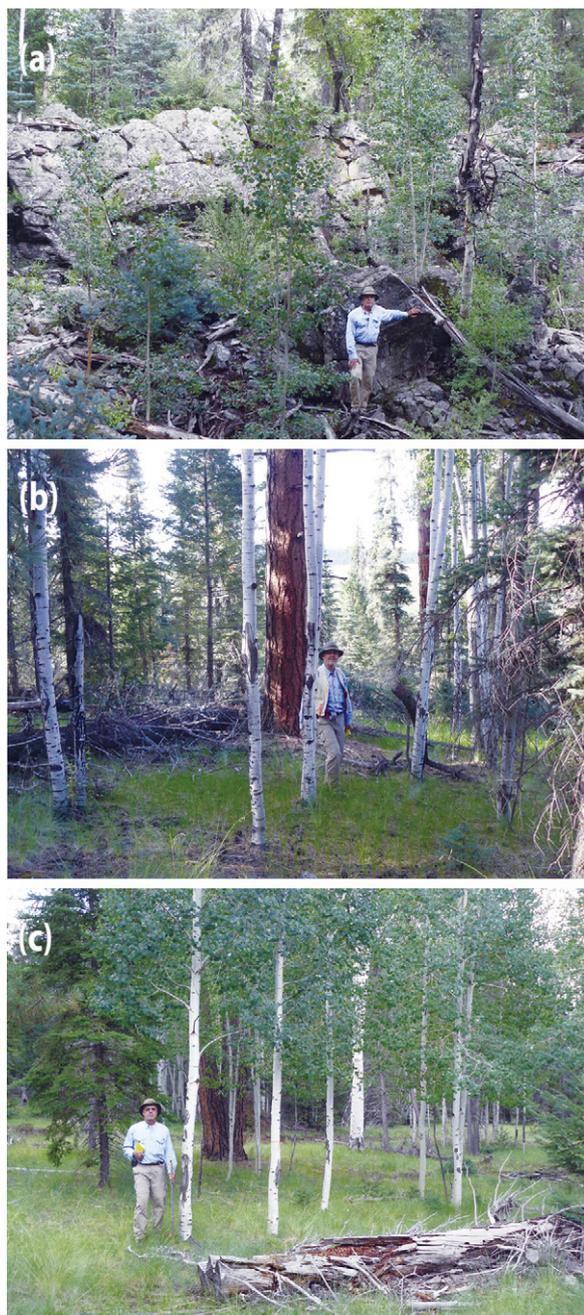


Fig. 2. (a) Refugium, (b) old-growth, and (c) thinned sites (July 2009 photographs). Note the presence of young seedlings/sprouts within the refugium site (where rocky ground reduces likelihood of access by elk) and the absence of seedlings/sprouts within the old-growth and thinned sites (both accessible to elk).

needs of a cow and calf over a period of one month) for the Udall and Big Lake Allotments; these allotments occur along the southern end of the Springerville District. Timber harvest volumes (board-foot/acre) were compiled for the adjacent Springerville and Alpine Districts; volumes were converted to m^3 using a conversion factor of 0.0024 bd-ft/m^3 (Manfredo and Sanders, 2008). Big game harvest records for Arizona game management unit 1 (which covers essentially all of the Springerville District and the northern portion of the Alpine District) were used to index the general abundance of elk, mule deer, and Coues white-tailed deer, as well as temporal trends in their populations (AGFD, 2009).

At each study site we measured diameter at breast height (DBH, cm) of aspen having a $DBH \geq 1$ cm. Because the refugium site com-

prised an area of only 0.1 ha, we sampled aspen within the entire site. However, at the old-growth (>5.0 ha) and thinned (~ 2.5 ha) sites we utilized belt transects to delineate areas within which aspen ≥ 1 cm in DBH were sampled. At the old-growth site, two parallel belt transects (each $25 \text{ m} \times 200 \text{ m}$, with a random start and 30-m offset between transects) were used; at the thinned site, two parallel belt transects (one $25 \text{ m} \times 200 \text{ m}$ and the second $25 \text{ m} \times 75 \text{ m}$, with a random start and 30-m offset) were used.

At each site we measured canopy cover (hemispherical densitometer), basal area ($4.6 \text{ m}^2/\text{ha}$ per stem basal area factor [BAF] wedge), and the height and density of aspen sprouts/seedlings within a circular 3-m radius plot (28.3 m^2). At the refugium site we undertook these measurements at two plot centers, 25 m apart, located near the center of the site. For the old-growth and thinned sites we undertook the same set of measurements at 25-m intervals along the centerline of each belt transect. We also measured the current annual growth (CAG, cm) of young aspen, not visibly affected by shepherd's crook (*Venturia* spp.), to illustrate the general productivity of each site. Shepherd's crook, a disease that causes a characteristic blackening and bending of young aspen stems, was relatively common on sprouts/seedlings at all three sites. Because these diseased stems eventually die and break-off in a manner that is similar to that of the stem having been browsed, we were unable to utilize plant architecture measurements for assessing browsing patterns on young aspen (e.g., Ripple and Beschta, 2007). All plant measurements were conducted in late July of 2009.

We selected 33 trees at the old-growth site and 30 trees at the thinned site from which increment cores were obtained. The probability of selection was based on the frequency distribution of DBHs at each site. Cores were placed in plastic straws, sealed, and transported to Oregon State University where they were subsequently dried and sanded. Annual growth rings were counted with a $10\times$ binocular microscope to establish the age (at breast height) represented by each core. From these ring counts, regression analysis was used to establish a relationship between tree age at breast height (yr) and DBH. We also obtained cross-sections (wafers) at ground level and at breast height (1.4 m) from three aspen saplings near the refugium site and determined the number of years required for them to attain breast height. The estimated age at breast height (from regression analysis) and the number of years to attain breast height were jointly utilized to estimate the establishment date of each measured aspen.

A histogram of stem frequency vs. establishment date was developed for each site to represent aspen age structure, by decade, over the period 1900–2008. Since annual estimates of elk populations were not available for this period we used annual elk harvest data to index general population trends (Toweill and Thomas, 2002). Based on harvest data we considered elk abundance to be “low” prior to 1990 and “high” after 1990. At each site we fitted an exponential regression through the age structure data from 1900 to 1989 (the period of “low” elk abundance) and used this relationship to assess if significant changes ($p < 0.05$) in aspen recruitment occurred after 1990 (“high” elk abundance).

In 2005, an elk enclosure (elevation 2500 m) was constructed approximately 1.2 km north of the Alpine, Arizona, on the city watershed. Along the southern edge of the enclosure, aspen sprouts were occurring both inside and outside of the fence. We undertook plant architecture measurements (Beschta and Ripple, 2007) of young aspen plants inside and outside of the fence to identify their relative patterns of height growth following construction of the enclosure.

Lastly, we utilized a ratio of predator/prey (wolves per 1000 elk) to index the potential ecological effectiveness of the Mexican wolf population in east-central Arizona. We calculated (a) the number of Mexican wolves per 1000 elk on the Apache National Forest (wolf and elk population estimates were obtained from the Mex-

ican Wolf Recovery Project, Alpine, Arizona) and (b) the number of gray wolves per 1000 elk in the northern range of Yellowstone National Park (Yellowstone National Park, Mammoth Hot Springs, Wyoming). These ratios were calculated annually from 1998 to 2008 for the Apache National Forest and from 1995 to 2008 for Yellowstone.

4. Results

Summaries of snowpack water equivalent, grazing use, timber harvest, and big game harvest on the Apache National Forest since 1970 indicated variability in temporal patterns of climate and land use (Fig. 3). Although snowpack conditions fluctuated considerably from year-to-year, since about 1995 snowpack water equivalents have been relatively low. For example, in 10 of the last 14 years water equivalents have been less than the long-term average of 11.0 cm (Fig. 3a) indicating that forest stands on the Apache National Forest have recently been experiencing relatively shallow winter snowpacks. Domestic grazing levels showed a slow increase in AUMs from 1970 to 1990 after which they decreased to less than half of their former levels (Fig. 3b). Timber harvests declined precipitously after the late 1980s and since 1995 have remained relatively low (Fig. 3c). Big game harvest data suggested that mule deer and Coues white-tailed deer on the forest have generally been less prevalent than elk, particularly in recent years (Fig. 3d). Furthermore, while mule deer harvests have been trending lower since the mid-1980s, elk harvests increased from the early 1980s until the mid-1990s, after which they remained relatively high.

The overstory canopy cover at our study sites ranged between 41 and 65% (Table 1). The old-growth site had the greatest basal area of conifer and aspen (10.5 and 19.6 m²/ha, respectively) while the refugium site had the lowest basal area in these categories (5.7 and 4.6 m²/ha, respectively). The thinned site had the highest densities of aspen sprouts/seedlings, perhaps reflecting the effects of overstory conifer removal in the early 1990s (Table 2). The CAG of sprouts/seedlings was greatest on the thinned site (49 cm) and least for the refugium site (35 cm).

Based on results from the 63 aspen increment cores, linear regression indicated the following relationship: tree age at breast height (yr) = 2.49 DBH ($r^2 = 0.85, p < 0.01$). Cross-sections obtained at the base and breast height of three aspen saplings indicated they had attained breast height within three years. Thus, the establishment date of each sampled aspen was calculated as: establishment date (yr) = 2009 - [(2.49 DBH) + 3].

At the refugium site, aspen age structure indicated recruitment had been ongoing since about 1940 and that a large number of stems were associated with younger age classes (Fig. 4a). In particular, recruitment had been relatively high during the last two decades. This age structure pattern is characteristic of an unevenaged forest where recruitment is an ongoing process. The old-growth (Fig. 4b) and thinned (Fig. 4c) sites also showed a

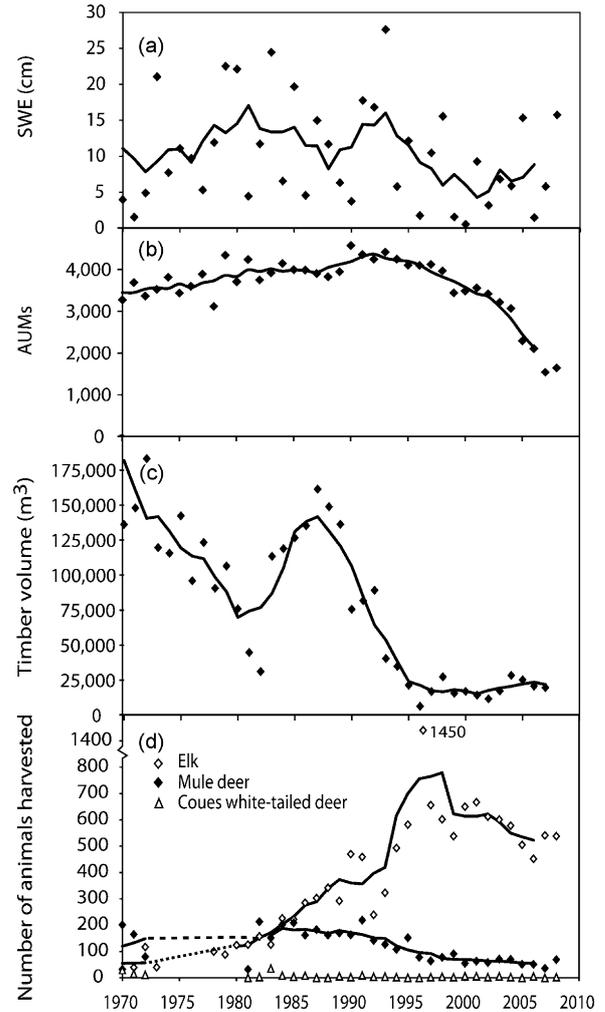


Fig. 3. Annual (a) snowpack water equivalent (SWE, cm) averaged from January 15 to April 1 for the Beaver Head, Coronado Trail, Hannagan Meadow, Maverick Fork, and Nutrioso snow courses, (b) grazing use in animal unit months (AUMs) for the Udall and Big Lake grazing allotments, Springerville District, (c) timber harvest volume (m³) on Alpine and Springerville Districts, and (d) harvest of elk, mule deer, and Coues white-tailed deer in game management unit 1, Apache National Forest. Solid lines are five-year moving averages. Data sources: (a) Natural Resources Conservation Service; (b) and (c) US Forest Service, Apache National Forest; and (d) Arizona Game and Fish Department.

Table 2

Average density, height, and current annual growth (CAG) of aspen <1.5 m in height at each study site (standard deviation in brackets).

| Study site | Density (#/ha) | Height (cm) | | CAG (cm) |
|------------|----------------|------------------------------|----------------------------|----------|
| | | Conifer (m ² /ha) | Aspen (m ² /ha) | |
| Refugium | 104 | 97 [27] | 4.6 [0.0] | 35 [15] |
| Old-growth | 1277 | 40 [25] | 19.6 [9.3] | 44 [10] |
| Thinned | 1905 | 22 [11] | 6.4 [4.8] | 49 [16] |

Table 1

General terrain and forest conditions at each study site (standard deviation in brackets).

| Study site | Elevation (m) | Aspect and slope (%) | n ^a | Canopy Cover ^b (%) | Basal area ^c | | |
|------------|---------------|----------------------|----------------|-------------------------------|------------------------------|----------------------------|----------------------------|
| | | | | | Conifer (m ² /ha) | Aspen (m ² /ha) | Total (m ² /ha) |
| Refugium | 2700 | S, 0–20% | 2 | 41 [20] | 5.7 [1.6] | 4.6 [0.0] | 10.3 [1.6] |
| Old-growth | 2675 | N, 20–30% | 18 | 65 [18] | 10.5 [9.0] | 19.6 [9.3] | 30.1 [10.4] |
| Thinned | 2715 | S, 0–10% | 13 | 54 [19] | 9.9 [11.7] | 6.4 [4.8] | 16.2 [13.7] |

Latitude and longitude of each study site: refugium site (33°51'26"N, 109°21'33"W), old-growth site (33°54'32"N, 109°21'12"W), and thinned site (33°51'46"N, 109°21'54"W).

^a n, number of plots for canopy cover and basal area measurements.

^b Canopy cover measured with a hemispherical densitometer.

^c Basal area measured with a 4.6 m²/ha basal area factor (BAF) wedge.

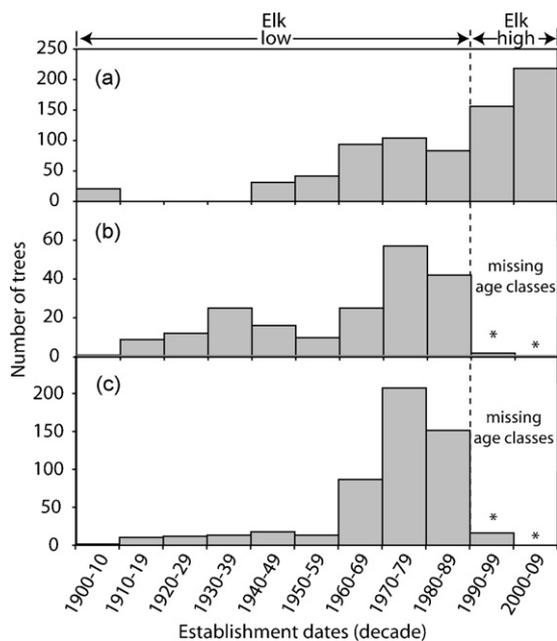


Fig. 4. Age structures of aspen (i.e., frequency of aspen by decade of establishment) from 1900 to 2008 for the (a) refugium, (b) old-growth, and (c) thinned sites (vertical scales vary). “Low elk” and “high elk” denote general elk abundance based historical harvest data. An asterisk (*) denotes recruitment significantly less ($p < 0.05$) than expected (see text).

pattern of nearly continuous recruitment from 1900 to 1989, during the period when annual elk harvests were relatively “low”. However, a significant decrease in recruitment ($p < 0.05$) occurred during the two most recent decades when annual elk harvests were relatively “high” (Fig. 3d).

Outside of the elk enclosure near Alpine, aspen sprouts remained suppressed by intensive elk browsing and unable to grow above a height of 50 cm in recent years. In contrast, aspen sprouts inside the enclosure and which averaged only 34 cm in height in 2005 had attained an average height of 241 cm in 2009, an annual height increase of 52 cm/yr (Fig. 5).

Over the last eight years (2001–2008 inclusive), an average of 2.9 Mexican wolves per 1000 elk (standard deviation = 0.8) have been present on the Apache National Forest. This ratio is significantly



Fig. 5. Fenceline view of elk enclosure 1.5 km north of Alpine, Arizona. Whereas aspen sprouts outside the enclosure (to the left of the fence) were sparse, heavily browsed, and averaged only 18 cm in height, those inside had attained average heights of 2–3 m since construction of the fence in 2005 (August 2008 photograph). Note also elk “barking” of aspen stems outside the enclosure that can increase the susceptibility of these trees to disease.

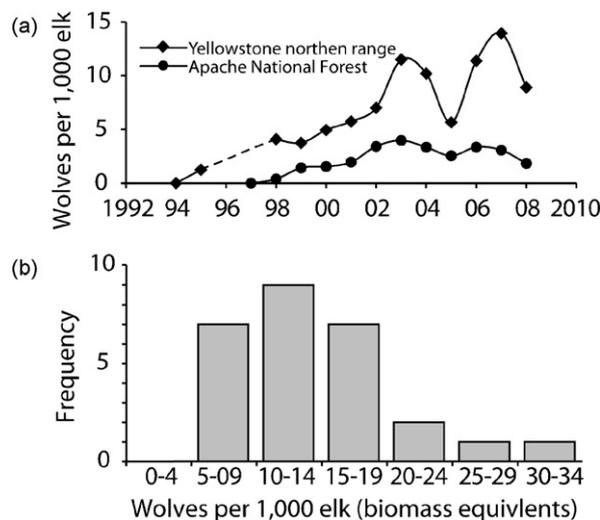


Fig. 6. (a) Number of wolves per 1000 elk for the Apache Forest in Arizona and the northern range of Yellowstone National Park and (b) relative frequency distribution of number of wolves per 1000 elk (biomass equivalents) for wolf populations in North America (see biomass conversions in Table 6.2, Fuller et al., 2003).

less ($p < 0.05$, t -test, unequal variances) than the 9.3 gray wolves per 1,000 elk (standard deviation = 3.0) that occurred in northern Yellowstone over the last eight years (Fig. 6a). Furthermore, 2.9 Mexican wolves per 1000 elk is a much lower ratio than has been reported for gray wolves in other portions of North America (Fig. 6b).

5. Discussion

Temporal patterns of several environmental and land-use variables specific to the Apache National Forest, variables that might directly or indirectly affect patterns of aspen recruitment, are summarized in Fig. 3. Relatively shallow snowpacks occurred during the most recent one and one-half decades, thus indicating reduced springtime and early summer soil moisture for plant communities. However, mountainous areas of east-central Arizona, like much of Arizona and New Mexico, normally experience a period of summertime thunderstorm precipitation. From 1990 to 2008, total July and August precipitation averaged 21.6 cm annually at Alpine, Arizona, or approximately 9% higher than the long-term average for the period 1970–2008.

The declines in annual snowpack water equivalent for snow courses on the Apache National Forest over recent decades are symptomatic of reduced winter snowpacks observed in other mountainous areas of the western US during this same period (Mote, 2006). While declining snowpacks may have implications for plant communities and patterns of streamflow, they may also influence elk populations. For example, Creel and Creel (2009) found that the steady growth of Montana elk populations in recent decades was inversely correlated with declining snowpacks. When they coupled their analysis with regional predictions of global climate change over the next 20–50 years, results indicated increased elk population growth rates were likely if snowpack amounts continue to decline as predicted. However, it is not known whether such results can be applied to Arizona where contemporary mountain snowpacks are often relatively shallow and thus may not limit elk populations like the deeper snowpacks of Montana’s mountains.

Range managers have long known that intensive annual browsing by domestic livestock can effectively curtail the recruitment of aspen and other palatable woody species over extended periods (Sampson, 1919; Houston, 1954). Relatively recently Kay (2001b) assessed the long-term status and trends of aspen stands across

central Nevada and found a widespread absence of recruitment extending back many decades. This lack of recruitment was not associated with climatic variation, fire suppression, forest succession, or browsing by wild ungulates, but instead was attributed to annual browsing by domestic cattle and/or sheep. During our 2008 field reconnaissance of aspen stands, a paucity of aspen recruitment along the edges of meadows utilized by cattle was observed in the Udall and Big Lake allotments. These reductions in recruitment appeared to have begun more than half a century ago, long before elk numbers had begun to increase.

The harvesting of overstory trees can greatly increase the amount of light available to the forest floor, thus increasing the above-ground biomass of herbaceous and browse species. Increased productivity of understory plants can provide additional food-web support for wild ungulates (Patten, 1974), particularly in forest stands not utilized by livestock. Thus, the relatively high levels of forest harvesting in the 1970s and 1980s may have contributed to the increase in elk abundance (as indicated by increasing harvest levels of elk) that occurred from the early 1980s to the mid-1990s (Fig. 3d). However, Coues white-tailed deer and mule deer harvests did not similarly benefit. Coues white-tailed deer harvests have remained extremely low from 1970 to the present and mule deer harvests have generally been in decline since the 1970s. The extent to which inter-specific competition may be a factor in the opposing trends in elk and mule deer harvests over the last three decades is not known, but elk are generally able to out-compete mule deer for limited forage resources (Murie, 1951).

Increased availability of light at the forest floor following timber harvesting can also trigger an increase in the density and vigor of aspen sprouts (DeByle and Winokur, 1985). The thinned site had the greatest density of aspen reproduction (1905 stems/ha) and the largest CAG (49 cm) of the three sites, perhaps as a consequence of thinning that occurred at this site in the early 1990s. Thus, the significant downturn in aspen recruitment ($p < 0.05$) at the thinned site (Fig. 4c) since 1990 represented an unexpected outcome of thinning. The significant downturn in aspen recruitment ($p < 0.05$) for the old-growth site since 1990 was similarly unexpected since there were numerous canopy openings where mature conifers had died or blown down in recent decades. These results indicate that high levels of elk herbivory now appear to be preventing aspen recruitment in mixed conifer stands not utilized by livestock. They further suggest that silvicultural treatments which would normally result in increased aspen recruitment are unlikely to be effective in areas where elk herbivory is relatively high.

The number of aspen stems attaining breast height during the last two decades was relatively high at the refugium site where aspen recruitment has been ongoing over many decades. These high levels of aspen recruitment indicated that diminished snowpacks, year-to-year fluctuations in summertime precipitation, or other environmental factors were not preventing recruitment. Continued height growth in recent years of young aspen within the elk enclosure near Alpine, Arizona similarly indicated that climatic patterns have not limited their growth. In contrast, significantly decreased aspen recruitment ($p < 0.05$) occurred during the last two decades at the old-growth and the thinned sites, during a period of relatively high elk abundance.

The general pattern of elk harvests reported for the Apache National Forest reflects a similar trend in elk harvest that has occurred on a state-wide basis. Approximately 1,000 elk were harvested across Arizona in 1970 with harvest levels increasing to 10,600–13,700 elk in the 1990s (AGFD, 2009). As of 2005, there were an estimated 35,000 Rocky Mountain elk in Arizona. On the Coconino National Forest in north-central Arizona, Fairweather and Tkacz (1999) found that browsing impacts to aspen sprouts/seedlings from cattle, along with elk and deer, were a common occurrence in aspen stands. They further observed that

young aspen stems were often “browsed all the way to the ground, year after year, until the resources [root reserves] are depleted and they stop sprouting altogether.” Browsing of aspen regeneration from large herbivores has been a major concern since the 1960s for the Coconino National Forest. Intensive ungulate herbivory was so prevalent that permanent exclusion fences were required to insure successful aspen recruitment following silvicultural treatments or fire (Bailey and Whitham, 2003; Stritar et al., 2010).

Although either elk or deer can damage aspen by persistently browsing new sprouts and by rubbing saplings or trees with antlers, DeByle and Winokur (1985) indicate that elk generally have a greater impact because: (1) elk are larger thus requiring more forage per animal, (2) elk are able to browse plants at higher levels, (3) elk chew the bark of aspen trees, and (4) elk may remain in aspen forests through most winters whereas snowpack depths usually force deer to lower elevations. Both barking and rubbing have been associated with increasing the susceptibility of aspen to the entry of pathogenic fungi which, in turn, can cause stem cankers and decay that contribute to the death of trees.

Browsing studies in the western US have often utilized aspen to assess temporal patterns of herbivory because it is a long-lived species and aspen sprouts/seedlings are highly palatable to ungulates. When combined with coring measurements that help establish the age structure of overstory aspen (or other tree species with palatable sprouts/seedlings), such approaches can provide important insights regarding historical browsing patterns associated with large herbivores (Beschta and Ripple, 2009). Although various studies have often confirmed that aspen in the western US is in serious decline (Bartos, 2001; Rehfeldt et al., 2009), little research has addressed the long-term impacts of increased herbivory on other woody browse or herbaceous species associated with aspen stands. Thus, there is a high need for public land managers to understand how historical and contemporary herbivory has not only affected the age structure of existing aspen stands, but also how it may have altered understory plant communities. While ungulate exclosures have various limitations (Sarr, 2002), they can quickly provide local information regarding the relative effects of large herbivores on plant communities and can be constructed (e.g., three-way exclosures) to help discern differences between the effects of wild vs. domestic ungulates.

Rocky Mountain elk, introduced following the extinction of Merriam elk, have been able to attain a relatively large population in Arizona in recent decades. The results of this study suggest that if contemporary elk population levels on the Apache National Forest are maintained into the future, a lack of aspen recruitment may continue even where aspen stands are inaccessible to livestock. In other areas of the western US where domestic livestock grazing has been absent, increased browsing by wild ungulates following the loss of large predators was similarly found to reduce/terminate the recruitment of palatable woody plants (Beschta and Ripple, 2009).

The introduction of Mexican wolves into the BMWRA was undertaken in an attempt to establish a sustainable population of this apex predator (USFWS, 1996). However, wolf numbers have no longer continued to increase in recent years and our results show that their presence has been ineffective at reversing declines in aspen recruitment within mixed-conifer stands, thus indicating this apex predator have not sufficiently affected elk behavior or populations to initiate a trophic cascade. This result contrasts with the Yellowstone experience where decreased browsing pressure and a spatially patchy increase in the heights of young aspen, cottonwood, and willow growth were measured within a few years following the reintroduction of gray wolves. We observed only a few locations on the Springerville and Alpine Districts in the general vicinity of our field sites were young aspen were beginning to increase in height in recent years, possibly indicating wolves were causing elk to avoid high-risk sites. However, the limited size of

these sites, the occurrence of recent fires and reduced grazing pressure in surrounding areas, both of which increase forage availability to wild ungulates, as well as the general occurrence of shepherd's crook (which precluded attempts to assess recent browsing history) prevented us from drawing any conclusions from these sites regarding a possible trophic cascade.

Soulé et al. (2003) indicate an ecologically effective density of highly interactive species (such as wolves in terrestrial ecosystems) is one that would maintain critical ecological interactions and help ensure against ecosystem degradation. With regard to a tri-trophic cascade involving wolves, elk, and aspen, this would be a predator density sufficient to mediate the behavior and/or density of native herbivores thus regulating potential impacts to plant communities. The relatively low ratio of Mexican wolves per 1000 elk on the Apache National Forest, in comparison to gray wolves in northern Yellowstone (Fig. 6a) and other areas of north America (Fig. 6b), appears to indicate that Mexican wolves have not achieved an ecologically effective density in Arizona. Why Mexican wolf populations in Arizona, as well as the New Mexico portion of the BMWRA, have not increased in recent years is a perplexing issue for wolf recovery biologists and administrators since elk, the primary prey of Mexican wolves in the BMWRA, remain plentiful. Part of the problem may lie with the prey base for Mexican wolves. For example, Rocky Mountain elk, the principal prey of Mexican wolves in the BMWRA, are considerably larger than Coues white-tailed deer which historically represented the primary prey of Mexican wolves in their historical range (Leopold, 1959; Brown, 1983). Additional impediments to the growth of the Mexican wolf population likely include human-caused wolf mortality and other types of management disruptions (Povilitis et al., 2006).

In the western US, the uncoupling of a tri-trophic cascades following the extirpation or displacement of large predators has been found across an array of biomes (Beschta and Ripple, 2009). For temperate and boreal forest ecosystems from around the world, there are additional examples of where tri-trophic cascades have become uncoupled with the loss of a large predator or, conversely, where tri-trophic cascades continue to exist or have become re-established with the reintroduction or recovery of a large predator (Jedrzejewska and Jedrzejewski, 1998; Ripple et al., 2010). Improving our understanding of the role of large predators within terrestrial ecosystems represents a major challenge to the scientific community. Allowing large predators to persist or reoccupy former habitats so that their ecological imprint can occur may be perhaps an even larger challenge to society.

6. Conclusions

Ongoing fluctuations and trends in climate do not appear to be the cause of reduced aspen recruitment in mixed-conifer forests in east-central Arizona. Where ungulate herbivory had been excluded (i.e., the refugium site and the ungulate enclosure near Alpine), young aspen sprouts/seedlings were able to grow taller regardless of climatic patterns. Instead, our results indicate that reduced aspen recruitment since the 1990s in mixed-conifer stands not accessible to livestock was likely due to increased elk herbivory. Thus, there is a need for additional assessments of the aspen age structure in stands across Arizona, as well as elsewhere in the western US, to determine the relative importance of wild vs. domestic ungulates in causing downturns in aspen recruitment. Such information would allow land managers to make more informed decisions regarding causes and potential solutions whenever a lack of aspen recruitment is encountered. Although Mexican wolves were introduced into the BMWRA in the late 1990s, they appear to not yet have attained an ecologically effective density as we were unable to document a trophic cascade (i.e., improved aspen recruitment). Unless

wolf densities increase, it is possible that the potential ecological benefits of these apex predators in the mixed-conifer forests of east-central Arizona will not be achieved.

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