

Sustainability and drivers of *Populus tremuloides* regeneration and recruitment near the southwestern edge of its range

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Abstract

Quaking aspen (*Populus tremuloides* Michx.) ecosystems are highly valued in the southwestern United States because of the ecological, economic, and aesthetic benefits they provide. Aspen has experienced extensive mortality in recent decades, and there is evidence that many areas in Arizona, United States lack adequate recruitment to replace dying overstory trees. Maintaining sustainable levels of regeneration and recruitment (i.e. juveniles) is critical for promoting aspen ecosystem resilience and adaptive capacity, but questions remain about which factors currently limit juvenile aspen and which strategies are appropriate for managing aspen in an increasingly uncertain future. To fill these critical knowledge gaps, we sampled aspen populations across Arizona and collected data representing a suite of biotic and abiotic factors that potentially influence juvenile aspen. Specifically, we addressed two questions: (i) Is aspen sustainably regenerating and recruiting in Arizona? and (2) Which biotic and abiotic factors significantly influence aspen regeneration and recruitment? We found that many aspen populations in Arizona lack sustainable levels of juvenile aspen, and the status of recruitment was especially dire, with 40% of study plots lacking a single recruiting stem. Aspen regeneration was less abundant on warmer sites than cooler ones, highlighting the threat that a rapidly warming climate poses to aspen sustainability. Aspen recruitment was significantly more abundant in areas with recent fire than in areas without fire, and recruitment had a strong positive relationship with fire severity. The most important limiting factors for aspen recruitment were ungulate browse, especially by introduced Rocky Mountain elk (*Cervus canadensis nelsoni*), and the invasive insect, oystershell scale (*Lepidosaphes ulmi*). We conclude with a discussion of how management can promote sustainability of aspen populations by addressing the array of threats that aspen faces, such as a warming climate, chronic ungulate browse, and outbreaks of oystershell scale.

Keywords: fire; forest health; oystershell scale; quaking aspen; structural equation modeling; ungulate exclosures

Introduction

Forests across the globe have experienced extensive mortality in recent decades due to climate change, insect and disease outbreaks, novel disturbance regimes, and interactions among these factors (van Mantgem *et al.* 2009; Anderreg *et al.* 2013; Senf *et al.* 2018; Stanke *et al.* 2021). A notable example of a tree species that has experienced widespread mortality in the western United States is quaking aspen (*Populus tremuloides* Michx.; hereafter aspen) (Worrall *et al.* 2013). Aspen mortality has received substantial attention because of the extent and severity of mortality events and because of aspen's role as a foundation species (Campbell and Bartos 2001; Ellison 2019; Rogers *et al.* 2020). Aspen ecosystems provide critical habitat for many plants, animals, invertebrates, and fungi (DeByle 1985; Rogers 2017) and make a disproportionately large contribution to biodiversity (Chong *et al.* 2001; Kuhn *et al.* 2011). Aspen also has important aesthetic and cultural value, making issues of aspen forest health relevant to the public and to local communities that benefit from aspen-driven tourism and recreation (McCool 2001; Assal 2020). Aspen

mortality events across western North America have been thoroughly studied, revealing two pathways of stand-scale mortality: (i) long-term successional replacement of aspen by conifers in the absence of stand-replacing disturbance (Kay 1997) and (ii) acute mortality events caused by interactions between predisposing, inciting, and contributing factors (Manion 1991; Worrall *et al.* 2013). Drought is the inciting factor driving acute aspen mortality, while specific site factors (e.g. aspen at low elevations and on south-facing aspects) predispose aspen to mortality and biotic agents [e.g. Cytospora canker (caused by *Cytospora* spp.) and bark beetles] contribute to mortality (Frey *et al.* 2004; Marchetti *et al.* 2011; Worrall *et al.* 2013; Singer *et al.* 2019). Despite the attention that recent aspen mortality events have received, there is also ample evidence of aspen expansion facilitated by severe disturbance, particularly from Colorado, United States (Zier and Baker 2006; Kulakowski *et al.* 2013; Andrus *et al.* 2021; Nigro *et al.* 2022). We argue that overstory mortality should only be a major concern when there is inadequate regeneration and recruitment (i.e. juveniles) to replace dying trees.

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Aspen populations along the southwestern edge of the species' range have experienced especially high levels of mortality (Fairweather et al. 2008; Ganey and Vojta 2011; Zegler et al. 2012; Ireland et al. 2014), and in many areas, there is inadequate recruitment to offset mortality (Martin 2007; Beschta and Ripple 2010; Zegler et al. 2012; Clement et al. 2019). Although the processes of aspen regeneration and recruitment have been studied less thoroughly than aspen mortality, we understand how individual factors influence juvenile aspen (Crouch et al. 2023). Regeneration refers to the process of new trees establishing, either as seedlings germinating from seed or suckers sprouting from an existing root system, whereas recruitment refers to the successful growth of regenerating stems into overstory trees (Crouch et al. 2023). Fire promotes abundant regeneration and recruitment (Rolf 2001; Bailey and Whitham 2002; Shepperd 2004; Higgins et al. 2015; Stoddard et al. 2018; Clement et al. 2019; Kreider and Yocom 2021), whereas ungulate browse has a strong negative influence on juvenile aspen (Shepperd and Fairweather 1994; Rolf 2001; Bailey and Whitham 2002; Binkley et al. 2006; Beschta and Ripple 2010; Zegler et al. 2012; Fairweather et al. 2014). Competition with conifers inhibits aspen regeneration and recruitment (Zegler et al. 2012; Clement et al. 2019), and certain insects and diseases contribute to mortality of aspen juveniles (Jacobi and Shepperd 1991; Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Zegler et al. 2012; Crouch et al. 2021). There is also evidence that drought negatively influences aspen recruitment (Zegler et al. 2012; Clement et al. 2019). However, the relative strength of, and potential interactions between, these influencing factors remain unknown (Crouch et al. 2023). In addition, previous studies of juvenile aspen were conducted before outbreaks of an invasive insect, oystershell scale (*Lepidosaphes ulmi*), began contributing to acute mortality of aspen in Arizona, United States and other western states (Crouch et al. 2021, 2024). The recent emergence of oystershell scale, paired with gaps in our knowledge about the relative strength of factors influencing regeneration and recruitment, have left scientists and managers unsure how to sustain aspen.

Maintaining healthy aspen ecosystems is an important land management objective in Arizona (USDA Forest Service 2014, 2018), which is situated near the southwestern edge of aspen's contiguous range (Little 1971; Zegler et al. 2012). To meet this objective, contemporary aspen management tends to conserve existing aspen stands at all costs (Crouch et al. 2023). For example, common management tactics include clearfelling declining aspen stands to establish a healthy cohort of regeneration and building fenced exclosures around existing aspen stands to reduce ungulate browse and, thereby, promote recruitment (Shepperd and Fairweather 1994; Rolf 2001; Shepperd 2004). However, these tactics alone are not sufficient for addressing the full array of threats to aspen sustainability (a term we use to refer to aspen's capacity for self-replacement via regeneration and recruitment, Dey 2014), which include a warming climate, increased fire activity, chronic ungulate browse, and outbreaks of oystershell scale (Crouch et al. 2023). Instead, management must shift its focus from conserving existing aspen stands to promoting aspen ecosystem resilience and adaptive capacity via sustainable regeneration and recruitment (Holling and Meffe 1996; Millar et al. 2007; Schoettle et al. 2019; Crouch et al. 2023). Resilience refers to an ecosystem's capacity to absorb disturbance and reorganize such that pre-disturbance composition, structure, and function are eventually reattained, whereas adaptive capacity refers to an ecosystem's ability to adjust its composition, structure, and function in response to external forces (Holling and Meffe 1996;

Millar et al. 2007; DeRose and Long 2014; Puettmann et al. 2013; Nagel et al. 2017). Management strategies to increase resilience and adaptability should include promoting diversity in age structure across the landscape by enhancing regeneration and recruitment and mitigating negative impacts of ungulate browse on recruitment (Crouch et al. 2023). Indeed, juvenile aspen success is considered a key indicator of ecosystem sustainability (Shepperd et al. 2006; Rogers 2017; Kitchen et al. 2019). To develop tactics consistent with these new strategies, managers must understand which biotic and abiotic factors currently inhibit aspen regeneration and recruitment and which tactics successfully promote juvenile aspen in the face of these threats.

To fill these critical knowledge gaps, we sampled aspen populations across Arizona to assess the abundance and health of juvenile aspen. We collected data representing a suite of biotic and abiotic factors that potentially influence aspen regeneration and recruitment, and we used structural equation modeling (SEM) to assess the direct and indirect influence of these factors on aspen juveniles. Specifically, we addressed two questions: (i) Is aspen sustainably regenerating and recruiting in Arizona? (ii) Which biotic and abiotic factors significantly influence aspen regeneration and recruitment in Arizona?

Materials and Methods

Study area

Our study area encompassed aspen ecosystems throughout AZ, United States (Fig. 1a, b) (Little 1971; Perala 1990). In contrast to more northerly latitudes, aspen ecosystems in Arizona are a relatively rare feature on the landscape, occupying less than 2% of forested land (Johnson 1994; Rolf 2001; Gitlin et al. 2006; Zegler et al. 2012). On the southwestern edge of its range, aspen is limited to relatively high elevations, where lower temperatures and higher precipitation allow this drought-intolerant species to survive (Perala 1990; Rehfeldt et al. 2009). Aspen can be found as low as 2000 m in elevation in the ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.) forest type, where small pockets of aspen occur on north-facing slopes or in drainages with increased water availability (Rasmussen 1941; Covington et al. 1983; Martínez González and González-Villarreal 2005; Fairweather et al. 2008; Zegler et al. 2012). As elevation increases into the mixed-conifer and, in some areas, spruce-fir forest types, the aspen component tends to be more abundant and less aspect-limited (Rasmussen 1941; Merkle 1962; Fairweather et al. 2008; Zegler et al. 2012). In these forest types, aspen occurs not only in pure stands but also in mixed stands with conifers, including ponderosa pine and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissn.] Franco) at lower elevations, white pine (*Pinus strobus* Engelm. or *Pinus flexilis* James var. *reflexa* Engelm.) and white fir (*Abies concolor* [Gord. & Glend.] ex Hildebr.) at mid elevations, and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt. var. *arizonica* [Merriam] Lemmon) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) at the highest elevations, where aspen reaches its upper limit above 3000 m.

Site selection

We sampled 220 aspen plots that represent the range of conditions under which aspen exists in Arizona (Fig. 1b). These plots were located across seven major areas: North Kaibab ($n=19$), South Kaibab ($n=26$), Flagstaff ($n=113$), Mogollon Rim ($n=13$), White Mountains ($n=25$), Prescott ($n=17$), and Coronado ($n=7$) (Fig. 1b). All data were collected during the 2020, 2021, and 2022 growing seasons (June–October), when aspen trees had leaves.

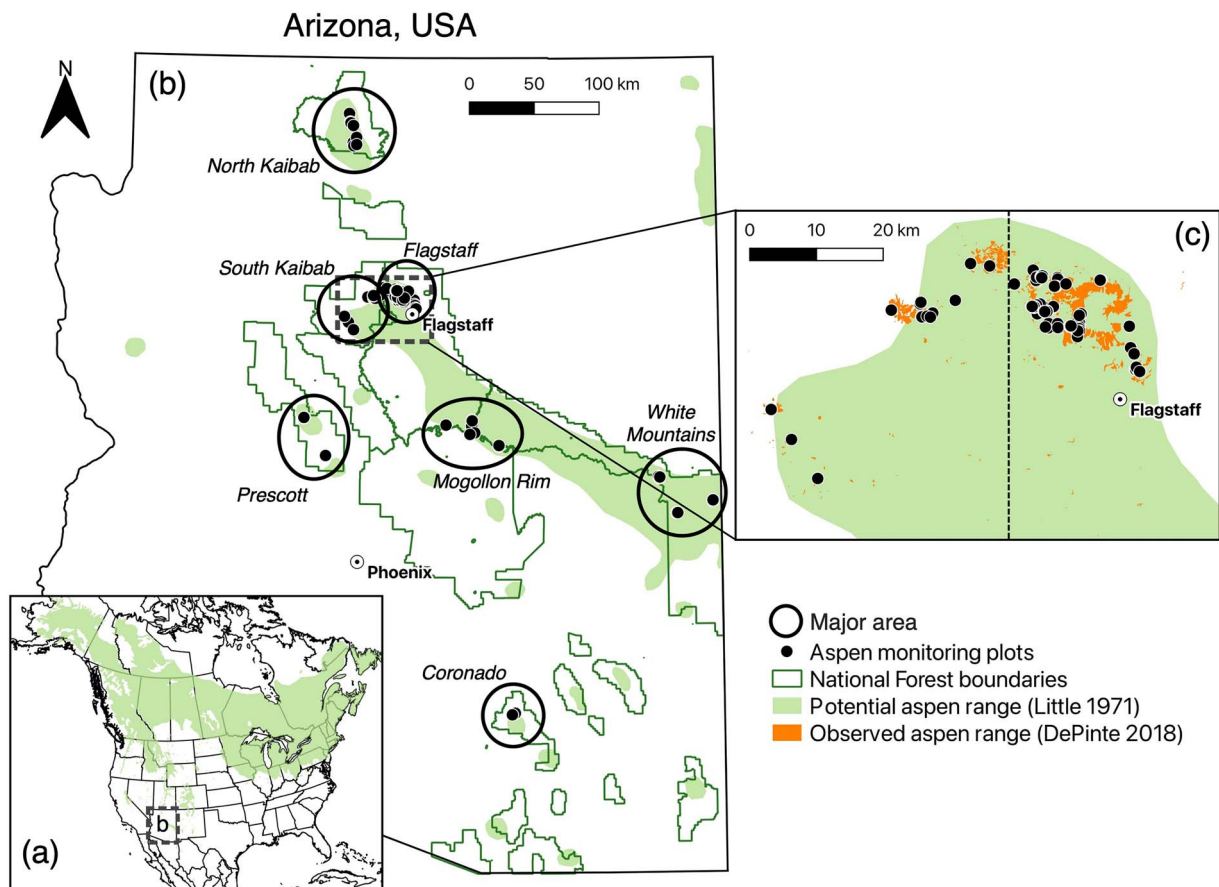


Figure 1. Maps showing (a) the location of our study area on the southwestern edge of aspen's range in North America, (b) the locations of our 220 aspen study plots across 7 major areas (in *italics*) where aspen occurs in AZ, United States, and (c) locations of study plots surrounding Flagstaff, AZ, which includes the South Kaibab (west of dotted line) and Flagstaff (east of dotted line) major areas; this map also shows the observed range of aspen (orange polygons) based on direct observations from an aircraft (DePinte 2018).

Most of our sampling occurred around Flagstaff because of the wide range of sites that aspen occupies in this area (Fig. 1c).

To ensure we obtained a representative sample of aspen sites and conditions, we stratified sites across four variables—elevation (≤ 2400 m, >2400 m); aspect (north/east, south/west); ungulate management [none, fenced exclosure (2-m-tall fences built around aspen stands to exclude ungulates) or jackstraw treatment (large piles of woody debris protecting aspen regeneration from ungulate browse)]; and fire history (0–2 years post-fire, 2–20 years post-fire, >20 years post-fire; included wildfire and prescribed fire)—resulting in 24 strata. We first sought to obtain one plot for each stratum, which we accomplished for 21 of the 24 strata, before building out a sample that was proportional to how much aspen actually occurs in each stratum. We assessed aspen's actual occurrence in each stratum using a GIS layer of aspen's observed range on three ranger districts surrounding Flagstaff (Flagstaff and Mogollon Rim Ranger Districts of the Coconino National Forest; Williams Ranger District of the Kaibab National Forest) (DePinte 2018). Although this layer covers only three of the nine ranger districts we sampled, it is the most accurate estimation of where aspen occurs in Arizona because it is a fine-scale layer of aspen's recent presence based on direct observations from an aircraft (DePinte 2018). We compared the proportion of aspen observed on the landscape, based on area from the GIS layer, to the proportion of aspen plots we sampled, based on the number of plots that fell into each stratum. We succeeded in obtaining a representative sample

across elevation, aspect, and fire history, with proportions of aspen observed in each stratum versus aspen sampled differing by less than 7% for each stratum (Table 1). Due to a lack of accurate GIS data documenting where fenced exclosures and jackstraw treatments occur across the three ranger districts, we were not able to assess how much aspen occurs in areas treated for ungulate management. Instead, we sampled these areas evenly across strata, resulting in roughly one-third of plots occurring in ungulate management treatments (Table 1).

When possible, we prioritized remeasurement of existing aspen monitoring plots to reduce the number of redundant plots on the landscape and to facilitate research permission on national forest land. We revisited plots previously established by the Coconino National Forest ($n=44$), the Apache-Sitgreaves National Forest ($n=5$), Zegler et al. (2012) ($n=20$), and Northern Arizona University's Ecological Restoration Institute ($n=12$). All four of these networks established plots using stratified or completely random sampling, ensuring the locations of these plots lacked bias. In addition to these existing plots, we established the remaining 139 plots by identifying aspen stands that filled target strata, standing on the edge of selected stands, laying out a linear transect longways based on stand shape, and establishing plots every 30 m along the transects. The Coconino National Forest, Apache-Sitgreaves National Forest, and Ecological Restoration Institute plots were also established along transects with plot spacings ranging from 100 to 300 m. The Zegler et al. (2012) plots that we re-sampled were initially established by randomly

Table 1. Proportion of aspen observed, based on area, compared with proportion of aspen sampled across AZ, based on number of plots in each stratum, across four elevation and aspect classes, fire occurrence in the past 20 years, and presence of ungulate management (fenced exclosure or jackstraw treatment).

Stratum	Aspen area observed (%)	Aspen plots sampled (%)	Aspen plots sampled (#)	Observed – sampled (%)
≤2400 m, SW aspect	3.7	6.4	14	–2.7
≤2400 m, NE aspect	12.8	13.2	29	–0.4
>2400 m, SW aspect	46.0	49.5	109	–3.5
>2400 m, NE aspect	37.6	30.9	68	6.7
Fire in past 20 years	35.6	36.8	81	–1.2
Ungulate management	unknown	32.3	71	na

Proportion of aspen observed was calculated using an aerial survey of aspen occurrence within the Flagstaff, Mogollon Rim, and Williams Ranger Districts of the Coconino and Kaibab National Forests (DePinte 2018).

locating points within known aspen stands and sampling four plots in each cardinal direction 20 m from the randomly located point.

Field data collection

Each study plot consisted of two fixed-area, circular plots: an overstory plot (8-m radius) and a nested regeneration plot (4-m radius) sharing the same plot center (adapted from Zegler et al. 2012). We collected GPS coordinates at the center of each study plot, recorded whether the plot fell in an area of ungulate management (i.e. fenced exclosure or jackstraw treatment), and noted whether there was evidence of recent conifer removal, as indicated by cut conifer stumps present in or directly adjacent to the plot. The objective of these conifer removal treatments varied depending on stand composition and location, but common objectives included mitigating high-severity wildfire risk, reducing likelihood of western spruce budworm (*Choristoneura freemani*) outbreaks, promoting aspen juveniles, or a combination of these. For a plot to be included in our study, it had to contain at least five live aspen stems between the 8-m overstory and 4-m regeneration plots combined (Looney and Waring 2012). In the overstory plots, all trees with diameter at breast height (dbh; height = 1.37 m) >12.7 cm were measured. In the regeneration plots, all trees >0.02 cm in height and <12.7 cm dbh were measured. In the regeneration plots, we classified stems into two size classes: regeneration (<1.37 m tall) and recruitment (>1.37 m tall and <12.7 cm dbh). We chose a regeneration-recruitment threshold height of 1.37 m to be consistent with previous studies of aspen juveniles in Arizona (Binkley et al. 2006; Zegler et al. 2012). We chose 12.7-cm dbh as the cutoff between recruiting and overstory trees to be consistent with how forest inventory data are typically collected by the USDA Forest Service (USDA Forest Service 2024). For all live aspen, we recorded dbh (except for stems that were <1-cm dbh) and height. For every dead aspen and live tree species other than aspen, we recorded size class and dbh.

For all live aspen, we documented the top three damaging agents present on each tree (Zegler et al. 2012). When more than three damaging agents were present, preference was given to agents with the greatest severity of impact (i.e. most likely to cause dieback and mortality) (Zegler et al. 2012). These damaging agents included insects, diseases, ungulate browse, other animal damage, and abiotic damages. For insects and diseases, we grouped individual species into functional groups to facilitate analysis and because some biotic damages (e.g. defoliating insects) were impossible to identify based solely on the damage they caused. These functional groups included sucking and gall-forming insects (excluding oystershell scale), bark beetles, wood-boring insects, defoliating insects, canker-causing diseases, foliar

and shoot diseases, and decay diseases (USDA Forest Service 2013; Steed and Burton 2015). We assessed oystershell scale and certain cankers individually because of their potential to have outsized impacts on aspen tree health compared with native insect species and less pathogenic diseases (Hinds 1985; Zegler et al. 2012; Crouch et al. 2021, 2023, 2024). The cankers we assessed individually were *Cytospora* canker, *Hypoxylon* canker (caused by *Entoleuca mammatum*), *Ceratocystis* canker (caused by *Ceratocystis* spp.), and sooty bark canker (caused by *Encoelia pruinosa*). We lumped all abiotic damages together, which included fire scarring of stems, foliar drought scorch, and foliar chlorosis. We assessed animal damage to aspen stems, including browse, ungulate barking (i.e. elk chewing aspen bark), and other animal damage. We also indirectly quantified ungulate impacts by counting ungulate scat piles within the 8-m overstory plot. We identified scat piles by species [i.e. elk (*Cervus canadensis nelsoni*), deer (*Odocoileus hemionus* or *Odocoileus virginianus couesi*), or cattle (*Bos taurus*)] and treated piles from the same species as distinct when piles were clearly separated, contained more than three pellets, and differed in color or size (Bunnefeld et al. 2006; Rhodes and St. Clair 2018).

Data calculations

Using tree height and diameter data, we calculated our three response variables: density (trees ha^{−1}) of live aspen regeneration, live aspen recruitment, and dead aspen recruitment. We did not use dead aspen regeneration density as a response variable because evidence of dead regenerating stems disappears quickly (Zegler et al. 2012). We also calculated density (trees ha^{−1}) of live overstory aspen, dead overstory aspen, live overstory tree species other than aspen, live overstory conifers, live regeneration of tree species other than aspen, and live conifer regeneration (Table 2). We used diameter data to calculate basal area for live aspen, dead aspen, live tree species other than aspen, and live conifers (Table 2). Using the presence/absence data for all damaging agents on each live aspen stem, we calculated the proportion of stems affected by each agent in each plot (Table 2).

Using the GPS coordinates we collected at each plot's center, we calculated elevation, aspect, and slope using a 30-m² digital elevation model (Table 2). We transformed raw aspect in radians (A) into a continuous variable (A') ranging from 0 to 2, with 0 representing southwest (225°) and 2 representing northeast (45°), using the following equation from Beers et al. (1966):

$$A' = \sin(A + 45) + 1. \quad (1)$$

We also calculated heat load (HL) and potential annual direct radiation (PAR), two indices that assess site-level temperature using slope (S), aspect (A), and latitude (L), all in radians, based

Table 2. List of 69 variables considered as potential influencing factors of aspen regeneration and recruitment, and plot-level ($n = 220$) mean and range are shown for continuous variables, whereas percentage of plots in each category is shown for categorical variables.

Influencing factor	Mean	Range
Stand structure		
Live aspen basal area ^a	10.3	0–55.9
Dead aspen basal area	4.3	0–47.1
Live non-aspen basal area	10.2	0–78.1
Live conifer basal area	10.0	0–78.1
Live aspen overstory density ^b	172	0–1194
Dead aspen overstory density	67	0–846
Live non-aspen density	1769	0–34 268
Live conifer density	1057	0–34 268
Live non-aspen regeneration density	1648	0–33 820
Live conifer regeneration density	939	0–33 820
Ungulate impacts		
Browse ^c	0.30	0–1
Ungulate barking ^c	0.03	0–0.85
Total ungulate scat ^d	2.6	0–35
Elk (<i>Cervus canadensis nelsoni</i>) scat	1.3	0–23
Deer (<i>O. hemionus</i> and <i>O. virginianus couesi</i>) scat	1.1	0–29
Cattle (<i>B. taurus</i>) scat	0.3	0–20
Damaging agents ^c		
Oystershell scale (<i>Lepidosaphes ulmi</i>)	0.15	0–1
Sucking and gall-forming insects (excluding oystershell scale)	0.09	0–0.80
Bark beetles	0.01	0–0.20
Wood-boring insects	0.22	0–0.83
Defoliating insects	0.60	0–1
Cytospora canker (caused by <i>Cytospora</i> spp.)	0.02	0–0.34
Hypoxylon canker (caused by <i>Entoleuca mammatum</i>)	0.002	0–0.10
Ceratocystis canker (caused by <i>Ceratocystis</i> spp.)	0.02	0–0.42
Sooty bark canker (caused by <i>Encoelia pruinosa</i>)	0.001	0–0.05
All cankers	0.33	0–1
Foliar and shoot diseases	0.19	0–0.94
Decay diseases	0.04	0–0.67
Abiotic damage	0.01	0–0.61
Other animal damage (excluding browse and barking)	0.01	0–0.15
Fire		
Fire strata ^e	1 (14.1%), 2 (22.7%), 3 (63.2%)	
Fire severity ^f	1 (65.5%), 2 (9.1%), 3 (11.4%), 4 (8.2%), 5 (5.9%)	
Burned twice ^g	0 (95.0%), 1 (5.0%)	
Management		
Ungulate management ^h	0 (67.7%), 1 (32.3%)	
Conifer removal ⁱ	0 (87.7%), 1 (12.3%)	
Site factors		
Elevation (m above sea level)	2543	1976–3038
Aspect ^j	0.98	0–2
Slope (°)	7.9	0.1–29.7
Heat load (MJ cm ^{−2} year ^{−1})	0.98	0.71–1.08
Radiation (MJ cm ^{−2} year ^{−1})	0.96	0.64–1.09
Major area ^k	1 (3.2%), 2 (51.4%), 3 (5.9%), 4 (8.6%), 5 (7.7%), 6 (11.8%), 7 (11.4%)	
UTM easting	453 804	358 542–674 303
UTM northing	3 880 092	3 589 116–4 052 723
Soils		
Soil order ^l	1 (2.7%), 2 (14.1%), 3 (13.2%), 4 (70.0%)	
Influencing factor		
Soil pH in H ₂ O (pHx10)	63.4	55.4–71.4
Cation exchange capacity (CEC) (mmol(c) kg ^{−1} at pH 7)	232.9	176.3–272.2
Nitrogen (cg kg ^{−1})	110.0	80.0–188.3
Soil organic carbon content (dg kg ^{−1})	135.2	93.8–193.9
Bulk density (cg cm ^{−3})	147.5	130.1–157.8
Sand content (g kg ^{−1})	321.7	187.5–592
Clay content (g kg ^{−1})	269.1	129.7–397.7
Volumetric fraction of coarse fragments (cm ³ dm ^{−3})	179.2	75.2–293.0
Climate		
Precipitation as snow (annual) ^m	125.8	22.0–380.8
Winter temperature (mean) ⁿ	−0.4	−3.8–4.1

(Continued)

Table 2. Continued

Influencing factor	Mean	Range
Spring temperature (mean)	6.4	3.1–10.6
Summer temperature (mean)	17.0	13.5–21.2
Autumn temperature (mean)	8.7	5.4–12.9
Summer temperature (maximum)	25.0	20.9–28.7
Winter temperature (minimum)	−7.1	−10.1– −1.7
Winter precipitation ^m	240.4	157.2–420.0
Spring precipitation	130.0	70.8–198.2
Summer precipitation	191.3	106.8–375.6
Autumn precipitation	130.7	80.4–291.0
Winter climate moisture index (CMI) ^o	19.1	11.5–35.3
Spring CMI	−5.2	−15.2–8.4
Summer CMI	−24.7	−38.8–3.7
Autumn CMI	−10.3	−18.3–5.9
Annual dryness index ^p	0.06	0.04–0.09
Monsoon index ^p	0.28	0.18–0.36

^abasal area = m² ha^{−1}. ^bdensity = trees ha^{−1}. ^cproportion of aspen stems affected by damaging agent. ^dscat = pellet piles/plot. ^ecategorical: 1 (0–2 years since fire), 2 (2–20 years since fire), and 3 (>20 years since fire). ^fcategorical: 1 (unburned in past 20 years), 2 (unburned/low), 3 (low), 4 (moderate), and 5 (high). ^gcategorical: 0 (burned <2 times in past 20 years) and 1 (burned twice in past 20 years). ^hcategorical: 0 (no ungulate management) and 1 (exclosure or jackstraw). ⁱcategorical: 0 (no treatment) and 1 (conifer removal). ^j0–2 (0 = 225°, 1 = 135° or 315°, 2 = 45°). ^kcategorical: 1 (Coronado), 2 (Flagstaff), 3 (Mogollon Rim), 4 (North Kaibab), 5 (Prescott), 6 (South Kaibab), and 7 (White Mountains). ^lcategorical: 1 (Inceptisols), 2 (Mollisols—Borolls), 3 (Mollisols—Ustolls), and 4 (Alfisols). ^mprecipitation = mm. ⁿtemperature = °C. ^oCMI = mm. ^psee Materials and Methods for equation. Seasons for climate variables are winter (December–February), spring (March–May), summer (June–August), autumn (September–November). See Supplementary Table 1 for means and standard errors of the 62 continuous variables across each of the seven major areas where aspen occurs in Arizona. See Supplementary Table 2 for the percentage of plots occurring in each level of the seven categorical variables we considered, along with their standard errors.

on the following equations from McCune and Keon (2002):

$$HL = 0.339 + 0.808 * \cos(L) * \cos(S) - 0.196 * \sin(L) * \sin(S) - 0.482 * \cos\left(\pi - \left[A - 5 * \frac{\pi}{4}\right]\right) * \sin(S) \quad (2)$$

$$PAR = 0.339 + 0.808 * \cos(L) * \cos(S) - 0.196 * \sin(L) * \sin(S) - 0.482 * \cos(\pi - [A - \pi]) * \sin(S). \quad (3)$$

We assessed fire occurrence at each plot for the past 20 years using wildland fire perimeters from the USDA Forest Service Region 3 GIS database (<https://www.fs.usda.gov/detail/r3/landmanagement/gis>) and prescribed fire perimeters obtained from national forest staff. We assessed fire severity at each plot using data obtained from the Monitoring Trends in Burn Severity program (<https://www.mtbs.gov/>), which provides fire severity data at 30-m resolution. We created categorical variables to represent both fire occurrence and severity in addition to a binary variable for plots that burned twice in the past 20 years (Table 2). Finally, we used GPS coordinates and maps obtained from national forest staff to verify whether plots fell inside areas of ungulate management and conifer removal treatments, and we created binary variables for both ungulate management and conifer removal (Table 2).

We obtained soils data from SoilGrids (<https://www.isric.org/explore/soilgrids>), which provides global soil mapping at 250-m resolution (Poggio et al. 2021). We used 9 of 12 available soil metrics to capture variables that represent soil moisture (e.g. sand content and bulk density), fertility (e.g. cation exchange capacity, nitrogen, and soil organic content), rooting environment (e.g. bulk density, clay content, and coarse fragments), and chemical environment (e.g. soil pH) (Table 2). We aggregated mean values for each variable to a depth of 1 m because most lateral aspen roots occur within the first 1 m of the soil (Jones and DeByle 1985a). We obtained climate data for each plot from ClimateNA (<https://climatenas.ca/>), which downscales PRISM data (Daly et al. 2008) at 800-m resolution (Wang et al. 2016). Specifically, we obtained

variables representing annual and, when available, seasonal temperature, precipitation, and drought [e.g. climate moisture index (CMI), which is calculated based on temperature, Wang et al. 2016] for the 5 years preceding when we sampled each plot (Table 2). We chose 5 years to be consistent with other studies that have assessed the influence of climate on juvenile aspen (Clement et al. 2019; Reikowski et al. 2022). In addition to climate variables obtained directly from ClimateNA, we calculated monsoon index (summer precipitation ÷ annual precipitation) and annual dryness index (annual degree-days above 5°C ÷ annual precipitation) because of the importance of the monsoon system in Arizona and the important influence of precipitation, in general, on aspen occurrence, growth, and mortality (Rehfeldt et al. 2009; Worrall et al. 2013; Kane et al. 2014; Ireland et al. 2020).

Analysis: sustainability of regeneration and recruitment

To determine whether aspen is sustainably regenerating and recruiting, we compared abundance of juvenile aspen to two different thresholds for self-replacement. The first set of thresholds, which we refer to as the WNA (western North America) thresholds, were 2500 stems ha^{−1} for regeneration and 1250 stems ha^{−1} for recruits as outlined in the literature (Mueggler 1989; Campbell and Bartos 2001; O'Brien et al. 2010). The WNA thresholds represent the minimum number of juvenile aspen trees that are necessary to replace existing overstory trees. However, these thresholds were developed for aspen in more northerly parts of its range, so we developed a second set of thresholds specific to aspen in Arizona using size class data from our study plots. These thresholds, which we refer to as the AZ (Arizona) thresholds, are site-specific and based on the overstory aspen present in each plot. We calculated these AZ thresholds based on data from 68 healthy study plots. To be considered healthy, a plot had to contain no oystershell scale and < 20% browse, which is considered the threshold of sustainable browsing (Jones et al. 2005; Rogers and Mittanck 2014). From these 68 plots, we calculated mean density of live regenerating (8575.1 trees ha^{−1}),

recruiting (4411.9 trees ha⁻¹), and overstory stems (201.9 trees ha⁻¹), and then we calculated the ratios between overstory trees to regenerating stems (1: 42.5) and overstory trees to recruiting stems (1: 21.9). For each study plot, we then multiplied the density of living and dead overstory aspen by both ratios. For plots with no overstory aspen, we defaulted to the WNA thresholds. We then compared observed densities of aspen regeneration and recruitment across our 220 study plots to both the WNA and AZ thresholds. To facilitate our understanding of where juvenile aspen were observed at sustainable levels, we categorized self-replacing status of regeneration and recruitment across the seven major areas where aspen occurs (Fig. 1b).

Analysis: factors influencing regeneration and recruitment

We considered 69 variables that could potentially influence aspen regeneration and recruitment, representing eight overarching categories: stand structure, ungulate impacts, damaging agents, fire, management, site factors, soils, and climate (Table 2). We conducted two analyses—random forests and SEM—to determine which of these factors significantly influence regeneration and recruitment. We analyzed all data in R version 4.2.1 (R Core Team 2022), using the *dplyr* package (Wickham et al. 2022) for data manipulation and the *ggplot2* package (Wickham 2016) for figure creation. First, we used random forests to determine which of the 69 predictor variables had the strongest influence on our three response variables (i.e. density of live regeneration, live recruits, and dead recruits). Random forests are a useful tool for assessing variable importance in regression and classification settings among an array of potential predictors (Breiman 2001). Specifically, we used the *VSURF* package (Genuer et al. 2015), which used 50 random forest runs, each of which was built using 2000 trees, to rank variable importance for each of our three response variables. *VSURF* is robust in noisy, high dimensional settings, and in the presence of highly correlated predictors (Genuer et al. 2010). *VSURF* outputs a ranked list of variables based on importance, which is calculated using out-of-box mean square error for each fitted tree, along with a group of variables highly related to the response that is geared toward interpretation (Genuer et al. 2010, 2015). We used both the ranked list of variables and the group of interpretation variables when building SEMs.

Once we obtained a list of the most important variables influencing each response, we used SEMs to quantify how those predictor variables and their interactions influence aspen regeneration and recruitment. SEMs are an insightful tool for ecological research because they allow the user to build models based on theoretical understanding of an ecological system, resulting in a network of causal, multivariate relationships with a complete accounting of direct and indirect relationships, and the relative strengths of those relationships (Grace 2006; Lefcheck 2016). SEMs are valuable in the specific context of our study because we understand how individual factors influence juvenile aspen (Crouch et al. 2023), but we do not understand how these various factors interact and which are the most important drivers of regeneration and recruitment. We used the results from both random forests and SEMs to determine which factors influenced regeneration and recruitment.

Our first step in building SEMs was to construct an *a priori* model based on our theoretical understanding of how biotic and abiotic factors influence juvenile aspen. This *a priori* model (Fig. 2) applied to all three response variables and accounted for all 69

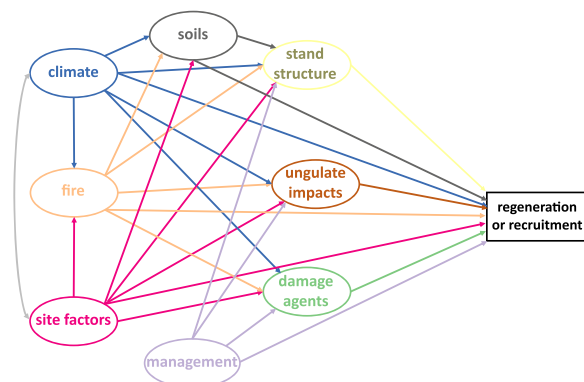


Figure 2. A priori SEM illustrating hypothesized directional relationships among influencing factors and aspen regeneration or recruitment, and arrows indicate causal relationships, and colors correspond to each of the eight categories of influencing factors; see Table 2 for complete list of measured variables included in each of these eight categories.

variables that potentially influence regeneration and recruitment using the eight categories of influencing factors (i.e. climate, fire, site factors, soils, management, stand structure, ungulate impacts, and damaging agents). For each of the three responses, we built a ‘full’ SEM, which included the highest ranked variable based on random forests from each of the eight categories of influencing factors. We then used a combination of backward and forward selection to optimize model fit (using AIC and Fisher’s C statistic) and explanatory power (using R^2 of the response variable). This optimization process included removing variables with low significance in the model and adding in more than one variable per category (e.g. adding a second climate variable) when two variables from one category had high importance values based on random forests. We also tested how swapping in one variable to replace another variable of the same category affected the model, but only one such swap resulted in improved model fit and explanatory power (spring CMI swapped in to replace winter CMI in the live aspen regeneration SEM).

We used the *piecewiseSEM* package to build SEMs because this package accommodates the use of mixed-effects models (Lefcheck 2016). Prior to fitting individual regressions that underlie the SEMs, we log-transformed the three response variables to satisfy normality assumptions. For the individual regressions that underlie *piecewiseSEM*, we used the *lme4* package (Bates et al. 2015) to fit linear mixed-effects models with the hierarchical, nested structure of plots [i.e. plots ($n=220$) within study sites ($n=87$), within minor areas ($n=19$), and within major areas ($n=7$)] modeled as random effects. Study site refers to a transect or group of plots that are clustered near each other, whereas minor area refers to a group of such transects or plots in a larger but still confined area (e.g. an individual mountain or fire footprint). Because study site location was accounted for implicitly as a random effect in these mixed-effects models, we did not explicitly include major area, UTM easting, UTM northing, or other spatial variables in SEMs.

Finally, we wanted to explore specific impacts of different ungulate species (i.e. elk, deer, and cattle) on recruitment. To do so, we fit six simple linear regression models with each of the three species’ scat counts as predictors and with density of live and dead recruits as responses. Similar to the linear models that were built for SEM, these linear models were mixed-effects models fit using the *lme4* package (Bates et al. 2015).

Table 3. Percentage of all study plots, including those inside and outside areas of ungulate management, in each major area with sustainable regeneration, recruitment, or either based on two different thresholds of self-replacement (WNA or AZ).

Major area	Sample size	Regeneration		Recruitment		Regeneration or recruitment	
		WNA	AZ	WNA	AZ	WNA	AZ
North Kaibab	19	68.4	47.4	47.4	47.4	78.9	63.2
South Kaibab*	26	61.5	34.6	26.9	15.4	65.4	38.5
Flagstaff*	113	50.4	28.3	32.7	15.9	71.7	38.9
Prescott	17	64.7	23.5	94.1	70.6	94.1	70.6
Mogollon Rim*	13	92.3	69.2	7.7	7.7	100.0	76.9
White Mtns*	25	52.0	20.0	28.0	28.0	68.0	36.0
Coronado	7	85.7	85.7	28.6	28.6	85.7	85.7
Total	220	58.2	33.6	35.9	24.1	75.0	46.8

*indicates area in which introduced Rocky Mountain elk are present. WNA self-replacement thresholds were 2500 stems ha^{-1} for regeneration and 1250 stems ha^{-1} for recruits (Mueggler 1989; Campbell and Bartos 2001; O'Brien et al. 2010). AZ thresholds were calculated by multiplying the total number of live and dead overstory aspen stems ha^{-1} in each plot by 42.5 for regeneration and by 21.9 for recruits. These multipliers were determined by calculating the ratio of regenerating and recruiting stem densities to overstory aspen density across 68 healthy study plots that had no oystershell scale and <20% browse. For plots with no overstory aspen, we used the WNA thresholds. See Materials and Methods section for additional details on these self-replacement thresholds.

Results

Sustainability of regeneration and recruitment

Across all 220 study plots, mean aspen regeneration density was 8694 trees ha^{-1} , and mean recruitment density was 2753 trees ha^{-1} . Mean density of live overstory aspen was 172 trees ha^{-1} , and density of dead overstory aspen was 67 trees ha^{-1} . Observed aspen regeneration density exceeded the WNA self-replacement threshold of 2500 regenerating stems ha^{-1} (Mueggler 1989; Campbell and Bartos 2001; O'Brien et al. 2010) in 58.2% of study plots, and observed recruitment density exceeded the WNA self-replacement threshold of 1250 recruiting stems ha^{-1} in 35.9% of plots (Table 3). Using the more conservative site-specific AZ self-replacement thresholds, regeneration density was sufficient to replace living and dead overstory aspen in 33.6% of plots, whereas recruitment density was sustainable in only 24.1% of plots. Aspen regeneration was absent from 6.4% of study plots, while recruitment was absent from 40.0% of plots. Concerningly, 25.0% of plots had unsustainable levels of both regeneration and recruitment based on the WNA thresholds, compared with 53.2% of plots with unsustainable regeneration and recruitment using the AZ thresholds (Table 3).

There were substantial differences in sustainability of juvenile aspen across the seven major areas where aspen occurs in Arizona (Fig. 3; Table 3). Across all areas, proportion of plots with sustainable regeneration and recruitment was typically higher when using the WNA thresholds compared with the more conservative, site-specific AZ thresholds (Table 3). The proportion of plots with sustainable regeneration was highest within the Coronado (85.7% for both thresholds) and Mogollon Rim areas (92.3% WNA; 69.2% AZ). The other five areas ranged from 50.4% to 68.4% of plots sustainably regenerating using the WNA threshold and from 20.0% to 47.4% using the AZ threshold (Table 3). The proportion of plots with sustainable regeneration was higher than proportion of plots with sustainable recruitment in every area except for Prescott, which had especially high levels of sustainable recruitment (94.1% WNA; 70.6% AZ). For every other region, the majority of plots lacked sustainable recruitment, with the Mogollon Rim having particularly low levels of sustainability (7.7% for both thresholds) driven by high mortality of recruiting stems (Supplementary Fig. 1, See online supplementary material for a colour version of this figure).

The only areas where we sampled plots inside of areas treated for ungulate management were South Kaibab, Flagstaff, and Mogollon Rim. In these areas, sustainability of regeneration tended to be higher outside of treated areas, whereas sustainability of recruitment tended to be much lower outside of treated areas (Table 4). In fact, in all three areas, no plot outside of exclosures or jackstraw treatments was sustainably recruiting using the AZ threshold (Fig. 3b; Table 4), while the sustainability rate was less than 10% for these areas using the WNA threshold (Table 4).

Factors influencing regeneration

The most important variables influencing density of live aspen regeneration (trees ha^{-1}) based on random forests were major area and HL (Table 5). The optimal SEM for live regeneration [AIC = -1351; Fisher's $C = 6.425$ with $P = .983$ (high P -value indicates better fit); response marginal $R^2 = 0.10$, conditional $R^2 = 0.41$ (marginal includes only fixed effects, conditional includes both fixed and random effects)] included six influencing factors: spring CMI, autumn precipitation, HL, fire strata, proportion of stems with abiotic damage, and proportion of stems with sooty bark canker (Fig. 4a). None of our SEMs included major area as an explicit influencing factor because it was accounted for as a random effect. Based on the optimal SEM, the only significant ($P < .05$) predictor of live regeneration density was sooty bark canker (effect size = -0.13; $P = .018$), with higher levels of sooty bark canker being associated with less aspen regeneration. Spring CMI had the highest path coefficient (0.14; $P = .233$), indicating that less arid conditions (i.e. higher spring CMI) were associated with increased regeneration. Variables with lower path coefficients included autumn precipitation (0.12; $P = .302$), abiotic damage (0.10; $P = .090$), HL (-0.09; $P = .200$), and fire strata (-0.12; $P = .316$). Increased aspen regeneration was associated with more autumn precipitation, a greater proportion of stems with abiotic damage, lower HL, and recent fire. Although their direct effects on regeneration were not significant, autumn precipitation (-0.51; $P < .001$) and HL (0.20; $P < .001$) had significant influences on fire strata. More precipitation in autumn and lower HL were associated with more recent fire. Thus, autumn precipitation indirectly increased live aspen regeneration density through its effect on fire strata, while HL indirectly decreased live regeneration density through its effect on fire strata. Both indirect effects were consistent with the

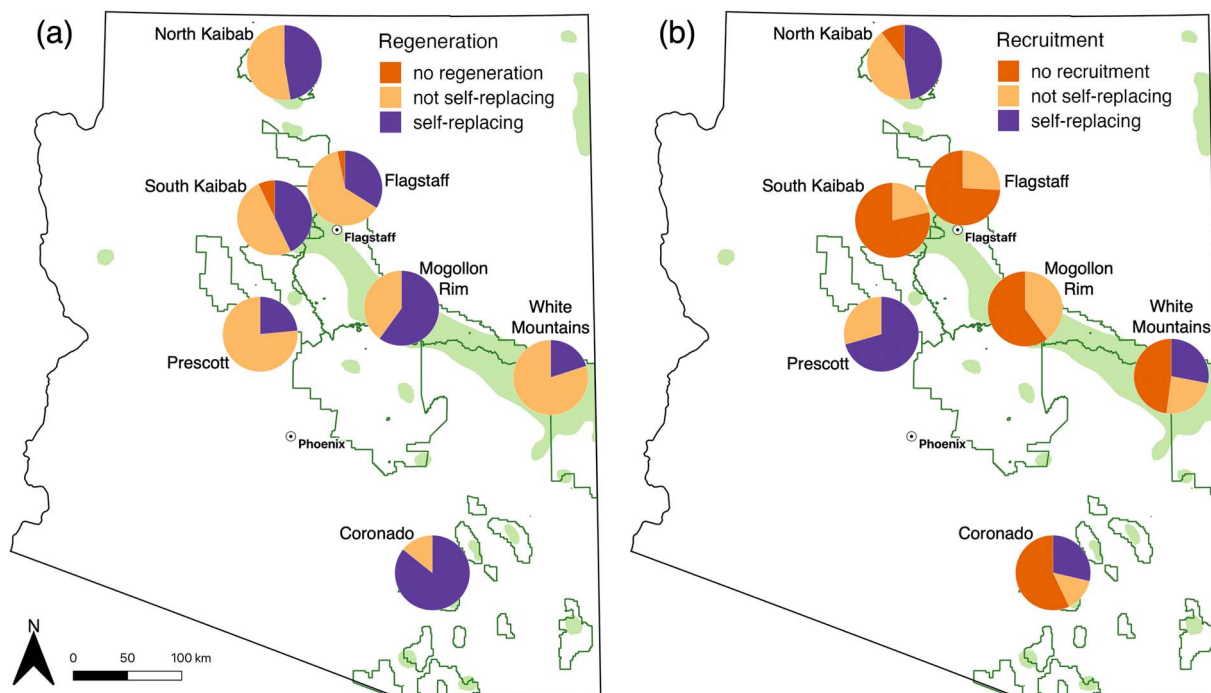


Figure 3. Maps showing sustainability status of (a) regenerating and (b) recruiting stems across seven major areas where aspen occurs in AZ, United States, and data shown here do not include the 71 study plots inside of exclosures or jackstraw treatments, and sustainability status is based on the site-specific AZ thresholds for self-replacement.

Table 4. Percentage of study plots outside versus inside areas of ungulate management with sustainable regeneration, recruitment, or either based on two different thresholds of self-replacement (WNA or AZ); only three major areas are shown because we did not sample inside areas of ungulate management in the other four areas (North Kaibab, Prescott, White Mountains, and Coronado).

Major area	Ungulate mngmnt	Sample size	Regeneration		Recruitment		Regeneration or recruitment	
			WNA	AZ	WNA	AZ	WNA	AZ
South Kaibab	outside	14	78.6	42.9	7.1	0.0	78.6	42.9
South Kaibab	inside	12	41.7	25.0	50.0	33.3	50.0	33.3
Flagstaff	outside	62	61.3	33.9	4.8	0.0	62.9	33.9
Flagstaff	inside	51	37.3	21.6	66.7	35.3	82.4	45.1
Mogollon Rim	outside	5	100.0	60.0	0.0	0.0	100.0	60.0
Mogollon Rim	inside	8	87.5	75.0	12.5	12.5	100.0	87.5

WNA self-replacement thresholds were 2500 stems ha^{-1} for regeneration and 1250 stems ha^{-1} for recruits (Mueggler 1989; Campbell and Bartos 2001; O'Brien et al. 2010). AZ thresholds were calculated by multiplying the total number of live and dead overstory aspen stems ha^{-1} in each plot by 42.5 for regeneration and by 21.9 for recruits. These multipliers were determined by calculating the ratio of regenerating and recruiting stem densities to overstory aspen density across 68 healthy study plots that had no oystershell scale and <20% browse. For plots with no overstory aspen, we used the WNA thresholds. See [Materials and Methods](#) section for additional details on these self-replacement thresholds.

direct effects of autumn precipitation and HL on live regeneration density.

Factors influencing recruitment

The most important variables influencing the density of live aspen recruitment (trees ha^{-1}) based on random forests were fire severity, fire strata, major area, ungulate management, snowfall, mean winter temperature, and proportion of stems browsed (Table 5). The optimal SEM for live recruitment ($\text{AIC}=1178$; Fisher's $C=18.786$ with $P=.845$; response marginal $R^2=0.43$, conditional $R^2=0.76$) included eight influencing factors: snowfall, mean winter temperature, HL, fire severity, fire strata, proportion of stems browsed, ungulate management, and proportion of stems with Cytospora canker (Fig. 4b). More severe fire (effect size = 0.52; $P < .001$), less recent fire (0.32; $P = .004$), presence of ungulate management (0.35; $P < .001$), higher levels of Cytospora canker (0.12; $P = .009$), and lower levels of browse (-0.34 ; $P < .001$)

resulted in significantly greater density of live recruitment. Although not significant, the path coefficients for snowfall (-0.33 ; $P = .069$) and winter temperature (-0.32 ; $P = .232$) were relatively high, indicating that less snowfall and cooler winter temperatures were more favorable for live aspen recruits. The influence of HL (0.01; $P = .862$) was negligible. Looking at indirect effects, ungulate management significantly decreased browse (-0.59 ; $P < .001$), meaning that ungulate management had positive direct and indirect effects on density of live recruits. Ungulate management was also associated with increased occurrence of Cytospora canker, a relationship that approached significance (0.16; $P = .082$). Fire strata had a negative effect on browse that approached significance (-0.16 ; $P = .090$), meaning that more recent fire was associated with more browse. Finally, both HL and winter temperature had significant influences on fire severity and strata. Higher winter temperatures were associated with more severe fire (0.23; $P < .001$) and more recent fire (-0.26 ; $P < .001$), whereas

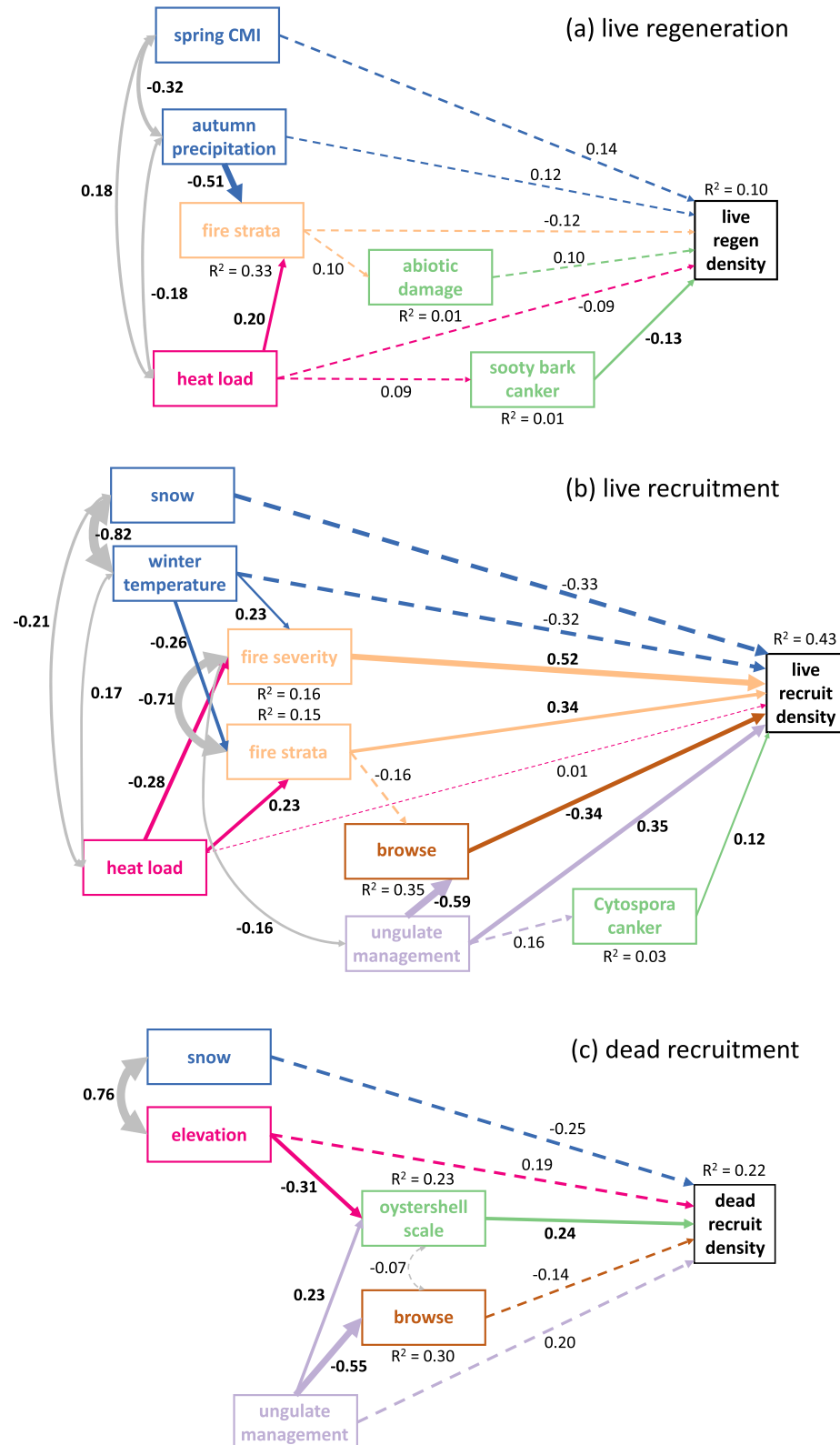


Figure 4. Optimal SEMs for density (trees ha⁻¹) of (a) live aspen regeneration, (b) live aspen recruitment, and (c) dead aspen recruitment; significant ($p < .05$) path coefficients are shown in bold, and their corresponding paths are depicted as solid lines; in contrast, insignificant coefficients are not bolded, and their corresponding paths are shown as dashed lines, and path thickness indicates strength of its coefficient, with wider paths indicating stronger relationships; see Table 2 for descriptions and summary statistics of influencing factors.

Table 5. Top 25 most important variables influencing each of our three responses (live aspen regeneration, live aspen recruitment, and dead aspen recruitment stems ha⁻¹) based on 50 random forest runs, each of which was built using 2000 trees.

Rank	Live aspen regeneration	Live aspen recruitment	Dead aspen recruitment
1	major area	<u>fire severity</u>	major area
2	<u>heat load</u>	<u>fire strata</u>	fire severity
3	<u>fire strata</u>	major area	<u>snow</u>
4	<u>sooty bark canker</u>	<u>ungulate management</u>	dead aspen basal area
5	slope	<u>snow</u>	<u>oystershell scale</u>
6	radiation	winter temp (mean)	coarse fragments
7	<u>abiotic damage</u>	<u>browse</u>	<u>browse</u>
8	UTM easting	winter temp (min)	<u>elevation</u>
9	winter CMI	<u>heat load</u>	summer precip
10	<u>autumn precip</u>	summer precip	soil organic carbon
11	<u>spring CMI</u>	spring temp (mean)	spring CMI
12	summer temp (max)	cation exchange capacity	UTM easting
13	summer CMI	autumn temp (mean)	UTM northing
14	spring temp (mean)	UTM easting	annual dryness index
15	winter temp (mean)	spring CMI	winter temp (min)
16	summer temp (mean)	spring precip	soil pH
17	annual dryness index	UTM northing	spring temp (mean)
18	fire severity	radiation	autumn temp (mean)
19	snow	elevation	<u>ungulate management</u>
20	winter precip	soil pH	defoliating insects
21	summer precip	<u>Cytospora canker</u>	summer temp (mean)
22	soil order	slope	monsoon index
23	winter temp (min)	soil organic carbon	winter CMI
24	autumn CMI	winter precip	autumn precip
25	UTM northing	summer CMI	winter temp (mean)

Variables in bold indicate those selected as important for interpretation by the VSURF package (Genuer et al. 2015). Underlined variables indicate those included in the optimal SEM for each response. These rankings include spatial variables, such as major area, UTM easting, and UTM northing, which were not included as predictors in SEM because they were accounted for using mixed-effects models that underly the SEMs.

higher HL was associated with lower fire severity (-0.28 ; $P < .001$) and less recent fire (0.23 ; $P < .001$).

The most important variables influencing the density of dead aspen recruitment (trees ha⁻¹) based on random forests were major area, fire severity, snowfall, and dead aspen basal area (Table 5). The optimal SEM for dead recruitment (AIC=637; Fisher's $C=2.219$ with $P=.898$; response marginal $R^2=0.22$, conditional $R^2=0.48$) included five influencing factors: snowfall, elevation, proportion of stems infested by oystershell scale, proportion of stems browsed, and ungulate management (Fig. 4c). The only significant predictor of dead recruitment density was oystershell scale (effect size=0.24; $P=.028$), which was associated with increased density of dead recruits. Although insignificant, snowfall (-0.25 ; $P=.172$) and browse (-0.14 ; $P=.079$) were associated with less dead recruitment, while elevation (0.19 ; $P=.341$) and ungulate management (0.20 ; $P=.066$) were positively associated with dead recruitment, indicating that more dead recruits were found at higher elevations and in areas of ungulate management. Looking at indirect effects, higher elevations had significantly less oystershell scale (-0.31 ; $P=.021$), resulting in higher elevations being indirectly associated with less dead recruits. Oystershell scale was significantly more abundant in areas of ungulate management (0.23 ; $P=.002$), whereas browse was significantly reduced in areas of ungulate management (-0.55 ; $P < .001$).

From the six linear regression models fit to assess the impacts of specific ungulate species on recruitment, we found that elk scat count had a significant negative relationship with a density of live ($P < .001$) and dead recruits ($P=.006$). In contrast, deer and cattle did not have significant relationships with either response ($P \geq .105$).

Discussion

Sustainability of regeneration and recruitment

Many aspen populations in Arizona lacked sustainable regeneration and recruitment. One-third to one-half of study plots had sustainable regeneration, depending on the self-replacement threshold used, but only one quarter to one-third of plots had sustainable recruitment. Notably, 25.0%–53.2% of plots lacked both sustainable regeneration and recruitment, depending on the threshold used. Although our study is the first to report state-wide unsustainability of both aspen regeneration and recruitment, numerous studies have previously identified a lack of regeneration or recruitment in specific areas of Arizona (Rasmussen 1941; Merkle 1954, 1962; Shepperd and Fairweather 1994; Rolf 2001; Binkley et al. 2006; Fairweather et al. 2008; Beschta and Ripple 2010; Ziegler et al. 2012; Martin 2014), with only one study highlighting a lack of recruitment across the state (Clement et al. 2019). Lack of juvenile aspen has also been documented in other areas of the western United States (Rogers et al. 2010; Kimble et al. 2011; Rogers and Mittanck 2014; Rogers and Gale 2017), although our study is novel because of the relatively large geographic area assessed (but see Refsland and Cushman 2021). The only study from Arizona that assessed status and health of both regeneration and recruitment was Ziegler et al. (2012), who studied aspen in the South Kaibab area and observed sustainable regeneration in 52% of sites and sustainable recruitment in just 4% of sites using the WNA thresholds. Their levels of sustainable regeneration were comparable to ours (58.2% state-wide and 61.5% for South Kaibab using WNA threshold), whereas recruitment sustainability was much greater in our study both across Arizona (35.9%) and in the South Kaibab area (26.9%). Notably, our levels of sustainable recruitment outside exclosures in the South Kaibab area (7.1%)

were more consistent with those reported in Zegler *et al.* (2012) who sampled only outside exclosures. Zegler *et al.* (2012) predicted a 'grim future' for aspen because of unsustainable regeneration and recruitment, and our findings suggest that the outlook for aspen sustainability has not improved in the South Kaibab area or in other areas of Arizona, especially outside of exclosures.

The state of aspen recruitment in Arizona is more concerning than that of regeneration because recruitment is a more direct indicator of sustainability (Rogers and Mittanck 2014; Rogers 2017) and because the situation for recruits is more dire. Sustainability of both regeneration and recruitment is important for maintaining a tree species on the landscape (Dey 2014), but unsustainable recruitment is arguably of greater concern because without sustainable recruitment, even abundant regeneration is not a good indicator of successful self-replacement. This is especially true for aspen, which regenerates reliably after fire, other disturbances, and management interventions that trigger sprouting (Crouch *et al.* 2023), but is susceptible to recruitment bottlenecks caused by ungulate browse, drought, and competition with conifers (Rolf 2001; Binkley *et al.* 2006; Beschta and Ripple 2010; Zegler *et al.* 2012; Martin 2014; Clement *et al.* 2019). Across Arizona, we observed higher levels of sustainability for regeneration than for recruitment (Table 3), indicating that recruitment bottlenecks are indeed occurring in Arizona. Of particular concern is our finding that 40.0% of study plots lacked a single recruiting stem. The only study that has assessed state-wide aspen recruitment was Clement *et al.* (2019), who found that 26.1% of sites lacked recruitment (defined in their study as stems >2-m tall and <5-cm dbh). For comparison, Zegler *et al.* (2012) found that 20.8% of sites lacked stems >1.37-m tall and <5.1-cm dbh, while 25% of sites lacked stems 5.1- to 10.1-cm dbh. Comparing these earlier studies to ours, the sustainability of recruitment has continued to decline. The outlook for aspen recruitment based on our study was especially bleak when using the site-specific AZ self-replacement thresholds, which were calculated based on the density of overstory aspen present in each plot. Although these AZ thresholds are more conservative than the WNA thresholds, we expect that they are a more accurate representation of aspen sustainability because they are based on Arizona-specific data. Regardless of which thresholds are used, current aspen recruitment is clearly unsustainable for replacing existing overstory trees across much of Arizona.

Factors influencing regeneration

Density of live aspen regeneration was influenced most strongly by damaging agents, fire occurrence, HL, and climate based on random forests and SEM. Only one influencing factor, proportion of stems with sooty bark canker, had a significant relationship with live regeneration density, and the strength of its path in SEM was similar to those of the other influencing factors (Fig. 4a). Sooty bark canker, which is an aggressive disease that affects older aspen trees in unhealthy stands (Hinds 1985; Marchetti *et al.* 2011), had a negative influence on regeneration density, suggesting that unhealthy, mature aspen affected by sooty bark canker might produce fewer suckers. However, interpreting the effect of sooty bark canker should be done with care because of the infrequency with which it occurred. Sooty bark canker was observed on 0.06% of the 9965 live aspen stems we sampled.

A novel finding from our study was the potential influence of HL and climate on aspen regeneration. HL had a negative influence on aspen regeneration density, whereas spring CMI and autumn precipitation had positive influences (Fig. 4a). Although these three relationships were insignificant according to SEM, all

three variables were among the most important influences of aspen regeneration abundance based on random forests (Table 5). Altogether, these findings indicate that aspen regeneration may be less abundant on hotter sites and in warmer, drier climates. Before our study, the influence of climate on aspen regeneration in Arizona was uncertain (Crouch *et al.* 2023). Wetter periods have been associated with patterns of aspen establishment in the North Kaibab area and throughout the western United States (Kaye 2011), but other demographic studies from Arizona have concluded that climate trends did not explain variations in aspen establishment in the 20th century (Binkley *et al.* 2006; Beschta and Ripple 2010). Similarly, Zegler *et al.* (2012) did not find that aspen regeneration mortality was influenced by HL in the South Kaibab area. However, our survey of aspen populations across Arizona indicated that climate may influence regeneration density, perhaps because our study had a larger spatial scale and included a wider range of climates than previous studies (Supplementary Table 1). This finding has important implications for aspen sustainability in a warming climate. Warmer, drier sites are already less suitable for aspen regeneration (Worrall *et al.* 2013), and as Arizona's climate continues to become more arid (Seager *et al.* 2007), aspen's regeneration potential is likely to decrease. This conclusion is supported by O'Donnell *et al.* (2018), who modeled climate change based on representative concentration pathways (RCP) 4.5 and 8.5 and predicted that loss of mesic conditions conducive to aspen regeneration will lead to the species' decline in the North Kaibab area. This influence of climate on aspen regeneration is an important consideration for aspen management in a rapidly changing climate, as we discuss in *Management implications* section below.

Despite including multiple variables representing stand structure in our analyses (Table 2), overstory density did not significantly influence aspen regeneration or recruitment. However, this does not mean that we can conclude that the overstory has no influence on juvenile aspen. Vegetative regeneration via suckering is triggered when the flow of two hormones, auxin and cytokinin, between roots and shoots is interrupted, which occurs when a stem dies or is cut (Schier *et al.* 1985). Without this hormonal trigger, an existing aspen overstory exerts apical dominance on the clone's root system and inhibits suckering, although apical dominance is not absolute and continuous suckering is common in undisturbed clones (Schier *et al.* 1985; Bates *et al.* 1988; Kurzel *et al.* 2007). Even though we sampled a wide range of aspen overstory conditions, from no overstory after high-severity wildfire to intact overstories in mature undisturbed stands, the overstory's influence on aspen juveniles must have been overshadowed by more important drivers of regeneration and recruitment across the landscape, such as damaging agents, fire occurrence, and climate.

Factors influencing recruitment

Interpreting drivers of aspen recruitment is complex because we explored influences on density of both living and dead recruits, which allowed us to compare processes driving survival versus mortality of recruits. The drivers of living and dead recruitment density were relatively consistent (Fig. 4b, c), with the exceptions of fire influencing density of living but not dead recruits and of different damaging agents influencing the two responses. Overall, fire and ungulate management were the most important positive influences promoting recruitment, whereas browse and oyster-shell scale were the primary factors limiting recruitment.

Fire had a strong positive influence on the density of live aspen recruits. Timing of fire and fire severity were the two

most important variables influencing live recruitment based on random forests. Moreover, both fire variables were significant influencing factors based on SEM, with fire severity having the strongest influence of any pathway in the live recruitment model. Live aspen regeneration was much more abundant in plots that burned 2–20 years ago compared with plots that burned <2 and >20 years ago. This indicates that less than 2 years is not enough time for most aspen regeneration to grow taller than 1.37 m (Jones and Schier 1985) but that recent fire in the past 20 years is clearly important for promoting aspen recruitment. Similar to regeneration, the importance of fire occurrence and severity in promoting aspen recruitment is well established in the literature (Jones and Trujillo 1975; Whittaker and Niering 1975; Fulé et al. 2002, 2003; Mast and Wolf 2004, 2006; Heinlein et al. 2005; Binkley et al. 2006; Margolis et al. 2011; Higgins et al. 2015; Clement et al. 2019). Higgins et al. (2015) found that the density of aspen recruits was significantly greater in mixed-conifer forests that had experienced high-severity fire than in low-severity areas. Similarly, Clement et al. (2019) studied how a wide array of biotic and abiotic factors influence aspen recruitment and found that high-severity fire had the strongest influence. In addition to influencing abundance of live recruitment, fire severity was also an important influence on the density of dead aspen recruits based on random forests. We would expect more dead aspen recruits in areas of high-severity fire because there are more recruits after high-severity fire, in general, and because stem exclusion in high-density, post-fire stands results in many dead recruits (David et al. 2001). However, the optimal SEM for dead recruits did not include fire severity, indicating that fire severity's influence on dead recruitment density was not strong enough to improve fit or explanatory power of the SEM.

Ungulate browse had a strong negative influence on aspen recruitment, while local management tactics to reduce the impacts of ungulate browse had a strong positive influence. Higher levels of browse resulted in significantly less live aspen recruitment, and ungulate management significantly reduced browse and increased live recruitment density. In the dead recruitment SEM, ungulate management also significantly reduced browse; however, higher levels of browse and lack of ungulate management were associated with fewer dead recruits. Although these dead recruitment results seem to contradict those for live recruitment, they can be explained by the fact that more dead recruits are likely to occur in areas where there are more live recruits. Therefore, areas with high levels of browse and no ungulate management resulted in fewer dead recruits because there were simply fewer recruits, in general, in these areas. The negative influence of browse on aspen recruitment in Arizona is well documented in the literature (Rasmussen 1941; Merkle 1954, 1962; Rolf 2001; Binkley et al. 2006; Fairweather et al. 2008; Zegler et al. 2012), as is the effectiveness of exclosures in promoting aspen recruitment (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Shepperd 2004; Bailey et al. 2007; Martin and Maron 2012; Martin 2014). Many studies have also found that aspen regeneration is negatively impacted by browse (Pearson 1914; Rasmussen 1941; Shepperd and Fairweather 1994; Binkley et al. 2006; Beschta and Ripple 2010; Zegler et al. 2012), but our study did not. Our study has a wider geographic scope than these previous studies, so perhaps local impacts of browse on regeneration were drowned out by more important drivers of regeneration across Arizona.

An important, yet unresolved question is whether different ungulate species have differential impacts on aspen recruitment. Our study indicates that introduced Rocky Mountain elk have an

outsized negative influence compared with deer or cattle. Rocky Mountain elk were introduced into Arizona in 1913 following the extinction of the native Merriam's elk (*C. canadensis merriami*), and these introduced elk now occur in larger population densities and occupy a broader area of Arizona than Merriam's elk did (Beschta and Ripple 2010; Fairweather et al. 2014). Despite not being included in the optimal SEMs for recruitment, linear regression indicated that elk scat count had a significant negative relationship with the density of live and dead recruits, whereas deer and cattle did not have significant relationships with either response. This general finding, where elk have greater impacts on aspen recruitment than other ungulate species, has also been found in more northerly parts of aspen's range (Bork et al. 2013; Rogers and Mittanck 2014; Rogers et al. 2015). To add further support to this finding, the areas in Arizona with the lowest levels of sustainable recruitment (South Kaibab, Flagstaff, Mogollon Rim, and White Mountains) were those where introduced elk are present (Table 3; Supplementary Table 1). Alarming, no plots outside of exclosures or jackstraw treatments had sustainable recruitment in the South Kaibab, Flagstaff, and Mogollon Rim major areas (Fig. 3b; Table 4), highlighting the dire threat to aspen sustainability posed by introduced elk in Arizona.

Two biotic agents—Cytospora canker and oystershell scale—were important factors influencing the density of live and dead recruits, respectively. Proportion of stems with Cytospora canker was positively associated with live recruitment, which is paradoxical because Cytospora is a common disease of aspen that kills stressed or damaged stems (Hinds 1985; Fairweather et al. 2008; Marchetti et al. 2011; Zegler et al. 2012). We hypothesize that this relationship is an artifact of our observational sampling approach, in which Cytospora is common in plots with dense aspen recruitment. The positive influence of ungulate management on Cytospora canker supports this hypothesis because we know that aspen recruits are more abundant in areas of ungulate management (Fig. 4b). Alternatively, intraspecific competition in stands with dense recruitment might increase tree stress and, thereby, susceptibility to Cytospora canker. A more clear and important influence on recruitment was the role of the invasive insect, oystershell scale, as a driver of recruitment mortality. This Arizona-wide finding is consistent with the initial report of oystershell scale's impacts on recruiting stems at two sites outside of Flagstaff (Crouch et al. 2021). The threat that oystershell scale poses is likely to increase in the future as the climate continues to warm and outbreaks occur in other areas of aspen's range (Crouch et al. 2021). The latter have already begun to occur, as aspen mortality events from oystershell scale have recently been observed in Utah, Nevada, and Idaho (Williams 2021; Grady et al. 2022). Our study also confirmed two other observations made by Crouch et al. (2021): oystershell scale invasions are significantly influenced by elevation and ungulate management (Fig. 4c). Specifically, the proportion of stems infested with oystershell scale increases at lower elevations and in areas of ungulate management, which is likely due to increased stem density, and therefore host availability, inside exclosures.

Climate and site factors seemed to influence aspen recruitment, albeit less strongly than fire, ungulate browse, and biotic damaging agents. Annual snowfall was one of the most important predictors of live and dead aspen recruitment density based on random forests and had a relatively strong but not significant negative influence on the density of living and dead recruits. These findings suggest that less aspen recruits, live and dead, occur in areas with more snowfall, a finding that differs from our expectation that wetter sites would have more recruitment

(Crouch *et al.* 2023) and from previous research on the relationship between snowfall and recruitment along the Mogollon Rim (Martin 2007; Martin and Maron 2012). Although insignificant, SEM indicated that warmer mean winter temperatures resulted in lower density of aspen recruits, which is consistent with our understanding that warmer, drier conditions inhibit recruitment both in Arizona (Martin 2007; Martin and Maron 2012; Zegler *et al.* 2012; Clement *et al.* 2019) and in more northerly latitudes (Kaye 2011; Shinneman and McIlroy 2019; McIlroy and Shinneman 2020). Another insignificant, yet surprising relationship was the positive influence of elevation on dead recruitment density, which is the opposite of what Zegler *et al.* (2012) found. We generally expect that aspen populations are healthier at higher elevations, where the climate is more favorable (Rehfeldt *et al.* 2009). However, increased recruitment mortality at higher elevations and fewer recruits in areas with more snowfall indicates that higher elevation aspen populations may be experiencing recruitment challenges, which is a concern for aspen sustainability under climate change. These recruitment challenges could be caused by reduced growth efficiency at higher elevations as resources are re-allocated from growth to offset abiotic stress (Carroll *et al.* 2019), providing motivation for future research on aspen growth versus defense tradeoffs in Arizona.

Management implications

The findings of our study can be used to guide management that seeks to increase resilience and adaptive capacity of aspen ecosystems by promoting regeneration and recruitment. Aspen ecosystem resilience and adaptive capacity are challenged by lack of historical fire, a rapidly warming climate, chronic ungulate browse, and outbreaks of oystershell scale. Managers must address these challenges to sustain aspen ecosystems and the multitude of species they support along the southwestern edge of its range and beyond (Rogers *et al.* 2020).

To sustain aspen in the future, management should maximize opportunities for aspen regeneration across the landscape. Aspen regeneration should be promoted both in areas where aspen currently exists, ensuring self-replacement and increasing diversity in age structure, and in areas where aspen is absent, thereby facilitating migration into potentially more suitable habitats in a warming climate. Promoting fire is a highly effective strategy for facilitating regeneration across the landscape, as the existing literature and our study demonstrate. Aspen's regeneration potential was limited throughout the 20th century due to fire suppression and exclusion, which began in the late 19th century (Jones and DeByle 1985b; Johnson 1994; Cocke *et al.* 2005; Binkley *et al.* 2006). As a result, many aspen stands are in advanced stages of succession to conifers (Johnson 1994; Shepperd and Fairweather 1994; Fairweather *et al.* 2008; Zegler *et al.* 2012). However, opportunities for aspen regeneration have increased in recent decades as climate change has facilitated more frequent, larger, and more severe wildfires (Singleton *et al.* 2019), a pattern that is likely to continue with continued climatic warming (Seager *et al.* 2007). An important advantage of high-severity fire over other regeneration tactics, such as clearfelling aspen stands, is that fire facilitates both asexual and sexual reproduction of aspen (Kreider and Yocom 2021). Post-fire sexual reproduction has the dual benefits of allowing aspen to establish in new areas via seedlings and increasing genetic diversity and potentially adaptation to a warming climate (Mock *et al.* 2008; Long and Mock 2012; Fairweather *et al.* 2014; Dixon and DeWald 2015; Kreider and Yocom 2021). Although more fire in a warmer climate is likely to benefit aspen (Kulakowski *et al.* 2013; Nigro *et al.* 2022), our study indicated that

warmer, drier conditions are unfavorable for aspen regeneration in Arizona. Across western North America, it is unclear whether decreasing aspen habitat due to climate warming (Rehfeldt *et al.* 2009; Worrall *et al.* 2013) or increasing opportunities for aspen establishment due to disturbance (Shinneman and McIlroy 2019; Andrus *et al.* 2021) will have greater impacts on aspen's future. In Arizona, managers should target areas with lower drought stress, more precipitation, and lower HL when considering areas for aspen regeneration treatments, ungulate management, and assisted colonization or gene flow (Kreyling *et al.* 2011; Aitken and Whitlock 2013).

Aspen regeneration success is contingent upon ensuing recruitment, which is far more difficult to promote as indicated by lower levels of sustainable recruitment compared with regeneration in Arizona. Based on the results of our study, we propose that successful management of aspen recruitment requires consideration of two important limiting factors: ungulate browse and oystershell scale. Ungulate management tactics, especially exclosures ($n = 65$), which were more common than jackstraws ($n = 6$) in our study, were extremely successful at reducing browse. However, exclosures have major drawbacks; they are costly to install and maintain (Shepperd 2004; Fairweather *et al.* 2008), limit aspen to confined areas which reduces adaptive capacity (Crouch *et al.* 2023), and are strongly associated with oystershell scale outbreaks (Crouch *et al.* 2021). Because oystershell scale is a primary driver of aspen recruitment mortality in Arizona, the long-term efficacy of exclosures may be compromised. Given the need to reduce local ungulate impacts and the limitations of exclosures, we suggest three paths forward for aspen management: (i) directly reduce ungulate population sizes and increase movement, particularly of introduced elk, to facilitate landscape-level recruitment, (ii) manage for aspen at higher elevations, which should be more suitable for aspen in a changing climate and less susceptible to oystershell scale, and (iii) mitigate damage from oystershell scale. Our future work seeks to address this last objective by assessing the extent, impacts, and drivers of oystershell scale invasions, answering critical questions about the insect's biology that are relevant to its management, and developing an integrated pest management program for oystershell scale.

Conclusion

Our study of aspen populations across Arizona is the first to report state-wide issues with sustainability of aspen regeneration and recruitment. We observed higher levels of sustainability in study plots for regeneration (33.6%–58.2%) than for recruitment (24.1%–35.9%), indicating that recruitment bottlenecks are occurring in Arizona. Of particular concern is our finding that 40% of study plots lacked a single recruiting stem. Using random forests and SEM, we assessed which biotic and abiotic factors significantly influenced aspen regeneration and recruitment. Aspen regeneration was less abundant on warmer sites, highlighting the threat that a rapidly warming climate poses to aspen sustainability. Aspen recruitment was significantly more abundant in areas with recent fire and had a strong positive relationship with fire severity. The most important factors limiting recruitment were ungulate browse, especially by introduced Rocky Mountain elk, and the invasive insect, oystershell scale.

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Author contributions

Connor Crouch (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing—original draft, Writing—review & editing), Nicholas Wilhelmi (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing—review & editing), Margaret Moore (Conceptualization, Methodology, Project administration, Writing—review & editing), Paul C. Rogers (Conceptualization, Methodology, Writing—review & editing), and Kristen Waring (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing—review & editing)

Supplementary data

Supplementary data is available at *FORESJ Journal* online.

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Data availability

We have published our data and R script via the Environmental Data Initiative, which can be accessed here: <https://doi.org/10.6073/pasta/6f69676d8665a62801c6aa1c739cd581>.

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