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Aspen (*Populus tremuloides*) stand dynamics and understory plant community changes over 46 years near Crested Butte, Colorado, USA

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ABSTRACT

Aspen stands in the Rocky Mountains form especially productive and diverse plant understory communities. However, little is known about canopy–understory relationships or understory dynamics, especially in light of widespread aspen decline. The purpose of our research was to assess recent aspen plant community dynamics by resampling 19 sites sampled in 1964 and 1994 near Crested Butte, Colorado. In 2010, we replicated previous sampling methods to measure canopy structure and understory composition at each site.

In contrast with the conclusions of previous work in the study area, sampled aspen stands did not exhibit long-term stability, nor were they succeeding to conifers. Over the 46-year sample period, live aspen density and basal area both decreased significantly (3151–1605 stems ha^{-1}; 39.2–33.7 m^2 ha^{-1}), with more pronounced decreases over the most recent sampling interval, 1994–2010. These changes appear linked to natural patterns of stand maturation, but may also have been enhanced by recent, drought-triggered mortality, as well as constraints on aspen regeneration imposed by elk and livestock. A striking decrease in the cover and frequency of fireweed (*Chamerion angustifolium*) was consistent with expectations of aging stands initiated by historic fire, and the expansion of Kentucky bluegrass (*Poa pratensis*) indicated strong effects of ungulate herbivory.

Recent overstory losses had little effect on understory communities, which were dominated by a suite of large perennial herbs that showed little change over the sampling interval, including Fendler's meadowrue (*Thalictrum fendleri*), oshá (*Ligusticum porteri*), elk and dryspike sedge (*Carex geyeri* and *C. siccata*), and blue wildrye (*Elymus glaucus*). Understory community composition was not closely related to current stand conditions or light levels, but was linked with regional elevational and geographic gradients and historic (1994) stand structure.

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1. Introduction

Aspen (*Populus tremuloides*) stands in the Rocky Mountains foster exceptionally rich and productive plant understories, yet little is known about the responses of these understory communities to recent, extensive canopy mortality (Anderegg et al., 2012). Aspen is the only deciduous tree species to develop extensive upland forests in this region, and creates a diffuse understory light environment (Chen et al., 1997) intermediate between the open meadows and the densely shaded conifer forests of this region. Because aspen leaves flutter or "quake," the light environment beneath their canopy is unusually evenly distributed (Roden and Pearcy, 1993) and supports particularly lush and diverse understory plant assemblages (Ramaley, 1927; Langenheim, 1962; Mueggler, 1985, 1988; Peet, 1981).

Throughout much of its range, aspen is an early-successional or "seral" tree species that achieves rapid post-fire dominance due to prolific resprouting and fast growth, but within a generation yields to more shade-tolerant conifers (Peet, 1981; Bartos, 2001). However, under some conditions, particularly in Utah and western Colorado, extensive stands of aspen appear to form a quasi-permanent, "stable" or "climax" forest type (Langenheim, 1962; Peet, 1981; Mueggler, 1987; Bartos, 2001; Kulakowski et al., 2004; Kurzel et al., 2007; Rogers et al., 2010). Such stands are characterized by a multi-layered aspen canopy, continuous or gap-phase regeneration from sucker shoots, and little or no conifer regeneration (Mueggler, 1987; Kurzel et al., 2007). The degree to which such aspen-dominated landscapes are indeed stable and persistent has historically been a question of lively debate (e.g., Sampson, 1916; Fetherolf, 1917; Daubenmire, 1943; Langenheim, 1962). Near Crested Butte, Colorado, Langenheim (1962) determined that aspen stands were stable, and did not succeed to spruce-fir forests over time. Conversely, working in the same area, Morgan (1969)

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concluded that aspen was indeed successional to a spruce-fir (*Picea engelmannii* and *Abies lasiocarpa*) forest type. Three decades later, Crawford et al. (1998) resurveyed Morgan's sample sites and reversed his conclusions, determining that the aspen-dominated forests around Crested Butte were persistent; however, these authors also noted that over centuries some aspen stands on N-facing slopes were likely to be replaced by spruce and fir.

Aspen stands have shown substantial recent decreases across the western US (Bartos, 2001; Worrall et al., 2008; Rogers et al., 2010), with potentially cascading effects throughout the ecological communities that aspen forms. Rapid, synchronous mortality of aspen clones in Colorado over the last decade (termed sudden aspen decline, or SAD) appears closely tied to recent high temperatures and drought (Rehfeldt et al., 2009; Worrall et al., 2008, 2010, 2013), and bioclimate models predict extensive future losses of aspen forests (Rehfeldt et al., 2009; Worrall et al., 2013). However, prior to the onset of SAD, gradual, chronic deterioration of many aspen stands had been widely noted, and attributed largely to shifting disturbance regimes rather than climate (Loope and Gruell, 1972; Schier, 1975; Romme et al., 1995; Ripple and Larson, 2000; Bartos, 2001; Kaye et al., 2005). Stand-level replacement of aspen in many cases may result from succession to shade-tolerant conifers in the absence of fire (Bartos, 2001). In Colorado, many aspen forests were initiated by stand-replacing fires associated with the mining boom and influx of settlers during the late 1800s (Kulakowski et al., 2004). As a consequence, extensive landscapes are dominated by relatively old (>100 years) trees, and in the absence of stand-replacing disturbance the replacement of these stands by conifers would not be unexpected. However, the long-term deterioration of stable, persistent aspen communities, in which aspen mortality is not balanced by recruitment, may have other causes, including intrinsic constraints on regeneration from root suckers (Schier, 1975; Mueggler, 1989), heavy elk or livestock use (Romme et al., 1995; Baker et al., 1997; Ripple and Larson, 2000; Kaye et al., 2005), and/or climatic factors (e.g., Hogg et al., 2002; Worrall et al., 2013).

Historic, long-term datasets provide the best tool available to measure changes in forest community composition (e.g., Rogers et al., 2008) and dynamics (e.g., van Mantgem et al., 2009). The purpose of our research was to assess relationships between aspen forest overstory and understory community changes by resampling 19 aspen stands originally surveyed in 1964 (Morgan, 1965, 1969) and 1994 (Crawford et al., 1998) in the Crested Butte area. Summary understory data from Morgan (1965) and the spatially explicit understory data of Crawford et al. (1998) provided a rare opportunity to assess recent changes in aspen understory plant communities. Successional shifts towards evergreen conifers would be expected to lead to decreases in light availability, understory productivity, and diversity, and drive a shift towards shade-tolerant understory species. Stam et al. (2008) reported shifts in aspen understory community composition and declining productivity even at very low (10–20%) levels of conifer encroachment. However, aspen canopy loss without replacement by conifers would be expected to increase light levels and drive shifts towards shade-intolerant species typical of more open environments. Anderegg et al. (2012) reported increased shrub cover in declining aspen stands in the San Juan mountains of southwestern Colorado. We examined these questions through comparisons of historic and current aspen stand structure and understory composition. Specifically, the objectives of our study were to:

(1) Evaluate changes in forest overstory structure and composition 1994–2010, and contrast with observed changes 1964–1994.
(2) Assess changes in aspen understory plant community composition 1994–2010.
(3) Examine the relationships between overstory structure (stand density, basal area, and canopy cover) and understory composition, and the relationships between changes in both.

2. Methods

2.1. Study area

We sampled 19 aspen stands originally surveyed in 1964 (Morgan 1965, 1969) and resurveyed in 1994 (Crawford et al., 1998) during July and August 2010. The study area spans approximately 20 km north–south and 35 km east–west across the West Elk and Elk mountain ranges in the headwaters of the North Fork (Anthracite Creek) and the Gunnison River (East River and Cement Creek), near the towns of Gothic, Crested Butte, and Crested Butte South, Colorado. Regionally, the climate is characterized as continental, but with temperature and precipitation largely influenced by elevation and topography. Study site elevations ranged from 2710 to 3170 m; this 460-m elevational spread suggests differences of 3 °C (given an average adiabatic lapse rate of 6.4 °C/km) in mean temperatures and further differences in precipitation. The west side of the study area also receives substantially more precipitation than the east due to the rain shadow effect of the West Elk and Elk mountains. The mean annual temperature at the nearest long-term climate station in Crested Butte is 1.5 °C (elevation 2710 m; period of record 1909–2006; WRCC, 2012). Mean annual temperature during survey years did not vary substantially from this long term average, though it was slightly cooler in the more recent sampling years: 2.2 °C in 1964, 0.8 °C in 1994, and 0.8 °C in 2010. Mean annual precipitation in Crested Butte is 599 mm. All study years were slightly drier than normal, particularly during more recent surveys; precipitation totaled 585 mm in the 1964 water year (October 1963–September 1964), 515 mm in 1994, and 515 mm in 2010.

2.2. Field methods

Originally, 25 stands were sampled in 1964 by Michael Morgan, a master's student working at the Rocky Mountain Biological Laboratory in Gothic (Morgan, 1965, 1969). Morgan did not explicitly state the criteria he used to determine sample locations, but noted that he sought to represent all the "aspect conditions" in which aspen occurred in the study area. In 1994, with the help of Michael Morgan, 19 of these stands (Fig. 1) were located and resampled by Jeremy Crawford, Seth McNulty, and John Sowell; 6 stands were not found (Crawford et al., 1998). To locate our sampling sites, we used a combination of UTMs, photos, and site locations and descriptions from Crawford et al.'s original field data sheets, archived at Western State Colorado University (WSCU). Generally, these 19 stands were easily found; in many cases, individual trees or other landscape features could be identified from photos taken in 1994. However, we did not find any plot markers from prior sampling efforts, and thus the exact locations of sample plots do not correspond precisely with those of the previous researchers. Similarly, Crawford et al. (1998) sampled the same stands as Morgan (1969) but did not sample identical transect or plot locations. Thus, variance between sample years due to spatial zheterogeneity within stands should be similar for all sample intervals 1964–1994, 1964–2010, and 1994–2010.

Sampling methods closely followed those of Morgan (1969) and Crawford et al. (1998). We sampled eight plots in each of the 19 stands, for a total of 152 plots. Within each historically surveyed stand, we established two parallel, 70-m transects, separated by 70 m. Four 10 × 10-m plots were located at 20-m intervals along

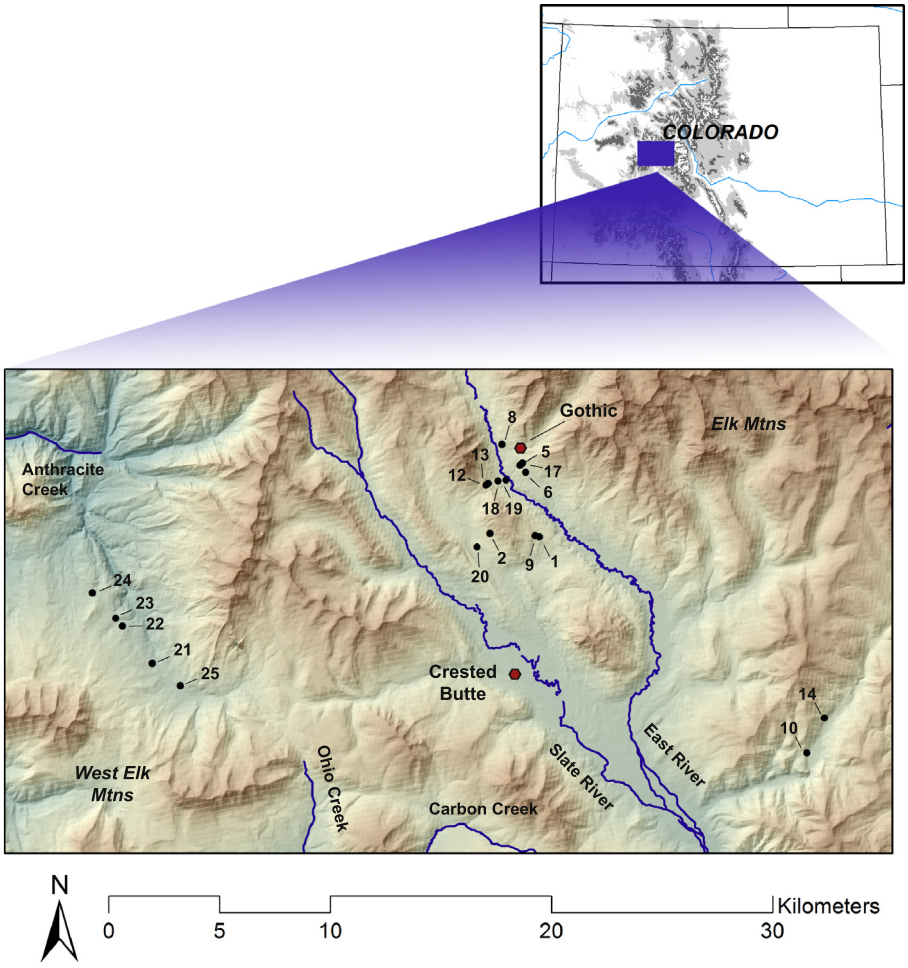

Fig. 1. Location of study area and sample sites near Crested Butte, CO; site numbering follows previous authors.

each transect. The edge of each plot was monumented with labeled rebar or wooden survey stakes. Within each plot, we measured the diameter at 1.37 m height (DBH) of all trees >2.5 cm diameter; stems > 1.37 m tall with diameters <2.5 cm were tallied. Stems <1.37 m tall were not recorded. At the center of each 100-m^2 plot, cover by each shrub and herb species was visually estimated in a nested 4×4-m and 2×2-m subplot, respectively. Following Morgan (1969) and Crawford et al. (1998), understory cover for each species was grouped into Braun-Blanquet cover classes as follows: <1% = 1, 1–5% = 2, 6–25% = 3, 26–50% = 4, 51–75% = 5, 76–100% = 6.

To explore relationships between understory cover and light levels, we also took a digital hemispheric photo at the center of each plot at a height of 1.37 m. Photos were taken during uniformly cloudy or twilight conditions. Canopy photos were analyzed with ImageJ (Rasband, 2012): we manually adjusted the contrast threshold to create binary, black-and-white images. From these images, the percentage of canopy foliar cover was calculated at each plot.

2.3. Data analysis

Prior to analysis, we digitized all available vegetation data from the earlier studies. Morgan (1965, 1969) provided the numbers of live and dead aspen and live conifer stems grouped by size classes, along with the total density and basal area of live aspen, for each of his 25 sample sites. The size classes he used were slightly different for live aspen (largest size class >33.0 cm dbh), dead aspen (largest class >10.2 cm dbh), and conifers (largest class >12.7 cm dbh). We used these data from the 19 sites that were resampled in both 1994 and 2010. Morgan did not include understory data specific to each site; instead, he presented cover and frequency of herbaceous and shrub species (for the most common 47 species; only percent constancy was given for the remaining 41 species) averaged across all of his 25 sites. These data could not be directly, quantitatively compared with data from the 1994 or 2010 resurvey but were still useful in qualitatively assessing long-term trends for particular plant species. We were able to obtain much more complete data from Crawford et al.'s field data sheets. From these we recorded the dbh of each stem, by species, for all live and dead trees. We also digitized the cover class measures of each shrub and herb species at each sample site, which allowed for direct, quantitative comparisons of individual plant species between 1994 and 2010. We used these data in subsequent analyses, rather than the summary data presented in Crawford et al. (1998). Though sites showed ecological variation along topographic and geographic gradients across the study area, we included all samples in our analyses because we wished to maximize statistical power and our ability to generalize most broadly to aspen stands across the study area, the statistical population of interest.

We used paired *t*-tests to test for differences in stand density and basal area of live aspen, and stand density of conifers and dead aspens, from the 19 stands for the periods 1964–1994 and 1994–2010. We also tested for differences between sample years in average live aspen basal area per stem for each stand. Additionally, we

utilized paired *t*-tests to test for changes in annual rates of change in stand density, stand basal area, and basal area per tree.

All plant nomenclature follows USDA NRCS (2013). To ensure taxonomic accuracy for analyzing understory vegetation, we first contrasted the species lists compiled by Morgan (1965) with the digitized data of Crawford et al. and our samples. We also took advantage of a partial set of plant collections made by Crawford et al., archived at WSCU, to ensure accurate plant identifications. Several discrepancies suggested misidentified species and required combining (''lumping'') taxa prior to analysis. In all cases these species pairs were (1) vegetatively morphologically similar and (2) recorded in the same locations in 1994 and 2010. Dryspike sedge (*Carex siccata*), a common species across the study area, was not recorded at all in 1994 and was probably misidentified as elk sedge (*Carex geyeri*), which was recorded in many sites both years, including some sites that only contained dryspike sedge in 2010. As such, in our analyses we treated these two species as a single taxon. For similar reasons, we combined bluntseed sweetroot (*Osmorhiza depauperata*) with western sweetroot (*Osmorhiza occidentalis*), cutleaf and western coneflower (*Rudbeckia laciniata* and *R. occidentalis*), Engelmann's aster (*Eucephalus engelmannii*) with alpine leafybract aster (*Symphyotrichum foliaceum*), and the two heart-leaved violets, hoodedspur violet (*Viola adunca*) and Canadian white violet (*Viola canadensis*). Unfortunately, several species listed as unknowns on the 1994 data sheets were apparently never identified. Consequently, species found in 2010 that were not recorded in 1994 may have been present but not identified, or may not have been present. We chose to address this problem conservatively by excluding from analysis all unidentified taxa and any identified taxon that was not present in both surveys. We therefore excluded 12 taxa from 1994 (representing 2.4% of total understory cover) and 9 taxa from 2010 (representing 1.3% of total cover). Following these adjustments, we retained 65 taxa found in both survey years in standardized datasets for all analyses unless specifically noted below.

We tested the significance of changes in total plant cover and richness at the stand level using paired *t*-tests. We also tested for differences in cover and richness separately for shrubs, forbs, and graminoids. Because these analyses might have been biased by exclusion of unidentified or misidentified taxa, we tested for changes using both the standardized and the original, non-standardized datasets described above. To test for the significance of changes in the frequency and cover of any of the 65 taxa identified in both 1994 and 2010, we utilized a bootstrap analysis. For each taxon, absolute frequency was calculated as a proportion of the 152 sample plots occupied, and the difference between 1994 and 2010 frequency was calculated. We then randomized the combined data from both years (304 samples) and recalculated the difference in frequency between two random draws (without replacement) of two 152-sample sets. From the distribution of differences of 10,000 randomized runs, we calculated the two-tailed *P*-value as the proportion of randomizations in which the absolute value of the differences was equal to or greater than that observed. Because we ran this analysis simultaneously for all 65 species, we adopted a conservative, Bonferroni-adjusted *P*-value of $\alpha = 0.05/65 = 0.00077$ for assessing statistical significance of any changes in frequency.

To assess relationships between aspen stand canopy structure and understory composition we conducted both indirect (nonmetric multidimensional scaling; NMS) and direct (Mantel tests) gradient analyses. We first conducted an NMS ordination using a dataset that combined all understory samples from both years [38 stands (19 from 1994 and 19 from 2010) × 65 taxa] to elucidate general patterns of understory compositional variation and explore differences between 1994 and 2010 samples. We used the ecodist package (Goslee and Urban, 2007) in R to run the ordination, finding the lowest-stress solution from 1000 iterations beginning with random coordinates. The ordination utilized a dissimilarity matrix of Sørensen (Bray-Curtis) distances of understory species frequency (presence–absence) data. We used frequency rather than cover class data because it was a more conservative measure; presence–absence differences between sample periods were more likely to reflect long-term shifts in composition rather than intra- or inter-annual variation in foliar cover. We used a joint-plot method to display correlations between ordination axes, environmental variables, and species abundances as vectors drawn from the centroid of the ordination, with vector length and direction corresponding to the correlation coefficients between each variable and sample scores on each ordination axis.

We used Mantel tests to more directly examine correlations between understory composition, canopy variables, and spatial distance (i.e., meters between sample units). Mantel tests analyze correlations between two or more dissimilarity matrices, and are particularly useful in quantifying the influence of spatial distance on bivariate relationships by calculating the partial correlation coefficient between two matrices when a third—spatial distance—is also included (Mantel, 1967; Smouse et al., 1986). Because our NMS ordination revealed associations between understory composition and spatial variables (UTM Easting, Northing, and elevation) we tested for relationships between understory variation and Euclidean distances between samples, and calculated partial correlation coefficients between understory, canopy, and spatial distance matrices. We examined relationships between understory species compositional dissimilarity in 1994 and 2010, and variation in live stand density, live stand basal area, live mean stem basal area, and the size class distribution of the live canopy [following the size classes of Morgan (1969) and Crawford et al. (1998)]. Similarly, we tested for correlates of 2010 understory compositional variation, but considered the canopy variables listed above from both 1994 and 2010, and canopy foliar cover, measured in 2010. Correlations between Sørensen dissimilarity matrices were generated for each variable of interest, including both understory species cover class and frequency data, with *P*-values calculated from 10,000 randomizations.

To determine whether changes in aspen canopies had driven changes understory composition, we first assessed how much the understory composition of each plot had changed between sample periods as measured by Sørensen distance between 1994 and 2010. We also calculated Sørensen distance between the 1994 and 2010 overstory size class structure, and the absolute and proportional differences in live stand density, live stand basal area, and live mean tree basal area for each stand 1994–2010. To test the hypothesis that stands showing the most canopy change from 1994–2010 would also show the most understory change, we used linear regression models with 1994–2010 canopy size class distance, stand density change, stand basal area change, and mean tree basal area change as predictors of 1994–2010 understory compositional distance, change in cover, and change in richness.

3. Results

3.1. Canopy change

Across the study area, aspen stands exhibited pronounced decreases over the sampling period (Figs. 2–4). Live aspen density dropped significantly, from 2360 ± 1480 ha^{-1} (mean ± 1 S.D.) to 1605 ± 1007 ha^{-1} between 1994 and 2010, a loss of 32% (paired *t*-test two-tailed $P = 0.009$, 18 d.f.; Fig. 2). Decreases in live aspen density occurred across all size classes of aspen except for the largest trees >33 cm DBH (Fig. 3). The decrease between 1964 and 1994 was from 3151 ± 1365 ha^{-1} to 2360 ± 1480 ha^{-1}, a 25% de-

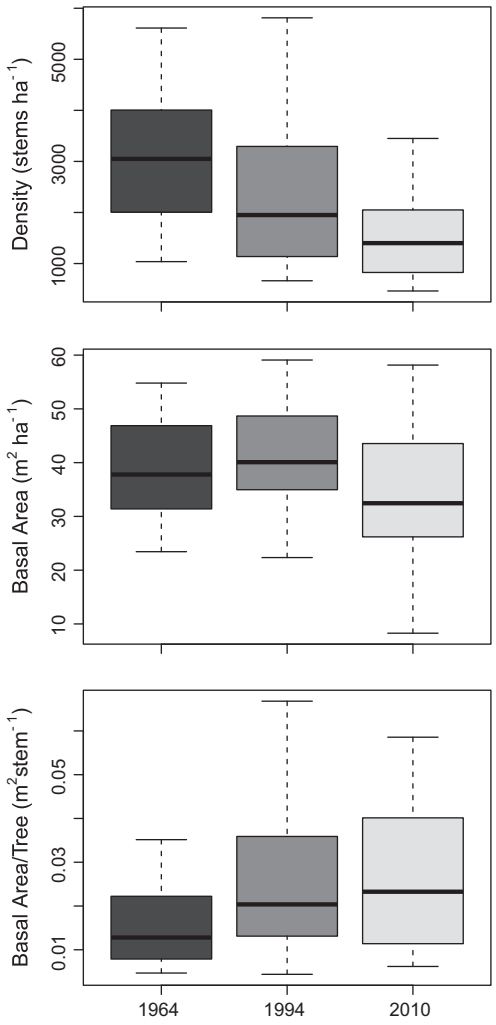

Fig. 2. Stand density, stand basal area, and mean tree basal area, for live aspen in the study area 1964, 1994, and 2010. Error bars represent 1 S.D.

crease ($P = 0.004$). Live stand basal area also fell markedly from 41.2 ± 10.8 m^2 ha^{-1} to 33.7 m^2 ha^{-1} ± 14.6 (paired *t*-test two-tailed $P = 0.03$, 18 d.f.) during the period 1994–2010 (Fig. 2). This decrease is entirely a recent phenomenon; live basal area was essentially unchanged during the period of 1964–1994 (39.2 ± 9.8 m^2 ha^{-1} to 41.2 ± 10.8 m^2 ha^{-1}; $P = 0.37$). Live basal area per tree increased significantly between 1964 and 1994 (from 0.015 ± 0.008 m^2 to 0.026 ± 0.017 m^2; Fig. 2; paired *t*-test two-tailed $P < 0.001$, 18 d.f.), but increased non-significantly to 0.030 ± 0.027 m^2 in 2010 ($P > 0.05$). Between the sampling periods of 1964–1994 and 1994–2010, the annual rate of density loss progressed non-significantly from −1.2% to −2.3% ($P = 0.14$, 18 d.f.). The rate of change of stand basal area change shifted significantly from 0.2% to −1.7% ($P = 0.03$). The rate of change of stem basal area also declined between sample intervals, but not significantly (1.4–0.7%, $P = 0.35$).

We also found fewer dead aspen stems (30 ± 381 ha^{-1}) than reported in 1964 (48 ± 604 ha^{-1}) or 1994 (51 ± 639 ha^{-1}); however, the decreases from 1964–1994 and 1994–2010 were not significant (paired *t*-test two-tailed $P > 0.05$; 18 d.f). Fewer dead stems were encountered in all but the largest size classes > 10.3 cm dbh (Fig. 3).

As in the prior surveys, conifers comprised only a very small fraction of the forest canopy. We found conifers in seven of 19 sampled stands; conifers were reported in six stands in 1964 and ten stands in 1994. The primary species of conifer encountered was subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*; 4 stands; 27 ± 55 ha^{-1}), but we also found Engelmann spruce (*P. engelmannii*; 3 stands; 11 ± 28 ha^{-1}), Colorado blue spruce (*Picea pungens*; 1 stand; 1 ± 3 ha^{-1}), and Douglas fir (*Pseudotsuga menziesii* var. *glauca*; 2 stands; 1 ± 3 ha^{-1}). Conifers have not become more abundant between 1964 and 2010 except in large size classes >12.7 cm dbh (Fig. 3). Though non-significant, live conifer density also appears to exhibit a long-term decrease, from 101 ± 245 ha^{-1} in 1964 to 82 ± 201 ha^{-1} in 1994 to 45 ± 91 ha^{-1} in 2010. Likewise, changes in conifer basal area were non-significant but not suggestive of any increases over the sampling period. Conifer basal area was 0.71 ± 2.35 m^2 ha^{-1} in 1964, 0.41 ± 0.93 m^2 ha^{-1} in 1994, and 0.42 ± 1.04 m^2 ha^{-1} in 2010.

3.2. Understory change

We found slight but significant increases in both understory species richness and cover between 1994 and 2010. Using the standardized, 65-taxa datasets, at the stand level (total sample area 36 m^2), understory species richness increased from 20.6 ± 3.6 to 23.0 ± 4.1 species (paired *t*-test two-tailed $P = 0.03$, 18 d.f) and total cover (sum of Braun-Blanquet cover classes for all species) increased from 133.5 ± 13.5 to 151.5 ± 28.9 ($P = 0.02$). Richness and cover of shrubs and forbs did not change significantly; however, richness of graminoids increased from 3.2 ± 0.8 to 3.9 ± 0.67 ($P = 0.009$) and cover (sum of Braun-Blanquet cover classes) by graminoids increased from 26.1 ± 7.5 to 33.2 ± 9.2 ($P = 0.004$). Because these findings may have been influenced by removal of unidentified species and lumping species we believe were misidentified in 1994, we performed these analysis using both the standardized and non-standardized datasets described above. In each case, the results of tests on the non-standardized datasets were comparable.

General patterns of understory species dominance remained relatively stable during the sampling intervals of 1964–1994 and 1994–2010 (Table 1). As with previous surveys, understory plant communities were dominated by a suite of large, long-lived perennial forbs and graminoids, including (in order of decreasing abundance in 2010) Fendler's meadow-rue (*Thalictrum fendleri;* mean cover class 1.40), oshá (*Ligusticum porteri*; 1.30), Geyer's and dryspike sedge (*C. geyeri* & *C. siccatta*; 1.30), wild bluerye (*Elymus glaucus*; 1.24), and bluntseed/western sweetroot (*O. depauperata* & *O. occidentalis*; 1.24). Fendler's meadow-rue accounted for the most understory cover in every sample period 1964–2010; Porter's licorice-root and the two sedges were among the five most abundant species in 1964 and the second and third most abundant in both 1994 and 2010 (Table 1).

Bootstrap analysis identified eight species of herbs that increased or decreased significantly in frequency, cover, or both between 1994 and 2010 (Table 2). Six species showed changes in frequency that were significant at our Bonferroni-adjusted α ($P < 0.00077$; Table 2); these changes included increases by fringed brome (*Bromus ciliatus*), Kentucky bluegrass (*Poa pratensis*), cutleaf/western coneflower (*Rudbeckia laciniata/R. occidentalis*), and Nuttall's violet (*Viola nuttallii*), and decreases in frequency by fireweed (*Chamerion angustifolium*) and tall fleabane (*Erigeron elatior*). Several of these species also showed highly significant changes in cover. We could not test 1964–1994 trends for significance, because we only had summary data from 1964, and the 1994 and 2010 samples represented a subset of the plots sampled in 1964. However, with few exceptions, the changes we found in the cover and frequency of these species appeared to continue long term population expansions or contractions exhibited from 1964–1994 (Table 2).

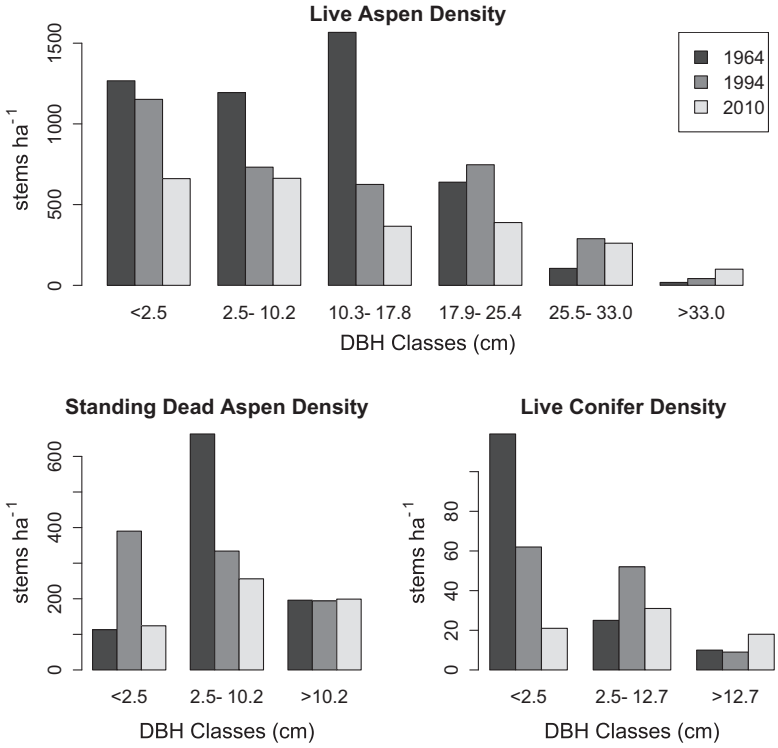

Fig. 3. Density of live aspen, standing dead aspen, and conifers by DBH size class, 1964–2010; size classes follow Morgan (1969). Following the methods of Morgan (1969) and Crawford et al. (1998), only standing dead aspen were measured; no attempt was made to measure fallen dead.

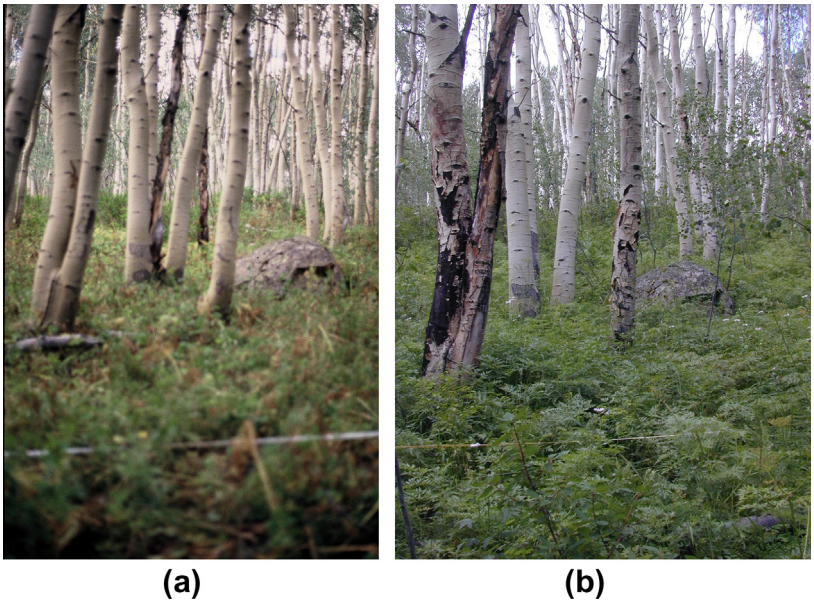

Fig. 4. Photos of aspen stand 6 in (a) 1994 and (b) 2010. The tape running along the sampling transect is visible in the foreground. Several trees (on the left and in the center) that were alive in 1994 are dead in 2010.

3.3. Understory community structure and canopy/understory relations

Non-metric multidimensional scaling produced a two-dimensional solution with a final instability of 0.25 and an r^2 of 0.75 (Fig. 5). Understory compositional variation corresponded well with geographic and elevational gradients. The first ordination axis (NMS 1) is correlated positively with mean basal area/tree ($r = 0.70$, $P < 0.001$) and negatively with UTM easting ($r = 0.67$, $P < 0.001$) and live stand density ($r = 0.59$, $P = 0.002$; Fig. 5b), appearing to represent a strong west-east gradient—stands with fewer, larger trees in the wetter western portion of the study area, and stands with smaller trees but higher density in the drier eastern portion. The second axis (NMS 2) illustrates a shift from lower elevations in the southern and western portions of the study area to higher elevations in the north and corresponds well with UTM northing ($r = 0.70$, $P < 0.001$) and elevation, which showed the strongest relationship to understory community structure ($r = 0.84$, $P < 0.001$; Fig 5b). Elevation also decreased on NMS 1,

Table 1
The twenty most dominant understory species, as measured by mean cover class in 2010, with their mean cover in 1964 and 1994. Three taxa include combinations of two morphologically, vegetatively similar species that were not adequately distinguished in previous surveys.

Species	1964 (*25 sites*)	1994 (*19 sites*)	2010 (*19 sites*)
Thalictrum fendleri	1.61	1.50	1.40
Ligisticum porteri	1.33	1.20	1.30
Carex geyeri/Carex siccata	1.19	1.30	1.30
Elymus glaucus	0.76	1.16	1.24
Osmorhiza depauperata/O. occidentalis	0.98	0.69	1.24
Vicia americana	0.67	0.63	0.89
Heracleum sphondylium	0.88	0.59	0.80
Lathyrus lanszwertii	1.49	0.70	0.80
Bromus ciliatus	0.45	0.46	0.76
Poa pratensis	0.00	0.24	0.70
Geranium richardsonii	0.66	0.59	0.65
Viola nuttallii	0.82	0.26	0.64
Pteridium aquilinum	1.20	0.41	0.55
Delphinium barbeyi	0.89	0.72	0.48
Senecio serra	0.86	0.50	0.40
Symphoricarpos utahensis	0.88	0.57	0.43
Hydrophyllum fendleri	0.56	0.16	0.43
Eucephalus engelmannii/Symphyotrichum foliaceum	1.19	0.17	0.36
Taraxacum officinale	0.68	0.31	0.34

Table 2
Mean frequency and cover of understory species that showed a significant change 1994–2010. Values in bold represent changes that were significant at $P < 0.00077$ ($\alpha = 0.05/65$ taxa tested in each analysis). Eight species showed such highly significant changes in frequency, cover, or both. Values from 1964 are based on summary statistics presented in Morgan (1969) and differences between 1964 and the other sample years could not tested for significance. Values from 1964 were also derived from a larger set of samples (25, rather than the 19 stands sampled in both 1994 and 2010).

Species	Frequency					Cover				
	1964	1994	2010	% Change 94–10	*P*-val	1964	1994	2010	% Change 94–10	*P*-val
Arnica parryi	NA	0.12	0.05	−56	0.0416	NA	0.22	0.14	−38	0.2927
Bromus ciliatus	0.45	**0.46**	**0.76**	**+66**	**0.0004**	0.42	**0.39**	**0.59**	**+53**	**0.0002**
Chamerion angustifolium	0.49	**0.20**	**0.03**	**−87**	**<0.0001**	0.71	**0.32**	**0.04**	**−88**	**<0.0001**
Cirsium eatonii	0.55	0.03	0.09	+180	0.0339	0.38	0.04	0.10	+150	0.0659
Delphinium barbeyi	0.60	0.49	0.34	−30	0.0102	0.89	0.72	0.48	−33	0.0091
Erigeron elatior	0.47	**0.47**	**0.11**	**−77**	**<0.0001**	0.38	**0.30**	**0.09**	**−70**	**<0.0001**
Eucephalus engelmannii/Symphyotrichum foliaceum	0.73	0.12	0.22	+89	0.0145	1.19	0.17	0.36	+108	0.0128
Fragaria virginiana	0.51	0.34	0.22	−35	0.0240	0.80	0.41	0.26	−35	0.0302
Hydrophyllum fendleri	0.40	0.14	0.30	+114	0.0008	0.56	**0.16**	**0.43**	**+164**	**0.0002**
Hymenoxys hoopesii	NA	0.04	0.10	+150	0.0386	NA	0.06	0.16	+178	0.0366
Maianthemum racemosum	0.38	0.05	0.01	−88	0.0168	0.59	0.07	0.01	−90	0.0192
Osmorhiza depauperata/O. occidentalis	0.59	0.47	0.58	+22	0.0628	0.98	**0.69**	**1.24**	**+80**	**<0.0001**
Poa pratensis	NA	**0.14**	**0.37**	**+155**	**<0.0001**	NA	**0.24**	**0.70**	**+187**	**<0.0001**
Rudbeckia laciniata/R. occidentalis	NA	**0.02**	**0.14**	**+633**	**0.0007**	NA	0.01	0.11	+700	0.0018
Sambucus racemosa	0.18	0.11	0.03	−71	0.0077	0.20	0.16	0.04	−75	0.0073
Vicia americana	0.55	0.46	0.53	+14	0.2552	0.67	0.63	0.89	+41	0.0151
Viola nuttallii	0.61	**0.23**	**0.42**	**+83**	**<0.0001**	0.82	**0.26**	**0.64**	**+148**	**0.0004**

consistent with the lower elevations of stands west of Kebler Pass. Live stand basal area increased moderately along both NMS 1 & 2 ($r = 0.47$, $P < 0.016$). Ordination scores were not correlated significantly with canopy foliar cover ($P < 0.05$).

Understory samples from 1994 had significantly higher scores, and those from 2010 had lower scores (two-tailed *t*-test $P = 0.0002$; 18 d.f.), on NMS 2 (Fig. 5a), suggesting that compositional shifts between 1994 and 2010 parallel shifts from higher-elevation, northern sites to lower-elevation, southern aspen understory communities. More than half (39) of the understory species showed significant ($P < 0.05$) correlations with ordination scores (Fig. 5c). Species with particularly strong relationships to the ordination (those that showed strong increases or decreases along either axis; for all $P < 0.001$; Fig. 5c) included several that increased strongly along NMS 1, indicative of increased presence in the wetter, western sample plots (e.g., cow parsnip (*Heracleum spondylium*; herspo) or decreased, suggesting higher abundance in the drier, eastern portion of the study area (e.g., Letterman's needlegrass (*Achnatherum lettermanii*; achlet). Likewise species such as brackenfern (*Pteridium aquilinum*; pteaqu) declined on NMS 2, consistent with increases at lower elevations and southern sites, while species such as blue wildrye (*E. glaucus*; elygla) showed the strong increases with elevation and northing on NMS 2.

Mantel tests revealed that understory dissimilarity was strongly correlated with spatial distance in both 1994 ($r = 0.57$) and 2010 ($r = 0.55$). Because spatial relationships were so strong, we included spatial distance in subsequent models assessing partial correlations between understory dissimilarity and canopy variation. No significant partial Mantel correlations were found between 1994 canopy and understory variation, or between 2010 canopy and understory variation, when spatial distance was also accounted for. However, partial correlation coefficients between 1994 canopy variation and 2010 understory dissimilarity were retained in models that also included spatial distance: 1994 live stand density (partial $r = 0.23$), live stand basal area (partial $r = 0.23$), live basal area per stem (partial $r = 0.44$), and canopy size

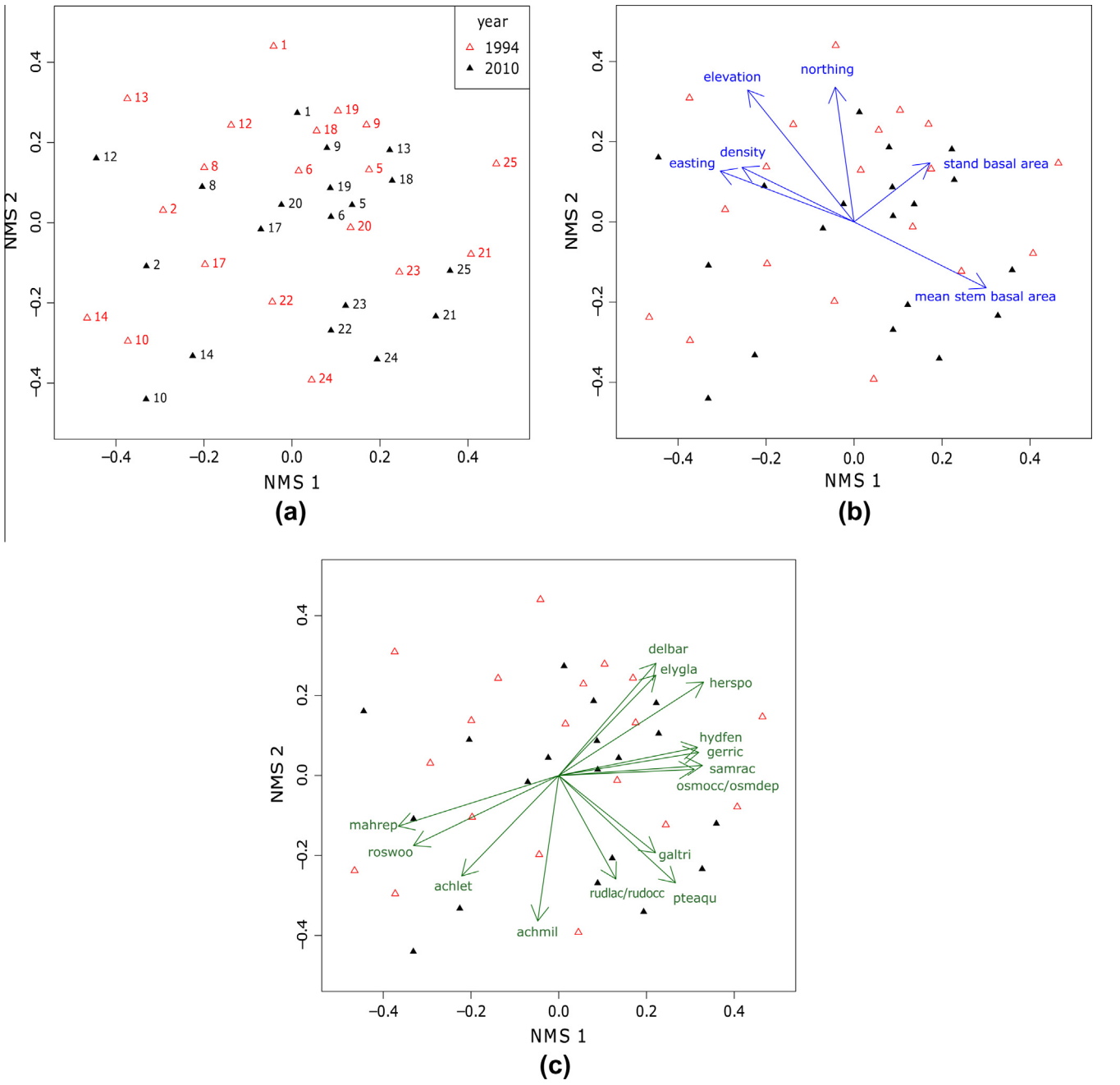

Fig. 5. Non-metric multidimensional scaling ordination of understory communities in 1994 and 2010, showing (a) positions of stands in both years, (b) relationships between ordination axes and environmental variables (only variables with $r > 0.40$ and $P < 0.05$ are shown), and (c) relationships between ordination axes and understory species (only species with $r > 0.60$ and $P < 0.001$ are displayed). Species abbreviations: achlet, *Achnatherum lettermanii*; achmil, *Achillea millefolium*; delbar, *Delphinium barbeyi*; elygla, *Elymus glaucus*; galtri, *Gallium triflorum*; gerric, *Geranium richardsonii*; herspo, *Heracleum spondylium*; hydfen, *Hydrophyllum fendleri*; mahrep, *Mahonia repens*; osmocc/osmdep, *Osmorhiza occidentalis/O. depauperata*; pteaqu, *Pteridium aquilinum*; roswoo, *Rosa woodsii*; rudlac/rudocc, *Rudbeckia laciniata/R. occidentalis*; samrac, *Sambucus racemosa*.

distribution (partial $r = 0.27$) all showed robust relationships to understory variation in 2010.

We found substantial changes between 1994 and 2010 in both canopy size class distribution and understory composition, as measured by Sørensen dissimilarity indices. Canopy dissimilarity from 1994–2010 was 0.37 ± 0.12, nearly identical to the 1964–1994 dissimilarity, 0.37 ± 0.13. Understory compositional distance from 1994–2010 averaged 0.30 ± 0.09. However, no measures of canopy change (1994–2010 canopy dissimilarity, live density change, or live basal area change) were significant predictors of 1994–2010 understory compositional distance, change in understory cover, or change in understory richness (for each, linear regression $r^2 < 0.2$, $P > 0.05$).

4. Discussion

4.1. Aspen loss in the study area

Aspen stands in the study area have lost substantial live density and basal area since 1964 (Figs. 2–4), and the rate of decrease has increased since 1994. Our findings suggest an unexpected resolu-

tion to an historic dilemma: are aspen stands in the study area temporary relics of historic disturbance that will ultimately give way to more shade tolerant conifers (e.g., Morgan, 1969), or stable and persistent landscape features that change little over thousands of years (e.g., Langenheim, 1962; Crawford et al., 1998)? The 46-year trajectory of accelerating loss we observed suggests the current answer to be "neither". The very low density of conifers across the study area has not changed significantly between 1964 and 2010 (Fig. 3). Several authors have suggested that seed source limitations alone may severely constrain conifer succession in aspen-dominated landscapes (Morgan, 1969; Peet, 1981). Even if stands were successional to spruce and fir over time scales of multiple centuries we would still have expected to find some measurable increases in conifer abundance, rather than the non-significant decrease we observed. However, the loss of aspen overstory, which has increased over the most recent sample interval, is clearly not balanced by increased aspen regeneration as would be expected if these stands were indeed stable features of the landscape. Such changes in aspen stand structure in our study area may reflect: (1) natural patterns of stand maturation and deterioration in the absence of stand-replacing disturbance, (2) diminished regeneration, possibly due to high elk and/or livestock use, and/or (3) enhanced mortality that may be due recent extreme drought stress, as has been implicated as a trigger for sudden aspen decline (SAD) at lower elevations in the region (Rehfeldt et al., 2009; Worrall et al., 2013). None of these tentative explanations excludes any of the others, in fact, minor but significant changes in understory composition offer evidence supporting all three.

Many aspen stands in the study area may have been initiated by extensive fires that occurred during mining boom of the late 19th C but ceased around 1905 when much of the area was incorporated into the Gunnison National Forest (Langenheim, 1962). Morgan (1969) noted the presence of charcoal in the soil in most of the study sites. As such, declining density and increasing tree size over a century later during our sampling period would be expected. The decreases in live stand density we observed were coupled with increased average tree basal area (from 0.015 ± 0.008 m^2 in 1964 to 0.030 ± 0.027 m^2 in 2010; Fig. 2), consistent with aging stands undergoing self-thinning. This interpretation is also supported by striking decrease in fireweed (*C. angustifolium*) from aspen understories over the entire sample period (from a frequency of 49% in 1964 to 20% in 1994 and only 3% in 2010; Table 2). Fireweed rapidly colonizes recent burns, both from off-site seed and on-site clonal spread from underground rhizomes, but gradually wanes in abundance as the tree canopy becomes re-established (Pavek, 1992 and references therein). Three years after high-severity fire in an aspen stand in Wyoming, fireweed increased from 68 to 1657 kg/ha, but had dropped to 1114 kg/ha by 12 years after fire (Bartos and Mueggler, 1981; Bartos et al., 1994). The large losses in fireweed we found are consistent with ongoing stand development following extensive historic fire. Bartos et al. (1994) also found large and persistent decreases in Fendler's meadowrue (*T. fendleri*) following even low- and moderate-severity fire; the high abundance of this species in our samples is also indicative of mature stands with no recent wildfire.

Even as aspen stands in the study area age in the absence of fire, it is not clear why mortality in the canopy is not balanced by regeneration of aspen root sucker shoots under the persistent-stand model. Abundant regeneration clearly occurred historically in the absence of stand-replacing fire. Morgan (1969) and Crawford et al. (1998) both noted aspen regeneration across the study area. Aspen age structure as reconstructed from tree rings (50 randomly selected stems; 14 sites) near Kebler Pass (Coop, unpublished data) over this period indicate nearly continuous aspen establishment from the late 19th C through the 1940s, decreases in the 1950s and 1960s, and a near total absence of establishment from the 1980s through the present. Intrinsic constraints on aspen root suckering due to apical dominance and shading may become more pronounced as trees mature, and may account in part for limited regeneration of older stands. Schier (1975) hypothesized that in old, deteriorating aspen stands, even a low density of live stems could suppress suckering through apical dominance if root density also decreased.

Browsing by elk and livestock is well known to severely constrain aspen regeneration (e.g., Fitzgerald and Bailey, 1984; Hessl and Graumlich, 2002), and such constraints may also exist in the study area. Elk browse the tips of new aspen sprouts during spring and fall (Romme et al., 1995). In the presence of high elk populations aspen regeneration occurs only at sporadic, low levels (Hessl and Graumlich, 2002). Elk were almost entirely extirpated from the Crested Butte area in the late 1800s, but reintroduced populations began to rise noticeably in the 1950s and 1960s, spiking in the 1980s until the mid-1990s before stabilizing at lower levels (Holland et al., 2005). These population trends largely mirror historic patterns of regeneration as reconstructed from tree rings in the Kebler Pass area (Coop et al. unpublished data). In addition to elk, cattle graze some stands across the study area, particularly those near large meadows. Finally, large herds of sheep utilize all of the sampled stands west of Kebler Pass during the late summer; browsing by sheep in these stands may exert particularly strong constraints on aspen regeneration (Smith et al., 1972). Combined, these impacts may account not only for limited aspen regeneration, but also the increases in Kentucky bluegrass (*P. pratensis*) across the sampled stands. Kentucky bluegrass is well known to replace native grasses and forbs in the presence of heavy grazing pressure (e.g., Uchytil, 1993 and references therein). Mueggler (1988) recognized an aspen-Kentucky bluegrass community as a "grazing-induced seral stage" across the Intermountain West, and cautioned that continued heavy grazing practices would ultimately result in loss of the aspen from these communities. While none of the stands we sampled approached the high levels of dominance by Kentucky bluegrass reported by Mueggler (1988), the expansion of this non-native grass across the study area is concerning.

Recent climate variation has caused extensive aspen mortality across the western US (Rehfeldt et al., 2009; Worrall et al., 2008) and may also have played a role in the accelerated loss of aspen from our study plots. Sudden aspen decline (SAD), characterized by rapid and extensive mortality imparted by agents not typically lethal to healthy trees, was triggered across much of the southern Rockies by increased temperatures and extreme drought in 2002 (Rehfeldt et al., 2009; Worrall et al., 2008, 2010). Similarly, drought and freeze–thaw events that occurred during years with unusually low snowpack were observed to lead directly to mortality and also predispose aspens to secondary insect and fungal attack in Alberta in the 1960s and 1980s (Hogg et al., 2002; Worrall et al., 2010). The stands we sampled were at higher elevations and more mesic settings than those that experienced SAD elsewhere in the region, and did not exhibit the dramatic patterns of mortality characteristic of SAD. However, the same extreme climatic conditions that led to the stand-scale mortality associated with SAD at lower elevations in the region undoubtedly increased water deficits for trees across all elevations, and may have directly or indirectly increased rates of mortality in the stands we sampled. Likewise, we did not observe any recent increases in the abundance of younger cohorts of aspen, paralleling the lack of a regeneration response to canopy mortality observed in stands experiencing SAD (Worrall et al., 2008). Interestingly, though non-significant, the increased rate of population loss we observed (from −1.2% between 1964 and 1994 to −2.3% between 1994 and 2010) closely matches the doubling in background tree mortality rates found for conifers across the western US by Van Mantgem et al. (2009), also attributed to climate-driven water deficit intensification. Shifts in overall patterns of aspen

understory composition between 1994 and 2010 (toward lower scores on NMS axis 2; Fig. 5) also parallel the transition from higher elevation, northern sites to lower elevation, southern sites. Expansion of low-elevation communities, and contraction of high-elevation communities is suggestive of a community-level response to warming conditions; however, this is a hypothesis requiring further testing—this shift may be due to unrelated increases or decreases in only one or two species, as we discuss below.

4.2. Understory community compositional dynamics

While aspen canopy structure changed substantially between 1964 and 2010, understory communities remained relatively stable overall, with high cover, richness, and dominance by the same suite of large perennial herbs (Table 1). The most abundant understory species in 1994 and 2010, Fendler's meadowrue (*T. fendleri*), oshá (*Ligusticum porter*), elk and dryspike sedge (*C. geyeri* and *C. siccata*), and blue wildrye (*E. glaucus*), showed little or no changes in cover (Table 1), and were also reported as dominant species of aspen stands by Morgan (1969) and Langenheim (1962). The relative stability of the understory in spite of pronounced decreases in live aspen density and basal area suggest that any concomitant increases in light levels have not yet exerted large influences on understory composition. It may be that canopy cover decreases associated with the loss of density and basal area were offset by expansion of the foliage of living trees. Alternatively, changes in canopy cover and light levels may not have substantially affected dominant understory species. Many of the most abundant species of aspen understories appear to be well-adapted to much higher light availability. Aspen understory dominants including Fendler's meadowrue, oshá, fringed brome, subalpine larkspur, American vetch (*Vicia americana*), Nevada pea (*Lathyrus lanszwertii*) are all abundant in both open, herb-dominated meadows and Thurber's fescue-dominated grasslands across the study area (Langenheim, 1962). Light levels did not appear to play a major role in structuring understory communities; we did not find any significant correlations between canopy foliar cover and community structure.

The lack of a strong signal of the current light environment may also be due to the apparent lag between understory composition and variation in stand structure—we found stronger relationships between composition and past canopy structure than current structure. Understory composition in 2010 was strongly correlated with 1994 canopy structure, particularly average tree size (mean BA/stem; partial Mantel $r = 0.44$), but showed no correlation to current canopy attributes. Likewise, composition in 1994 was not significantly correlated with canopy factors in 1994, once patterns of spatial similarity were taken into account. Aspen understory communities are dominated by long-lived perennials and the dynamics of these communities are likely to be protracted, even relative to our 46-year sampling period. The most abundant species in our study, Fendler's meadowrue, has been estimated to have an average life expectancy of 12 years (Treshow and Harper, 1974). Another species found in our sample sites, monument plant (*Frasera speciosa*), can live over 90 years (Taylor and Inouye, 1985). Given the longevity of these species, it should perhaps not be surprising that understory composition does not reflect current canopy conditions.

Rather than showing strong associations with canopy conditions, aspen understory composition our study area reflected strong spatial relationships and geographic variation. Non-metric multidimensional scaling identified strong gradients in community composition that were clearly related to the basic geography of the study area, including a west-east precipitation gradient and a temperature- and moisture-related shift from lower elevation, southern sites to higher elevation, northern sites (Fig. 5). As discussed above, we found that composition in 1994 averaged higher scores, and 2010 lower scores on this second axis, suggesting a general compositional shift from northern, higher-elevation taxa towards the southern, lower-elevation species. However, it may reflect grazing-induced changes in only two taxa that had disproportionately large effects on the ordination. Subalpine larkspur showed marginally significant decreases in frequency (−30%) and cover (−33%) between 1994 and 2010, consistent with an apparent reduction between 1964 and 1994; this species is documented as decreasing with livestock grazing (Johnston et al., 2001). Conversely, *Rudbeckia* species showed the large increase in frequency (+633%) and cover (+700%) 1994 and 2010 (Table 2); *Rudbeckia* are known to be toxic to livestock (e.g., Cronin et al., 1976; Allred, 2010). As such, changes in the both species may be related to patterns of grazing in the study area.

In contrast to the minor but significant increases in total understory richness and cover that we found, Anderegg et al. (2012) reported significantly lower herb cover and richness in severely SAD-affected stands than healthy stands in the San Juan Mountains. Anderegg et al. (2012) also found that stands that had experienced SAD contained significantly greater shrub cover (primarily by one species, mountain snowberry, *Symphoricarpos oreophilus*), which has not changed in our study area. Stands with high cover by mountain snowberry tend to occur at lower elevations and more xeric sites than other aspen community types (Johnston et al., 2001), where SAD is also more severe (Worrall et al., 2008). Sites with substantial mountain snowberry cover in our study (sites 10 and 14, both in the Cement Creek drainage at the easternmost extent of our study area) also experienced some of the largest decreases in live aspen density (74% and 65% losses, respectively), but shrub cover in both sites was nearly identical in 1994 and 2010.

5. Conclusions

Despite abundant research, there remains considerable uncertainty surrounding the dynamics of aspen communities in the western United States. Our results illustrate the importance of detailed historic data and long-term research in gaining insight into ecological change in aspen communities. Such research is essential to broaden the temporal scale of our understanding of aspen forest dynamics (Kulakowski et al., 2013). However, the 46-year period of this study is still too short to determine whether most of the changes we observed fall within a natural progression of stand development, maturation, and deterioration in the absence of fire, or whether these processes have been substantially anthropogenically influenced.

Key findings of our study include an ongoing decrease of live aspen density, a recent decrease in live aspen basal area, and insufficient regeneration of either aspens or conifers to compensate for these losses. This pattern seems to defy traditional categorization of such aspen stands as either stable or successional (e.g., Mueggler, 1988; Kurzel et al., 2007; Rogers et al., 2010). The trajectory of these apparently healthy aspen stands also raises questions about their long-term persistence, or what kinds of communities might replace them, should observed trends persist. Understory plant species composition in our study area was relatively stable despite pronounced overstory changes, in sharp contrast to findings based on comparisons of healthy and unhealthy stands elsewhere (Anderegg et al., 2012). The stability we observed suggests a degree of resistance in aspen understory communities that may be imparted by species characteristics (e.g., tolerance to a broad range of light regimes), or that the decreases in aspen density and basal area we observed have not substantially influenced understory light availability. These findings also raise further questions,

including the rate and extent of understory changes should overstory density and basal area continue to decrease.

Future sampling efforts will be essential to improving our understanding of canopy and understory trends and temporal relationships, including the apparent lag between canopy losses and understory compositional responses. In addition to continuing long-term observational research, our findings raise questions that should be the focus of experimental approaches designed to provide managers with detailed, site-specific information. Our research suggests several key hypotheses that require further testing to understand drivers of aspen overstory and understory dynamics. These include (1) exclosure studies to determine the effects of elk and livestock on aspen regeneration and understory composition and (2) research on the effectiveness of management treatments in promoting aspen regeneration, and the consequences of such activities on understory plant communities. Accelerating losses of aspen from apparently healthy stands in the Crested Butte area suggest the maintenance of aspen communities—for both their ecological and economic value—may require applied science and informed, active management.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.01.019.

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