



The relative importance of biotic and abiotic factors influencing aspen recruitment in Arizona

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ABSTRACT

Poor recruitment in some quaking aspen (*Populus tremuloides*) stands has led to debate over which factors play the largest role in aspen forest persistence. Understanding the relative importance of the many relevant factors over a large landscape could inform management strategies regarding aspen recruitment by focusing efforts on the most important factors. Therefore, between 2011 and 2016 we collected data on 29 biotic and abiotic factors thought to affect aspen recruitment from 92 randomly-selected aspen stands growing along the southwestern limit of its distribution in Arizona, USA. We assessed the condition of selected aspen stands by quantifying the number of recently recruited aspen stems (saplings > 2 m tall and < 5 cm dbh) in each sampling plot. We used negative binomial regression to estimate the relationship between aspen recruitment and the measured covariates. We fit a balanced set of models, calculated AIC weights for those models, and summed the weights of the models containing each covariate as a measure of covariate relative importance. Six covariates had relative importance values that were significantly greater than random: fire severity in 2011, conifer encroachment, rust presence, fire severity in 2015, blight presence, and the standardized precipitation-evapotranspiration index. There were no significant differences in the ranking of these six covariates by relative importance. Although we estimated that cattle and elk had a significant negative impact on aspen recruitment, these factors were relatively unimportant. This seemingly counter-intuitive result arose because many sites lacked ungulates, but still failed to recruit aspen, indicating that other factors were more important for aspen recruitment. Our results indicate that conifer removal and increased fire activity could be among the most effective management tools to help promote aspen recruitment.

1. Introduction

Quaking aspen (*Populus tremuloides*) is the most widespread tree in North America and in the Rocky Mountain region (Little, 1971). In large portions of the interior western United States that are dominated by coniferous trees, aspen make a disproportionately large contribution to biodiversity (White et al., 1998). As an early-successional species, aspen reproduces prolifically after significant disturbance events via seeds or root suckers (Schier, 1973), although disturbance is not always required for reproduction (Kurzel et al., 2007). In some areas in its range, however, aspen have experienced very low recruitment for decades (Ripple and Larsen, 2000; Hessler and Graumlich, 2002). Aspen stands that consistently fail to recruit new trees become decadent, experiencing declines in tree vigor followed by tree death (Bartos, 2001; Smith and Smith, 2005; Kashian et al., 2007). Accordingly, understanding which factors affect aspen recruitment is a prerequisite for

developing management plans for sustaining aspen.

Multiple factors affect aspen recruitment. For example, trees must have adequate soil and moisture conditions to regenerate (Romme et al., 1995; Strand et al., 2009; Kaye, 2011). These conditions can vary spatially with latitude and elevation (Worrall et al., 2013; Rogers and Mittank, 2013), as well as with recent precipitation and drought conditions (van Mantgem and Stephenson, 2007; Rehfeldt et al., 2009). Even when climatic conditions are adequate, competition with shade-tolerant conifers can lead to poor recruitment (Kaye et al., 2005; Smith et al., 2011). Browsing by elk (*Cervus canadensis*) and other ungulates can also inhibit recruitment by stunting or removing aspen suckers (Baker et al., 1997; Kay and Bartos, 2000). Similarly, insects and disease can contribute to mortality of aspen saplings and suckers (Ziegler et al., 2012). In contrast, fire can spur aspen regeneration and recruitment by reducing competitors and stimulating seed production and sprouting (DeByle et al., 1987; Loope and Gruell, 1973).

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It is likely that all of the above factors and more affect recruitment of aspen (Kashian et al., 2007). However, most previous studies have been limited in the number of factors investigated or in the geographic area addressed (but see Wan et al., 2014; Rhodes et al., 2017). While previous univariate studies have demonstrated the effects of various factors on aspen recruitment, the diversity of studies has led to debate over which factors play the greatest role in aspen forest health in the interior western United States (Hessl, 2002). For example, ungulate browsing and fire are often identified as significant factors in aspen recruitment (Romme et al., 1995), but uncertainty about the most important factors makes it difficult to select effective management actions to counter aspen decline (Hessl, 2002). Simultaneously investigating a greater number of relevant factors over larger geographic regions will help identify factors that consistently affect aspen recruitment across a variety of conditions and better inform management strategies. Therefore, our objective was to estimate the relative importance of a large suite of biotic and abiotic factors for aspen recruitment across a large landscape in Arizona.

2. Methods

2.1. Sampling plots

Our area of interest was all aspen stands in national forests in Arizona. Identifying and selecting stands for inclusion in the study was a multi-step process. First, we obtained a geodatabase of known aspen stand locations in the Kaibab, Coconino, and Apache-Sitgreaves national forests from the U.S. Forest Service. We also obtained LandSat images covering high-elevation forested areas of Arizona in 1984 and 2014 (<https://glovis.usgs.gov>). We then used a GIS (ArcGIS 10.2, ESRI, Redlands, California) to examine LandSat image data of known aspen stands. Specifically, we quantified the reflectance of map pixels and computed a normalized difference vegetation index for each map pixel in known aspen stands. We then developed a supervised classification model (in ArcGIS 10.2, Spatial Analyst extension; Campbell, 2008) that created training samples and signature files to identify additional aspen stands within national forests using matching spectral characteristics from the LandSat data. We randomly selected 229 potential aspen stands to visit to verify the accuracy of the classification model. We classified all visited aspen stands as increasing, decreasing, or stable, based on the relative area of the stands in the LandSat images from 1984 and 2014. Finally, we used stratified random sampling to select 25 increasing, 37 decreasing, and 30 stable stands, resulting in 92 selected stands. The selected stands were located in the Kaibab ($n = 23$), Coconino ($n = 44$), Apache-Sitgreaves ($n = 22$), and Coronado ($n = 3$) national forests (Fig. 1). Aspen stands were located in larger forest areas dominated by Douglas-fir (*Pseudotsuga menziesii*), western white pine (*Pinus strobiformis*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), or Engelmann spruce (*Picea engelmannii*). Big toothed maple (*Acer grandidentatum*), Gambel's oak (*Quercus gambelii*), and New Mexican locust (*Robinia neomexicana*) were also frequently present. Sites varied in elevation from 2110 to 2934 m.

Plot design followed the Forest Inventory and Analysis of the US Forest Service (Bechtold and Scott, 2005). At the center of each of the 92 selected stands, we established a sampling plot composed of four subplots: one central subplot with three radial subplots at azimuths of 0°, 120°, and 240° (Fig. 2). The distance between the centers of the central and radial subplots was 37 m. Each subplot was circular, with a radius of 7.3 m (168.1 m²). Each subplot also contained a microplot of radius 2.1 m (13.5 m²) located 3.7 m from the center of the subplot at an azimuth of 90°. We collected field data between April 1 and November 1 in 2014, 2015, and 2016.

2.2. Data

We empirically assessed the condition of aspen stands by

quantifying the number of recently recruited aspen in each sampling plot (Wan et al., 2014; Rhodes et al., 2017). We quantified aspen recruitment as the number of saplings, i.e., trees > 2 m tall and < 5 cm dbh, as in other studies (e.g., Painter et al., 2015). While some studies have focused on other size classes, we focused on saplings because mature aspen (≥ 5 cm dbh) do not provide a useful measure of recruitment and very few suckers (≤ 2 m tall) actually recruit into the adult population (Durham and Marlow, 2010), leaving saplings as the size class most likely to contribute to aspen sustainability (Shepperd et al., 2001). We counted the number of saplings in the four microplots and used the sum as the response variable in our analysis.

We also collected data for 29 biotic and abiotic factors expected to affect aspen recruitment for use as predictor variables (Table 1). The 11 biotic factors consisted of three ungulates that browse aspen suckers (elk, deer [*Odocoileus hemionus* and *O. virginianus*] and domestic cattle [*Bos taurus*]), five diseases that affect aspen, insects that affect aspen, encroachment by competing conifers, and non-structural carbon storage. The 18 abiotic factors consisted of two measures of stand position (latitude and elevation), three terrain measures (ruggedness, percent slope, and substrate size), five aspects of climate (solar radiation, drought, precipitation, temperature, and snow), four components of soil conditions (cation exchange capacity, soil pH, carbon:nitrogen ratio, and soil type), and four types of abiotic disturbance (fire intensity in 2011, fire intensity in 2015, previous logging, and wind throw damage).

To address the question of whether ungulate presence affected aspen recruitment, we quantified ungulate activity in each sampling plot using counts of recently deposited fecal pellet piles (Ripple et al., 2001; Painter et al., 2015). We chose this metric because fecal pile counts correlate with ungulate abundance (Forsyth et al., 2007; Rhodes and St. Clair, 2018). Although some studies use measures of browse to quantify ungulate use of plots, our intent was to obtain an index that reflected all ungulates using the plot and not just those that browsed aspen within the plot. In addition, fecal pellet piles enabled us to reliably differentiate among elk, deer, and cattle. During autumn 2015, we removed fecal piles or marked them with spray paint so we could measure the deposition of new fecal piles (Lucas et al., 2004). During spring and autumn surveys in 2016, we counted all new fecal piles in the four subplots, continuing to remove or paint piles after counting them. We assigned fecal piles to species (elk, deer, or cattle) and used the number of fecal piles found during 2016 as our measure of ungulate activity for each species. Because we only counted fecal piles in 2016, our data may not reflect annual variation in ungulate use during aspen recruitment, but rather served as an index of relative ungulate activity among aspen stands, an approach previously used to assess relative habitat use (Wan et al., 2014; Rhodes et al., 2017).

During sampling plot visits, we inspected each subplot for evidence of common diseases of aspen (Hines, 1985). Specifically, we searched for blight (*Venturia tremulae*), leaf rust (*Melampsora* spp.), taphrina (*Taphrina johansonii*), canker (*Encoelia pruinosa*, *Ceratocystis fimbriata*, *Valsa sordida*, *Cryptosphaeria populina*, and *Nectria galligena*), and heart rot (*Phellinus tremulae*). We also searched for destructive insects, such as western tent caterpillars (*Malacosoma californicum*) and oystershell scale (*Lepidosaphes ulmi*; Fairweather et al., 2006). For insects and for each disease type mentioned, we recorded the percentage of the four subplots with evidence of disease or insects and used this percentage (e.g., insects detected in 3 of 4 subplots = 75%) as a metric of disease or insect use in the aspen stand.

We measured conifer encroachment during sampling plot visits because conifers compete with aspen for resources (Smith and Smith, 2005). We counted all adult (dbh > 5 cm) aspen and conifers (Douglas-fir, Engelmann spruce, limber pine [*Pinus flexilis*], ponderosa pine, western white pine, white fir) in all subplots and calculated conifers as a percent of total adult aspen and conifer trees.

We also quantified non-structural carbohydrates (NSCs) in aspen distal branches as a measure of ephemeral carbon storage. NSCs

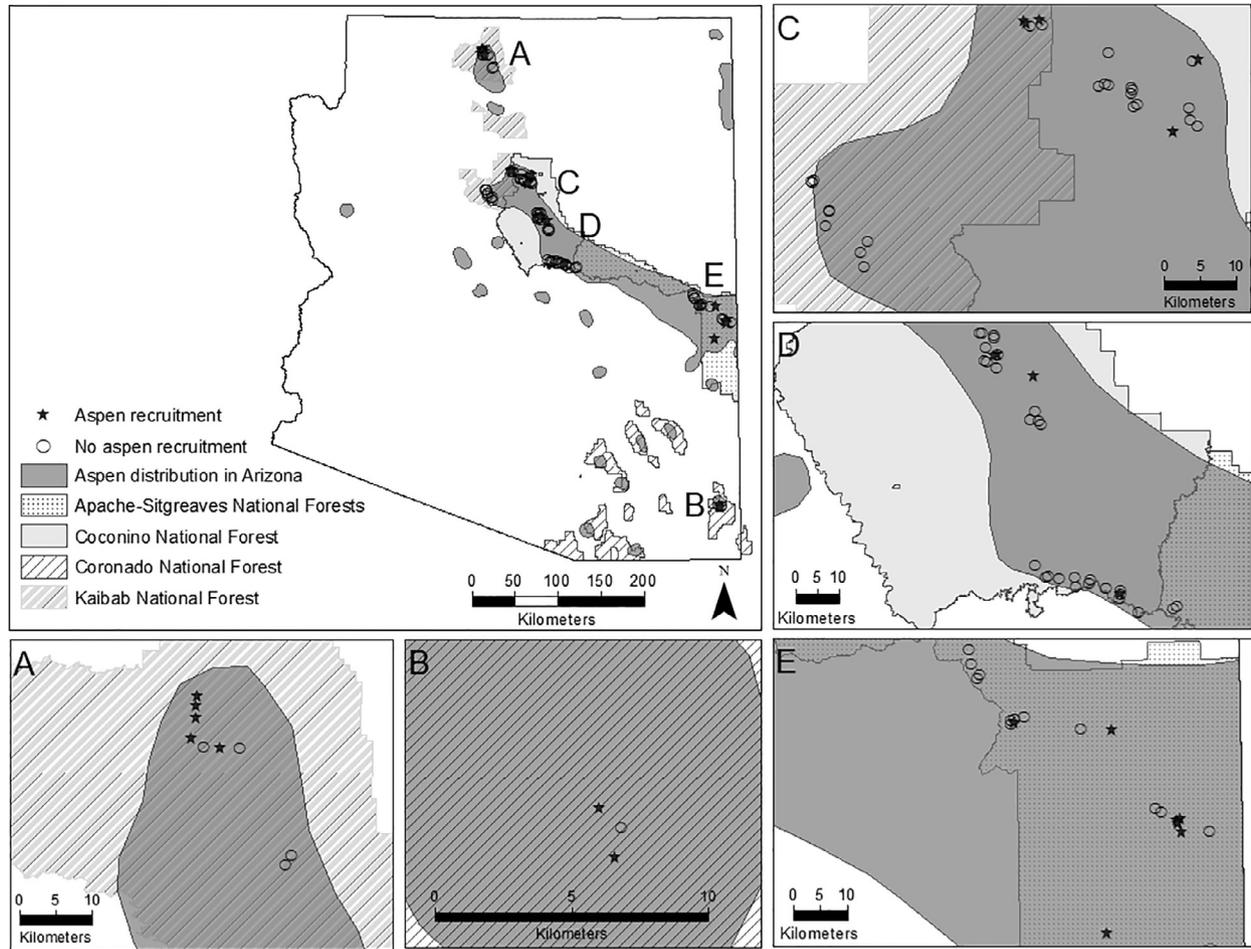


Fig. 1. Aspen distribution and sampling plots, with and without aspen regeneration, in national forests of Arizona. Aspen distribution follows Little (1971).

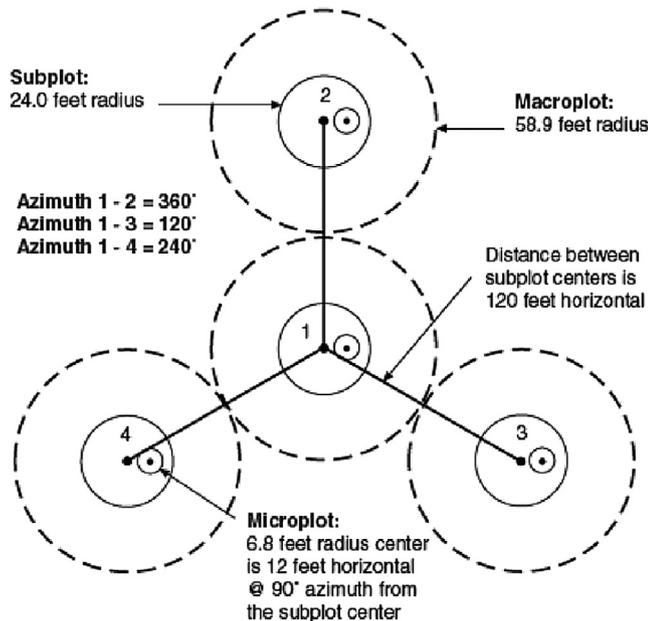


Fig. 2. USDA Forest Service forest inventory and analysis plot design (Bechtold and Scott, 2005).

contribute to plant survival and growth by contributing to transport of carbohydrates, metabolism, osmoregulation, and other functions (Anderegg, 2012). We collected 10-cm sections of distal branches

containing petioles and leaves from the upper canopy, with one branch sample collected per microplot. We quantified the soluble sugar content of the samples by drying and grinding the branch samples, extracting the soluble sugars using hot 80% ethanol, and used colorimetric analysis on the extractant to estimate soluble sugar content. We quantified starch content in the residue using enzymatic digestion and colorimetric measurement of the resulting glucose hydrolyzate (Chow and Landhäusser, 2004). We then summed the soluble sugar and starch as an estimate of NSCs.

We determined the position of sampling plots, using a GIS to extract latitude and longitude. We then used a digital elevation model to extract elevation for sampling plots. We also quantified the terrain at sampling plots because it might affect the vigor of aspen and competing trees, and because it might affect site accessibility for ungulates. We calculated the percent slope in a 30-m² cell centered on each plot and generated a ruggedness index for a 150-m² area centered on each plot (Sappington et al., 2007). We also characterized the surface substrate size at each plot by establishing a 35-m transect at each of the three radial subplots and measuring the diameter of the largest rock at each 5-m interval. We calculated the average of these 21 measured diameters at each sampling plot. We noted a bimodal distribution, with plots containing rocks either substantially larger or smaller than 50 cm diameter, and so we created a dichotomous variable indicating if the average substrate size was ≥ 50 cm (1) or < 50 cm (0).

We obtained five climate-related covariates for each sampling plot. We calculated incident solar radiation using the Solar Radiation tool in ArcMap 10.3. This tool estimated annual Watt hours/m² in a 30-m² cell centered on each plot. While aspect has been used historically as a measure of sun exposure, solar radiation is a more direct measure that

Table 1
Factors potentially affecting aspen regeneration and mean and range of values measured at 92 sampling plots in Arizona.

Factor	Units	Mean	Range
Elk (<i>Cervus canadensis</i>)	Pellet piles/plot	13.1	0–80
Deer (<i>Odocoileus hemionus</i> and <i>O. virginianus</i>)	Pellet piles/plot	2.6	0–25
Cattle (<i>Bos taurus</i>)	Pellet piles/plot	1.5	0–27
Blight (<i>Venturia tremulae</i>)	Portion of subplots with blight present	0.52	0–1
Rust (<i>Melampsora</i> spp.)	Portion of subplots with rust present	0.23	0–1
Taphrina (<i>Taphrina johansonii</i>)	Portion of subplots with taphrina present	0.16	0–1
Canker (<i>Encoelia pruinosa</i>)	Portion of subplots with canker present	0.52	0–1
Heart rot (<i>Phellinus tremulae</i>)	Portion of subplots with heart rot present	0.57	0–1
Insects	Portion of subplots with destructive insects present	0.64	0–1
Conifers	Portion of mature aspen and conifers in subplot that are conifers	0.45	0–0.96
Non-structural carbohydrates (NSC)	NSC as % of dry matter in aspen distal branches	8.6	2.4–25.6
Latitude	Degrees north	34.8	31.9–36.7
Elevation	100 m above sea level	25.12	21.10–29.34
Ruggedness	Scaled dimensionless standardized measure of vector strength in 150-m ² area	–1.05	–1.99–4.70
Slope	% slope in 30-m ² area	16	1–59
Large substrate	1/0, average substrate size \geq 50 cm	0.08	0–1
Solar radiation	annual 0.1 MWatt hours/m ² in a 30-m ² area	16.99	12.07–19.45
Standardized precipitation- evapotranspiration index	Standardized deviation of water balance from local averages over 12 months, averaged across 2011–2015	–0.75	–1.24– –0.32
Precipitation	Total annual precipitation in 100 mm, averaged across 2011–2015	6.4	5.0–9.2
Temperature	Mean annual temperature in degrees centigrade, averaged across 2011–2015	8.4	5.9–11.3
Snow	Mean snow depth in mm on Jan 1, Feb 1, and Mar 1, averaged across 2011–2015	265	27–581
Cation exchange capacity	Moles of positive charge/kg of soil	3.58	1.93–8.24
Soil pH	Negative logarithm of molar concentration of hydrogen ions in organic soil layer	6.0	4.7–7.0
Carbon-nitrogen ratio	Ratio of mass of carbon to mass of nitrogen in organic soil layer	22.0	11.4–70.6
Soil type	1: shallow, gravelly; 2: fine-textured; 3: deep, gravelly	NA	4% type 1, 85% type 2, 11% type3
Fire severity in 2011	0: no fire; 1: unchanged; 2: low; 3: moderate; 4: high	0.27	0–4
Fire severity in 2015	0: no fire; 1: unchanged; 2: low; 3: moderate; 4: high	0.08	0–2
Logging	1/0, man-made stumps present	0.69	0–1
Wind throw	% of subplots with wind throw present	20	0–100

accounts for the orientation of the plot, as well as the position on the globe and other factors (Dubayah and Rich, 1995). We also retrieved annual temperature and precipitation data from the PRISM database (Daly et al., 2008; <http://www.prism.oregonstate.edu/>). We used the mean annual temperature and total annual precipitation for the 2011–2015 time period to characterize the climate at each sampling plot. We selected this time period because it likely corresponded to the time that current saplings were growing. We obtained snow depth data from the Snow Data Assimilation System (SNODAS), maintained by the National Snow and Ice Data Center (<http://nsidc.org/data/g02158>). We extracted snow depth data at each sampling plot for January 1, February 1, and March 1 for each year, and used the mean value to characterize snow depth. To characterize drought in our study area, we used the standardized precipitation-evapotranspiration index (SPEI). The SPEI calculates a water balance from precipitation and potential evapotranspiration, with negative values indicating drought (Vicente-Serrano et al., 2010). We acquired 12-month SPEI data with 4-km spatial resolution for 2011–2015 from the West Wide Drought Tracker (Abatzoglou et al., 2017; <https://wrcc.dri.edu/wwdt/index.php>). We extracted SPEI values for each sampling plot and used the average value over 2011–2015 as a predictor.

We also acquired four measures of soil conditions. We obtained soil type data for each sampling plot from the Arizona Soils Map (Hendricks, 1985). This map divides Arizona into 64 soil associations. The sampling plots occurred in six associations, and we further aggregated these into a shallow, gravelly category (Lithic Haplustolls–Lithic Argiustolls–Rock Outcrop association and Roundtop–Tortugas–Jacks association), a deep, gravelly category (Gordo–Tatiyee association), and a moderately deep, fine-textured category (Soldier–Hogg–McVickers association, Soldier–Lithic Cryoborolls association, and Sponseller–Ess–Gordo association). We also collected 16 soil samples from each sampling plot during late autumn of

2014 to quantify soil nutrient availability. Each sample consisted of a 2.5-cm diameter soil sample from the top 10 cm of the organic soil. All soil samples from a sampling plot were combined, air dried, and sifted through a 2-mm diameter sieve.

We determined pH, the carbon:nitrogen (C:N) ratio, and cation exchange capacity (CEC) in the composite soil samples. Soil pH was determined using a 3:1 volumetric mixture of deionized water to air-dried soil. Additional analyses were carried out at the Utah State University Analytical Lab. The masses of C and N were determined using dry combustion and quantification with a TruSpec C/N autoanalyzer (LECO Corp., St. Joseph, Mo., USA). The CEC, which measures the ability of soil to hold nutrients, was determined by summing the exchangeable acidity (i.e., H and Al ions) and the exchangeable base cations (i.e., Ca, Mg, K, and Na; Martinelli et al., 1999). Base cations were extracted with 1 M ammonium acetate solution adjusted to pH 5 and concentrations were quantified with an iCAP inductively-coupled plasma spectrophotometer (Thermo Fisher Scientific, Waltham, Mass., USA). Exchangeable acidity was determined by titration of 10.0-g samples of air-dried soil (Martinelli et al., 1999).

We collected data on abiotic disturbances for each sampling plot. We obtained fire severity data from the National Monitoring Trends in Burn Severity database (Eidenshink et al., 2007; <http://mtbs.gov>) because fire promotes early successional trees such as aspen (Brown and DeByle, 1987). This database includes raster images of burn severity, with five levels of burn severity (unchanged, increased greenness, low, moderate, and high) and an unknown category. Unburned sites were recorded as 0. We coded the two lowest severity categories (unchanged and increased greenness) as 1, and the remaining categories (low, moderate, and high) as 2, 3, and 4. For two sampling plots with unknown severity, the majority (97% and 60%) of the area (excluding “unknown”) within 150 m was classified in the lowest severity category, so we classified these as category 1. We extracted burn severity

values for all sampling plots for each year from 2011 to 2015. We selected this time period because it likely corresponded to the time that current saplings were growing. Furthermore, our sampling plots experienced little fire activity between 1984 and 2010. No fires occurred in the sampling plots during 2012–2014, so we discarded these years. Although these data are ordinal, we treated them as interval data, assuming an equal effect between each category. Given our sample size, this seemed a practical approximation. We also recorded evidence of past logging because it may benefit early successional species, such as aspen (Shepperd, 2001). Specifically, we recorded the presence of stumps indicating previous logging activity as a dichotomous variable, with 1 indicating stumps present. We also recorded the presence of windthrow in each subplot because such disturbance might stimulate aspen growth and recruitment by reducing the canopy or hastening conifer succession (Man et al., 2013). We treated the percentage of subplots with windthrow (at least one uprooted or broken tree) as a metric of wind disturbance in each aspen stand.

2.3. Analyses

Our general approach was to use information theoretic methods to estimate the relative importance of the different covariates we examined in relation to aspen recruitment. We fit a balanced set of models (described below), calculated AIC weights for those models, and then summed the weights of the models containing each covariate as a measure of relative importance (Burnham and Anderson, 2002). The relative importance of each covariate can be interpreted as the probability that the covariate is in the best model in the model set (Galipaud et al., 2014).

Before fitting models, we addressed missing data points. For various reasons, 2.7% of our final data set consisted of missing values. These were concentrated in insect damage (14.1% missing), the five disease measures (13.9%), non-structural carbohydrates (8.7%), logging (6.5%), and windthrow (6.5%). Our counts of aspen saplings included no missing values. Historically, researchers have substituted mean values for missing values, which maintains the mean value of the covariate, but distorts the standard deviation. Here, we used a newer method, called multivariate imputation by chained equations (MICE; van Buuren, 2007), to fill in missing values. MICE iteratively solves a series of conditional regression models to stochastically impute missing covariate values (van Buuren, 2007). This approach maintains the mean and standard deviation of the original data set while preserving the maximum amount of usable data. We performed the imputation using the ‘mice’ package (van Buuren and Groothuis-Oudshoorn, 2011, v. 2.25) in Program R (R Core Team 2016, v. 3.2.5). We also estimated the Pearson correlation matrix for all covariates. We identified any pairs with an $R^2 > 0.5$ and eliminated one covariate from that pair from the analysis.

Our response variable, number of sapling trees > 2 m and < 5 cm dbh, was inherently limited to non-negative integers and included many zeros, as is common in tree recruitment data (Zhang et al., 2012). While sites with recruitment are required for analysis, sites lacking successful recruitment provide an informative contrast to sites with recruitment. Furthermore, discarding sites with zero saplings overestimates recruitment (Zhang et al., 2012). To avoid this bias, we retained sites lacking recruitment and considered generalized linear models for count data: poisson, negative binomial, and zero-inflated negative binomial (Atkins and Gallop, 2007; Cameron and Trivedi, 2013). These count models avoid the bias arising from analyzing count data with linear regression (O’Hara and Kotze, 2010; Zhang et al., 2012). Count models estimate the effect of covariates on the natural logarithm of the count of aspen. Exponentiated coefficients yield rate ratios, which express the multiplicative change in aspen counts for a one-unit increase in a predictor. We fit negative binomial regression models using package ‘aods3’ (Lesnoff and Lancelot, 2013, v. 0.4-1), zero-inflated negative binomial regression models using package ‘pscl’

(Zeileis et al., 2008, v. 1.4.9), and Poisson regression in the ‘base’ package in Program R. We used a likelihood ratio test to compare the fit of a negative binomial model to a Poisson model and a Vuong test for non-nested models (Vuong, 1989) to compare the fit of a zero-inflated negative binomial model to a negative binomial model. We further used parametric simulations (i.e., we fit an intercept-only model to obtain parameter estimates, and then repeatedly simulated data using the estimated parameters) to check model fit by comparing the number of zeros, ones, and the mean count size in the simulated data to the original data set (Gelman and Hill, 2007, p. 158).

After selecting the most appropriate regression type using the above tests, we developed our model set. Given our sample size of 92 sampling plots, we made an *a priori* decision to limit each model to six estimated parameters (Giudice et al., 2012), which included four covariates, as well as the intercept and the dispersion parameter. (The dispersion parameter allows the negative binomial model to estimate the variance independently of the mean, in contrast to a Poisson model, which constrains the variance to equal the mean.) We used ‘all sets’ modeling, including all possible combinations of one, two, three, or four covariates, to develop a balanced set of models (i.e., each covariate was in the same number of models). ‘All sets’ modeling is susceptible to over-fitting in the best-supported model, yielding estimated relationships that are biased away from zero (Burnham and Anderson, 2002). Because our conclusions are based on the entire model set, and not just the top model, the problem of over-fitting is ameliorated (Burnham and Anderson, 2002). After fitting the complete set of models, we calculated generalized variance inflation factors to assess multi-collinearity of covariates using package ‘car’ (Fox and Weisberg, 2011, v. 2.1–6) in Program R. We reviewed variance inflation factors and eliminated covariates, where warranted (Zuur et al., 2010).

We then fit all models, calculated AIC weights for those models, and summed the weights of the models containing each covariate as a measure of relative importance (Burnham and Anderson, 2002). We assessed the significance of the estimated relative importance in two ways. First, for each covariate, we assessed whether its relative importance was significantly higher than that expected for a random variable. We adapted an approach proposed by Burnham and Anderson (2002; p. 345–346) and, sequentially, for each covariate, randomly permuted the covariate values. We then recalculated the relative importance of covariates and determined if the relative importance of the focal covariate had increased or decreased after permutation. We repeated this permutation and calculation many times and used the incidence of increased importance after permutation as a one-tailed test of significance for covariate relative importance. Because recalculating the relative importance was computer intensive, we initially performed 100 permutations per covariate (> 6 days on two Intel Xeon quad-core X5560 processors at 2.8 GHz). Then, only for covariates that were close to significant ($0.05 < \alpha < 0.20$), we performed 400 additional permutations to obtain more precise significance tests (an additional 7 days of computing). Second, we used a bootstrap procedure to assess the significance of covariate rankings, relative to each other. Specifically, we used bootstrap resampling of sampling plots to generate 1000 bootstrapped datasets and calculated relative covariate importance for each bootstrapped data set. We made bivariate comparisons of covariate rankings across the bootstrapped data sets (e.g., covariate A outranked covariate B in 95% of data sets) and used twice the complement (e.g., 10%) as a two-tailed test of significance for the relative ranking of covariates. For both significance tests, we set $\alpha = 0.10$. We used an $\alpha > 0.05$ because of the high variance in sapling numbers, although we report the exact results of the permutation test, so readers can apply any desired significance level. We then calculated model-averaged coefficient estimates and unconditional variance estimates for each covariate to assess the size and direction of the estimated relationship with aspen sapling density (Burnham and Anderson, 2002).

3. Results

Aspen sapling counts varied widely across sampling plots, as did measured values for several factors that we anticipated might be important to aspen recruitment. All 92 sampling plots had aspen, with mature aspen (dbh > 5 cm) at 91 plots, aspen shoots (height < 2 m) at 78 plots, and aspen saplings (height ≥ 2 m, dbh ≤ 5 cm) at 24 plots. At the 24 sampling plots with saplings, the mean count was approximately 24 saplings (SD = 31) in the four microplots (4259 saplings/ha; SD = 5593), with a minimum of one sapling (180/ha) and a maximum of 118 saplings (21,293/ha). Elk, deer, and cattle fecal piles were found at 69, 51, and 27 sites, respectively. At sites with elk fecal piles, the average count summed across the four subplots was 18 piles (SD = 15 piles; equals 268 piles/ha; SD = 231 piles/ha), with a maximum of 80 (1190 piles/ha). At sites with deer fecal piles, the average count was five piles (SD = 5; equals 74 piles/ha; SD = 77 piles/ha), with a maximum of 25 (372 piles/ha). At sites with cattle fecal piles, the average count was five piles (SD = 7 piles; equals 74 piles/ha; SD = 103 piles/ha), with a maximum of 27 (402 piles/ha). Conifers were widespread in sampling plots and made up 45% of the number of mature aspen and conifer trees. If we define seral stands as stands with at least 10% conifer trees (Rogers and Mittanck, 2013), then 74 stands (80%) were seral, while 18 stands (20%) were stable. Eleven sampling plots were located in areas that had been burned by the 2011 Wallow Fire (the largest fire in Arizona history) and three sampling plots were located in areas that had been burned by the 2011 Horseshoe 2 Fire. In 2015, five additional sampling plots were burned by three smaller fires: Bull, Camilo, and Springs.

Based on goodness-of-fit tests, we determined that negative binomial regression was the most appropriate of the model types considered. A likelihood ratio test indicated the negative binomial model fit the data much better than the Poisson model $\chi^2(df = 1) = 938.3$, $p < 0.0001$. A Vuong test for non-nested models (Vuong, 1989) did not favor the zero-inflated negative binomial ($z = -0.12$, $p = 0.45$). We further checked the fit of the negative binomial model via 1000 parametric simulations. The average number of zeros (67.8), ones (4.6), and mean count (6.0) in the simulated data were nearly identical to the original data set (68 zeros, 4 ones, and mean count 6.1), further indicating that negative binomial regression was appropriate for the data set.

We eliminated two covariates due to excessive correlation with other covariates. Our Pearson correlation matrix indicated that elevation and mean temperature were strongly correlated. Furthermore, our initial all-sets regression analysis indicated that annual precipitation exhibited multicollinearity. Specifically, the maximum variance inflation factor was moderately elevated (4.9; Zuur et al., 2010), and we also noted large estimated coefficients and standard errors, which were sensitive to the covariates included in the regression, all signs of multicollinearity. Therefore, we removed mean temperature and annual precipitation from the analysis, although both were still indirectly included via the SPEI drought index.

After removing correlated covariates, we were left with 27 covariates. All combinations of up to four covariates yielded 20,853 regression models. After running all regression models, fire intensity in 2011, percent conifers, and rust presence had the greatest relative importance (Table 2). Our permutations of covariates indicated that the relative importance of six out of 27 covariates were significant ($p < 0.10$): fire severity in 2011, percent conifers, rust, fire severity in 2015, blight, and SPEI (Table 2). Our bootstrap analysis indicated no significant differences in the ranking of these six covariates by relative importance. Among the top covariates, fire severity, rust, blight, and reduced drought (i.e., high SPEI score) were all associated with increased aspen saplings (as indicated by rate ratios > 1, Table 3), although there was substantial uncertainty around the estimated effects. In contrast, conifers were associated with decreased numbers of aspen saplings.

Table 2

Relative importance of factors related to aspen saplings per sampling plot. Significance indicates the fraction of permutations in which covariate relative importance exceeded the relative importance of the covariate using the original data (* indicates significance of 1-tailed permutation test, with $\alpha = 0.10$). Factors with the same letter listed under Rank did not significantly differ in ranking (2-tailed bootstrap test, with $\alpha = 0.10$). Number of permutations or bootstrap samples in parentheses.

Factor	Relative importance	Significance (Permutations)	Rank (Bootstraps)
Fire severity in 2011	0.724	0.010* (100)	a (1000)
Conifers	0.575	0.000* (100)	a b (1000)
Rust	0.436	0.034* (500)	a b (1000)
Fire severity in 2015	0.400	0.010* (100)	a b (1000)
Blight	0.361	0.020* (100)	a b (1000)
Standardized precipitation-evapotranspiration index	0.298	0.040* (100)	a b (1000)
Canker	0.096	0.140 (500)	a b (1000)
Large substrate	0.087	0.152 (500)	a b (1000)
Taphrina	0.081	0.160 (500)	a b (1000)
Soil type	0.081	0.176 (500)	a b (1000)
Soil pH	0.074	0.204 (500)	b (1000)
Non-structural carbohydrates	0.071	0.210 (100)	b (1000)
Heart rot	0.064	0.220 (100)	b (1000)
Elevation	0.063	0.264 (500)	a b (1000)
Insects	0.062	0.250 (100)	b (1000)
Deer	0.057	0.210 (100)	a b (1000)
Latitude	0.052	0.210 (100)	b (1000)
Cattle	0.048	0.340 (100)	b (1000)
Slope	0.048	0.260 (100)	b (1000)
Elk	0.042	0.380 (100)	b (1000)
Solar radiation	0.036	0.410 (100)	b (1000)
Snow	0.035	0.470 (100)	a b (1000)
Logging	0.033	0.600 (100)	b (1000)
Carbon-nitrogen ratio	0.031	0.480 (100)	a b (1000)
Ruggedness	0.030	0.640 (100)	b (1000)
Wind throw	0.026	0.750 (100)	b (1000)
Cation exchange capacity	0.024	0.840 (100)	b (1000)

4. Discussion

This study focused on estimating the relative importance of a wide suite of biotic and abiotic factors across Arizona to help guide management strategies for supporting aspen recruitment at a large scale. We outline the major inferences we can draw from the model results and discuss each of them in more detail below. We found that recent fires (Kulakowski et al., 2013), conifer encroachment (Smith and Smith, 2005), and drought (Rehfeldt et al., 2009) were among the most important predictor variables for aspen recruitment. A more novel finding was that disease factors, such as rust and blight, were also important predictors of aspen recruitment. Furthermore, our model results estimated a relatively unimportant role for elk and other ungulates, in contrast to a number of previous studies (e.g., reviewed in Hessler, 2002). While our findings are intended to guide forest management strategies at large scales in the southwest, local management options may need to be tailored to reflect conditions at a given site.

Our analysis indicated that fire in 2011 was the single most important factor associated with aspen sapling numbers in 2015. Fire can promote aspen regeneration by removing conifers, stimulating reproduction, and reducing competition for light and nutrients (Kulakowski et al., 2013). These effects are maximized by intense, stand-replacing fires (Kashian et al., 2007; Kurzel et al., 2007). Similarly, we found that sapling numbers increased with fire intensity (Table 3). We did not age saplings in our sampling plots, but we believe many saplings on burned sites sprouted after the 2011 Wallow fire in eastern Arizona because post-fire monitoring indicated that young aspen grew up to 6 m in 3 years (A. Hartzell, AZGFD, personal communication). Similarly, unbrowsed and unburned aspen at a different location in Arizona reached sapling size in just three years (Beschta and

Table 3

Model-averaged rate ratios and confidence intervals from negative binomial regression models. The rate ratio indicates the multiplicative change in counts of aspen for a one unit increase in the given factor.

Factor	Rate ratio	Confidence interval
Fire severity in 2011	5.620	1.723–18.338
Conifers	0.017	0.000–0.889
Rust	17.152	2.099–140.189
Fire severity in 2015	9.793	0.921–104.098
Blight	45.283	0.350–5864.267
Standardized precipitation- evapotranspiration index	162.669	0.011–2323982.914
Canker	0.088	0.002–3.983
Large substrate	18.571	0.010–35316.491
Taphrina	15.039	0.051–4424.186
Soil type 2	0.676	0.000–36417.342
Soil type 3	0.011	0.000–200678.023
Soil pH	0.102	0.000–32.006
Non-structural carbohydrates	0.827	0.806–0.849
Heart rot	0.149	0.007–3.127
Elevation	1.548	1.263–1.897
Insects	5.345	0.163–175.205
Deer	1.104	1.090–1.117
Latitude	1.910	0.899–4.058
Cattle	0.788	0.727–0.854
Slope	0.951	0.947–0.955
Elk	0.963	0.955–0.970
Solar radiation	1.402	1.111–1.769
Snow	0.996	0.996–0.996
Logging	1.139	0.034–38.554
Carbon-nitrogen ratio	0.960	0.956–0.963
Ruggedness	0.799	0.524–1.219
Wind throw	0.759	0.022–26.741
Cation exchange capacity	0.797	0.499–1.273

Ripple, 2010). Fire size might also influence aspen recruitment (Mueggler and Bartos, 1977). A large-scale fire, such as the Wallow fire, may stimulate more aspen regeneration and saturate herbivores, increasing survival of young aspen. However, we were not able to analyze the effects of fire size due to a lack of replication.

We also found that fire in 2015 was the fourth most important factor associated with aspen sapling recruitment. While fire may promote aspen regeneration, it seems unlikely that new sprouts could have grown 2 m in the time between the fires and our field measurements. However, none of the 2015 fires were stand-replacing fires, with a maximum intensity of “low.” Instead these fires may have aided existing sprouts in attaining recruitment height, perhaps through removing some fire-sensitive competitors. We suspect that any stand-replacing fires in 2015 would have reduced the number of saplings, although we have no relevant data. We note that just five sites burned in 2015 and that the estimated confidence interval was wide and included (barely) 1, which would indicate no effect (Table 3). Therefore this result should be evaluated in the context of the sample size and resulting precision.

Model results indicated that mature conifers were the second most important factor affecting aspen recruitment, with a strong, negative relationship between mature conifers and aspen saplings. Aspen is an early successional species that regenerates after disturbances, but is shade intolerant (Kulakowski et al., 2013). Mature conifers may reduce aspen recruitment by increasing canopy cover and therefore creating unfavorable light conditions. Alternatively, mature conifers may indicate soil that is inhospitable to aspen (Calder et al., 2011). Conifers may be found in soils that are low in nutrients, micronutrients, and organic matter, conditions that inhibit aspen growth (Calder et al., 2011). Accordingly, shade-tolerant conifers compete well with aspen, absent disturbance (Strand et al., 2009). Among aspen stands in Colorado and Idaho with > 25% conifers, aspen recruitment was poor, and aspen overstory declined in Colorado (Smith and Smith, 2005; Strand et al., 2009). Our sites generally had a high level of conifer

encroachment, with conifers comprising 45% of mature aspen and conifer trees, indicating widespread challenges for aspen recruitment.

We also found that disease agents were of significant importance to aspen recruitment, with rust ranked third and blight ranked fifth. Interestingly, both were positively associated with aspen recruitment. Prior to analysis, we expected diseases that kill mature trees, such as cankers and heart rot, to function as disturbance events, promoting regeneration in aspen stands by stimulating root sprouts and increasing light penetration (Worrall et al., 2008; Rogers et al., 2014). In contrast, we expected diseases that affect shoots (blight) or flowers (taphrina) might reduce regeneration (Frey et al., 2003) and foliar diseases (rust) to have less impact. However, our estimates differed from our expectations, with canker and heart rot associated with reduced recruitment, while rust, blight, and taphrina were associated with increased recruitment. The unexpected result could be due to diseases responding to the density of aspen, with blight, for example, more common in sampling plots with more recruitment. Although disease agents were important in our results, few studies emphasize that relationship (Hessl, 2002). Disease agents are typically described as “contributing” or “secondary” factors that attack trees that are already weakened by drought or another primary factor (Worrall et al., 2008; Zegler et al., 2012; Kulakowski et al., 2013). Our unexpected results may warrant further study to elucidate the mechanisms at work.

The final factor with significant importance was drought. On an individual level, drought may kill trees via hydraulic failure or carbon starvation (Anderegg, 2012). Accordingly, drought has been linked to both dieback of mature aspen trees and lack of regeneration at the continental scale (Hogg et al., 2008; Rehfeldt et al., 2009; Worrall et al., 2013). In contrast, other studies have found that observed drought levels did not limit aspen regeneration (Baker et al., 1997; Ripple and Larsen, 2000; Hessl and Graumlich, 2002). Over the five years prior to surveying aspen, our study sites were typically in mild or moderate drought conditions (SPEI of -0.3 to -1.2). While not as severe as drought levels associated with large diebacks (Worrall et al., 2013), our analysis suggests this level of drought was sufficient to reduce recruitment in Arizona.

Previous studies indicate ungulates sometimes significantly inhibit aspen recruitment (Baker et al., 1997; Kay and Bartos, 2000; Kay, 2001a, 2001b; Hessl, 2002; White et al., 2003; Swanson et al., 2010; Kulakowski et al., 2013; Seager et al., 2013), including in Arizona (Rolf, 2001; Bailey and Whitham, 2002). For example, when an enclosure fence in northern Arizona was removed five years after a clearcut, the number of stems was reduced by 40% and the height of stems was reduced by 1/3 in the first year (relative to control plots), with smaller size classes most severely affected (Shepperd and Fairweather, 1994). Eleven years after a fire in northern Arizona, 316 aspen stems were established inside fenced plantations, while 2 stems were established outside fences (Fairweather et al., 2014). However, the impact of ungulates on aspen regeneration has been more muted in other studies. For example, ungulate browsing did not prevent aspen recruitment in several national forests in Utah (Smith et al., 1972). Similarly, after fires in Dixie National Forest in Utah, aspen sucker (< 2 m tall) density and height differed by just $\leq 8\%$ between sites with and without evidence of browsing (Smith et al., 2011). Still other studies found divergent results within small areas. For example, an enclosure study in Utah found that deer virtually eliminated aspen recruitment inside 0.18 ha plots, yet within a few miles, healthy aspen recruitment was observed on the site of a 1500-ha fire (Mueggler and Bartos, 1977). In southwestern Montana, elk and cattle limited aspen recruitment in unburned areas, but not in burned areas (Durham and Marlow, 2010). Aspen in the Arapaho-Roosevelt National Forest in Colorado included a mix of stable and declining stands in areas under heavy browsing pressure, suggesting factors beyond ungulate browsing affected aspen recruitment (Kashian et al., 2007).

At our sampling plots, we estimated that the effect of cattle and elk (but not deer) on aspen recruitment was significantly negative,

indicating lower sapling density at sites with higher ungulate density. Nonetheless, ungulates were relatively unimportant compared with other factors we studied. This seemingly counter-intuitive result is because other factors (e.g., fire, conifers) were more likely to belong to the best-supported model. Although a single cattle fecal pile was associated with 21% fewer aspen saplings (Table 3), many sites lacked both ungulates and aspen saplings, indicating that other factors were also important for aspen recruitment. Accordingly, our estimates of the relative importance of ungulates were relatively low.

The density of ungulate pellet piles we observed was lower than in some other studies, although differences may also reflect differences in field methods or fecal pile decomposition rates. We recorded a mean density of deer, elk, and cattle pellet piles of 39, 195, and 22 piles/ha, respectively. Figures of 394, 445, and 401 piles/ha were reported for deer, elk, and cattle from national forests in Utah (Wan et al., 2014), while 40% of sites in Utah contained more than 800 elk pellet piles/ha (Rhodes et al., 2017). In Yellowstone National Park, elk pellet pile density was 2000–4000 piles/ha before wolves were reintroduced (Ripple et al., 2001) and 400–1700 piles/ha after wolves were reintroduced (Painter et al., 2015), although these figures included both old and new pellet piles.

While recent fires, conifer encroachment, and rust were the highest ranked factors affecting aspen sapling recruitment, our rankings included a high level of uncertainty. We attribute this to a small sample size and high variation in sapling numbers. Although our 92 sampling plots were more numerous than in many previous studies, only 24 sampling plots had aspen saplings, which increased uncertainty in our estimates. Furthermore, the four sites with > 40 aspen saplings had the greatest effect on parameter estimates. Accordingly, estimates of importance varied across bootstrap samples, resulting in uncertain rankings. For example, conifers generally were one of the five most important covariates (50.1% of bootstrap samples), but ranked as low as 27th (out of 27 covariates) in 1.0% of bootstrap samples. While analyzing such overdispersed data is a challenge, the variation in sapling numbers we observed reflects the reality of aspen recruitment in Arizona.

We found recruitment into the sapling size class at 24 of 92 sites (26%). The implications for the long-term sustainability of aspen, however, remain unclear. Certainly, if 74% of sites never recruit new aspen saplings, future aspen persistence at those sites is unlikely. However, it is common for tree stands to go years with no recruitment (Zhang et al., 2012), especially for a disturbance-dependent species like aspen (Kurzel et al., 2007). At one extreme, aspen recruitment was rare among unburned sites in Montana (3%; Durham and Marlow, 2010), among unfenced sites in Wyoming (14%; Kay, 2001b), and at sites in northern Arizona (21%; Ziegler et al., 2012). However, recruitment was more common at unfenced plots in Utah (50%; Kay and Bartos, 2000) and in northern Colorado (72%; Kashian et al., 2007), and recruitment was relatively widespread at selected unfenced sites in Utah (92%, Rhodes et al., 2017) and in Colorado (100%; Kurzel et al., 2007). Additional studies of long-term aspen dynamics could better inform the amount of recruitment that is required for sustainable aspen forests.

A particular feature of our study was the large geographic span, covering the range of aspen within Arizona (Fig. 1). Our study therefore covered a wide range of biotic and abiotic conditions that could affect the relationship between elk and aspen. The range of conditions created an opportunity to generate inferences across a large geographic and environmental range, and allowed us to measure a suite of covariates across a range of naturally-occurring values (see also Wan et al., 2014; Rhodes et al., 2017). These covariates provided a means to develop a multivariate analysis designed to estimate the relative importance of various factors that are suspected to affect aspen recruitment. In contrast, spatially-restricted studies may not represent the larger landscape, yielding unrepresentative results (Barnett and Stohlgren, 2001; Kaye et al., 2001). While not unique to this study, we argue that our random selection of study sites strengthened our inferences (Kaye et al.,

2001). In contrast, if study plots are subjectively placed in areas thought to incur severe elk damage, elk impacts may be overestimated (Barnett and Stohlgren, 2001; Kaye et al., 2001).

Because our study sites were near the southern limits of the range for aspen, our results may not hold across the range of aspen. In Arizona, aspen are found in areas that are relatively warm, dry, high elevation, and rugged with limited snowfall. The ungulate species and competing tree species found in Arizona differ from those found in some portions of the range. Therefore, the relative importance of these factors may differ in other regions in ways that are difficult to predict.

Our cross-sectional study essentially represents a “snapshot” of a long-term dynamic process. The saplings we studied sprouted several years before we began data collection and sprouts emerged, grew, and died during those years. We were not able to measure biotic and abiotic conditions throughout those years, nor record the growth and survival processes that yielded the saplings we observed. Our study could be complemented by future longitudinal studies that might yield additional inferences about aspen recruitment.

4.1. Management implications

We found that recent fire intensity, conifers in the overstory, several disease factors and drought had the greatest relative importance for aspen recruitment in Arizona, although there was some uncertainty about the rankings of these factors. In contrast, we found that our index of ungulate activity was relatively unimportant to aspen recruitment. Our results suggest that conifer removal and application of moderate to high intensity fire would be the most useful management tools to benefit aspen recruitment, consistent with findings in Oregon and California (Jones et al., 2005; Endress et al., 2012; Krasnow et al., 2012). We note that studies in other regions have raised concerns that fire may exacerbate aspen decline in areas with high elk density if fire kills mature trees, while elk consume new shoots (Bartos et al., 1994; White et al., 1998; Kay, 2001a; Smith et al., 2016). In these areas, management options include using mechanical conifer removal instead of prescribed fire, or implementing large or multiple simultaneous prescribed fires to saturate herbivores.

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