REGENERATION AND RECRUITMENT FOR RESILIENCE: SUSTAINING ASPEN ECOSYSTEMS THREATENED BY CLIMATE CHANGE, UNGULATE BROWSE, AND OYSTERSHELL SCALE

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ABSTRACT

REGENERATION AND RECRUITMENT FOR RESILIENCE: SUSTAINING ASPEN ECOSYSTEMS THREATENED BY CLIMATE CHANGE, UNGULATE BROWSE, AND OYSTERSHELL SCALE

CONNOR DAVIDSON CROUCH

Quaking aspen (*Populus tremuloides*) ecosystems are highly valued in the southwestern United States because of the ecological, economic, and aesthetic benefits they provide. Concerningly, aspen has experienced extensive mortality in recent decades, and there is evidence that many areas in Arizona, USA lack adequate recruitment to replace dying overstory trees. Maintaining sustainable levels of regeneration and recruitment is necessary for facilitating resilience to biotic and abiotic disturbance agents and for maximizing aspen's ability to adapt in an increasingly uncertain future. However, questions remain about which factors currently limit aspen regeneration and recruitment in Arizona and which strategies are appropriate for promoting aspen sustainability. Moreover, recent outbreaks of an invasive insect, oystershell scale (*Lepidosaphes ulmi*; OSS) pose a new threat to aspen forest health. Because these are the first documented outbreaks of OSS in aspen ecosystems, there is an urgent need to survey the extent and impacts of these invasions and to better understand the insect's biology and ecology on aspen in Arizona. To fill these knowledge gaps, we conducted a systematic literature review of aspen in the Southwest to understand how biotic and abiotic factors, including management, influence aspen forest dynamics (Chapter 1). We also sampled aspen populations across Arizona to quantify the sustainability and drivers of aspen regeneration and recruitment (Chapter 2) and impacts and drivers of OSS invasions (Chapter 3). Finally, we used repeated measurements of OSS-infested aspen stands to quantify short-term rates of OSS intensification on trees, OSS spread among trees, and aspen mortality, and we collected OSS from these stands to document the insect's phenology in northern Arizona (Chapter 4).

We found that many aspen populations in Arizona lack sustainable regeneration and recruitment. The status of recruitment was especially dire, with 40% of study plots lacking a single recruiting stem. Aspen regeneration was less abundant on warmer, drier sites, highlighting the threat that a warming climate poses to aspen sustainability. Aspen recruitment was significantly more abundant in areas with recent fire and more severe fire. The most important factors limiting recruitment were OSS and browsing by ungulates, especially Rocky Mountain elk (*Cervus canadensis*). OSS was widespread in Arizona and was associated with increased aspen crown damage and mortality. Climate was the most important driver of OSS abundance, with warmer, drier conditions resulting in significantly more OSS. OSS was also associated with less recent fire, presence of ungulate management strategies such as fenced exclosures, and stands with a greater density of aspen saplings. We also found that immature OSS life stages persist throughout the year and that there are two waves of first-instar crawlers in northern Arizona, one throughout the summer and the second in mid-winter. The first wave seemed to be driven by warming temperatures, but the cause of the second wave is unknown and might represent the initiation of a second generation. We also found that OSS causes high levels of mortality and spreads rapidly within aspen stands. We conclude by discussing how our findings can inform contemporary management of aspen and OSS (Chapter 5).

Acknowledgements

Although an aspen tree may look like a single individual aboveground, it is supported by a network of roots shared with its neighbors that allows it to thrive. Obtaining a PhD also requires an extensive network of supportive individuals, and I am incredibly grateful for the mentors, colleagues, friends, and family that have supported me over the past four years.

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Preface

This dissertation is presented in journal format with four chapters written as independent manuscripts followed by a fifth chapter, which is intended to be a research brief summarizing the dissertation's management implications. The first chapter, titled "Building ecosystem resilience and adaptive capacity: a systematic review of aspen ecology and management in the Southwest," is a systematic literature review that was published in *Forest Science* on February 23, 2023 (https://doi.org/10.1093/forsci/fxad004). The second chapter, titled "Sustainability and drivers of aspen regeneration and recruitment near the southwestern edge of its range," is formatted for *Ecological Applications*. The third chapter, titled "Extent, impacts, and drivers of oystershell scale invasions in aspen ecosystems," is formatted for *Biological Invasions*. The fourth chapter, titled "Oystershell scale phenology, intensification, and spread on aspen in Arizona, USA," is formatted for *Environmental Entomology*. Acknowledgements, references, tables, figures, and supplementary materials are included at the end of each individual chapter. Some redundancy exists among chapters, which is necessary to conform with journal formatting standards.

Chapter 1: Building ecosystem resilience and adaptive capacity: a systematic review of aspen ecology and management in the Southwest

Abstract

Quaking aspen (*Populus tremuloides* Michx.) has high conservation value on the southwestern edge of its range, which extends from the southwestern United States (i.e., Arizona, New Mexico, and Texas) to central Mexico. This value is driven by aspen's ecological importance, positive impact on local economies, and aesthetic and cultural values. Generally, the scant aspen populations that remain in the Southwest lack resilience and adaptive capacity, and managers are unsure how best to maintain the species in an uncertain future. This systematic review seeks to address that need by reviewing existing literature from the Southwest on which biotic and abiotic factors influence aspen forest dynamics and by synthesizing that literature with a discussion of how management can promote aspen ecosystem resilience and adaptive capacity. We found that fire and silvicultural treatments promote aspen regeneration, but chronic ungulate browse inhibits recruitment. Moreover, drought is a driver of overstory mortality and has a negative influence on recruitment. In the second half of this review, we propose three management objectives for increasing aspen resilience and adaptive capacity: (1) promote diversity in age structure, (2) mitigate ungulate impacts, and (3) enhance complexity. We consider how various management strategies could meet these objectives and highlight potential threats to aspen forest health and resilience.

Keywords: decline, ecological silviculture, exclosures, *Populus tremuloides*, Rocky Mountain elk, wildfire

Introduction

Quaking aspen (*Populus tremuloides* Michx.; hereafter aspen) is the most widely distributed tree species in North America (Little 1971; Perala 1990). Despite its abundance across the continent, aspen has a limited extent along the southwestern edge of its range, which extends from the southwestern United States (hereafter the Southwest) to central Mexico (Little 1971; Perala 1990; Martínez González and González-Villarreal 2005). Aspen has high ecological importance (Campbell and Bartos 2001; Rogers et al. 2020), a positive impact on local economies (McCool 2001; Rogers 2017), and important aesthetic and cultural values (Dahms and Geils 1997; McCool 2001; Assal 2020). Compared to other areas of aspen's expansive range, the importance and value of aspen ecosystems is even more pronounced in the Southwest, where they are scarce but make an outsized contribution to biodiversity, especially in comparison to neighboring conifer-dominated ecosystems (Chong et al. 2001; Gitlin et al. 2006; Kuhn et al. 2011; Riva and Fahrig 2022).

Aspen's conservation value has been heightened further in recent decades due to the species' ongoing decline, a term we use to refer to the loss of aspen at the landscape level. There are three pathways of aspen decline: (1) advancing succession to conifers caused by lack of disturbance (Kay 1997), (2) acute mortality events, especially at lower elevations, caused by interactions among predisposing, inciting, and contributing factors (Manion 1991; Worrall et al. 2013), and (3) failure of regenerating stems to recruit due to chronic ungulate browse, which can intensify both successional and acute decline (Bartos and Campbell 1998; Fairweather et al. 2008). The compounding effects of these three processes have resulted in high levels of aspen mortality in the Southwest, with cumulative mortality rates in northern Arizona exceeding 50% in the early 21st century (Fairweather et al. 2008; Ganey and Vojta 2011; Zegler et al. 2012; Ireland et al. 2014). Chronic ungulate browse is especially concerning because it diminishes aspen ecosystem resilience and adaptive capacity (*sensu* Millar et al. 2007). Resilience refers to an ecosystem's capacity to absorb disturbance and reorganize such that pre-disturbance composition, structure, and function are eventually reattained (Millar et al. 2007; Puettmann et al. 2013; DeRose and Long 2014; Nagel et al. 2017). Adaptive capacity refers to an ecosystem's ability to adjust its composition, structure, and function in response to external forces such as a changing climate or disturbance regime (Millar et al. 2007; Puettmann et al. 2013; Nagel et al. 2017). Further constraining aspen's adaptive capacity is the limited area that is suitable for aspen in the Southwest, where it occurs on less than 2% of forested land (Johnson 1994; Rolf 2001; Gitlin et al. 2006; Halbritter and Bender 2011; Zegler et al. 2012). Aspen in the Southwest is living on the fringe of its realized climatic niche, and populations are limited in size, extent, and landscape position by the arid environment (Rehfeldt et al. 2009).

Given aspen's ecological importance and ongoing decline in the Southwest, maintaining aspen ecosystems has become an important management objective. However, the management strategies that worked in the past may not be effective in an increasingly warm and dry future. Instead, managers need to promote aspen ecosystem resilience and adaptability (Millar et al. 2007). To do so, they need information on potential aspen trajectories in response to various biotic and abiotic influences, such as ungulate browse, insects and diseases, drought, and fire. Although the individual impacts of these factors have been well studied, few experimental or observational studies have considered them together because of logistical constraints. Therefore, a systematic review and synthesis of the existing literature provides a unique opportunity to consider, in concert, the many factors that influence aspen forest dynamics. There is also need for a review of aspen management strategies and their potential to promote and maintain resilient aspen ecosystems. Numerous reviews have been published on various aspects of aspen ecology and management (e.g., DeByle and Winokur 1985; Shinneman et al. 2013; Rogers et al. 2014, 2020; Singer et al. 2019; Refsland and Cushman 2021). Many of these encompass large geographic areas and highlight the variability of aspen throughout its expansive range, yet the only review to date that has focused specifically on the Southwest was published by Jones (1974), who reviewed mixed-conifer forests, with specific sections devoted to aspen, and focused primarily on managing for timber. Scientific understanding of aspen ecology and management has advanced dramatically since then, and new challenges have arisen, necessitating a contemporary review of aspen ecology and management in the region. Finally, an important, yet understudied, geographic area of aspen's expansive range is Mexico, where the species reaches its true southern limit. Mexico is rarely mentioned in broader reviews or syntheses of aspen, and we will highlight this geographic gap in our scientific understanding of aspen.

Our review is structured around the concept of aspen forest dynamics, which we use to refer to the cycle of aspen regeneration, recruitment, and overstory survival. Regeneration, which we define as stems shorter than 1.4 m, is the process of new trees establishing, either as seedlings germinating from seed or suckers sprouting from an existing root system.

Recruitment refers to the successful growth of regenerating stems into overstory trees. The range of sizes considered recruits in our review was stems taller than 1.4 m but smaller than 10.1 cm in diameter at breast height (dbh). Although recent research from Yellowstone National Park suggests aspen stems do not escape elk (*Cervus canadensis nelsoni* Bailey) browse until they exceed 3 m in height (Brice et al. 2022) and research from Arizona suggests an even taller escape height of 4–5 m (Shepperd and Fairweather 1994; Rolf 2001; Shepperd 2004), we chose to include the lower height range in this review because many studies from the Southwest have used 1.4 m as the cut-off for recruitment (e.g., Binkley et al. 2006; Zegler et al. 2012). The final stage in our three-step cycle is survival, or conversely mortality, of mature, overstory trees (> 10.1 cm dbh). This three-step cycle not only allows us to easily classify the literature but also has important implications for aspen management which typically targets one of these three processes. Unlike for other tree species, management of aspen rarely seeks to optimize growth or productivity, except as these processes might relate to improving survival, because aspen has low value for wood products in the Southwest (Gottfried 1983; Dahms and Geils 1997). Instead, management typically seeks to maintain healthy aspen ecosystems for multiple uses, such as wildlife habitat, watershed stability, and aesthetic and recreational purposes (USDA Forest Service 2018).

This systematic review has two objectives: (1) to synthesize existing literature on how climate, fire, ungulates, insects, and diseases influence aspen forest dynamics (i.e., regeneration, recruitment, and overstory survival) in the Southwest and (2) to discuss how management can promote aspen ecosystem resilience and adaptive capacity while synthesizing existing literature on aspen responses to management.

Methods

Study Area

This review is focused on the southwestern edge of aspen's range, so only studies conducted in the Southwest and Mexico are considered here. We defined the Southwest as Arizona, Texas, and New Mexico, excluding where the Rocky Mountains extend into northern New Mexico (Fig. 1.1). Most of where aspen occurs in our definition of the Southwest is classified as a single ecoregion (Arizona and New Mexico Mountains) in the Level III Ecoregions Map, except for a few isolated pockets of aspen in the Madrean Archipelago of southeastern Arizona (US EPA 2013) and scattered populations in northeast New Mexico and west Texas. Level III Ecoregions have been used for previous aspen classification (Shinneman et al. 2013), and our definition of the Southwest closely aligns with one of the regions (Upper Gila Mountains) identified in Worrall et al. (2013). To add further support, Shaw (2004) found that aspen populations located in Arizona and New Mexico were more similar to each other based on stand structure and tree species composition than they were to aspen in any other western state.

Southwestern aspen is limited to higher elevations, where lower temperatures and higher precipitation allow the drought-intolerant species to survive (Perala 1990; Rehfeldt et al. 2009). Aspen can be found as low as 2,000 m in elevation in the ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) 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). Aspen stands tend to be small (0.1–25 ha in size), especially compared to more northerly latitudes of aspen's range (Zegler et al. 2012).

Inclusion Criteria

To be included in our review, studies had to either (1) quantify aspen regeneration, recruitment, or overstory survival responses to climate, fire, ungulates, insects, or diseases or (2) quantify aspen regeneration, recruitment, or overstory survival responses to management strategies or provide specific guidelines for aspen management. We chose the five influencing factors in criterion #1 because they have all have been implicated in the ongoing decline of aspen in the Southwest (Shepperd and Fairweather 1994; Binkley et al. 2006; Fairweather et al. 2008; Beschta and Ripple 2010; Zegler et al. 2012). In this review, we included site factors, such as elevation, under the category of climate because climate's influence can be inferred from comparing low- and high-elevation sites. We also considered conifer encroachment under the category of fire because succession to conifers is the result of lack of fire or other stand-replacing disturbance in seral aspen populations (Jones and DeByle 1985). For ungulate impacts, we included both domestic and wild ungulates. Finally, although a wide range of insects and diseases affect aspen (Hinds 1985; Jones et al. 1985), we focused only on the agents that commonly contribute to mortality. Studies were excluded if they did not directly quantify aspen responses or failed to explicitly relate those responses to observed influences. For example, if a study observed aspen regeneration after fire but did not quantify its abundance, the study was excluded from our review. Similarly, if a study documented overstory aspen survival over time without explicitly relating survival to climate, except to hypothesize that drought likely contributed to mortality, then the study was excluded. Only studies of aspen in wildland (i.e., non-urban or ornamental) settings conducted in the Southwest were included in our review. Studies that included sites both inside and outside the Southwest (e.g., a study with sites in Arizona and Utah) were excluded unless the Southwest-specific results could be gleaned separately from the non-Southwest results.

Search Methods

We searched Web of Science, CAB Abstracts, BIOSIS Citation Index, Utah State University's Aspen Bibliography, and ProQuest Dissertation and Theses. We prioritized inclusion of peer-reviewed papers but also included grey literature (e.g., conference proceedings, dissertations and theses, and technical reports) when they presented new information not already reported in the peer-reviewed literature. Failure to include grey literature can result in a biased review (Côté et al. 2013; Haddaway et al. 2020). This is especially true for the field of forest science because USDA Forest Service researchers in the 20th century commonly published results in government research papers, some of which were subject to an informal peer review, rather than peer-reviewed journals. We used the following search term string: (aspen OR "Populus tremuloides" OR tremuloides) AND (southwest* OR Arizona OR "New Mexico" OR Mexico). We also conducted separate searches using aspen's common name in Spanish (álamo temblón) to identify literature from Mexico. We identified relevant literature through references in papers identified from the systematic search, personal knowledge of existing literature that was not found via the systematic search, suggestions from colleagues in

Mexico, and undigitized documents in Northern Arizona University's Silviculture Laboratory. The latter consisted primarily of pre-1990s USDA Forest Service research papers and technical reports. Our systematic database searches occurred in December 2021, and we continued to consider literature published after that through December 2022 by establishing new paper alerts in Google Scholar using "aspen" and "Populus tremuloides" as keywords. Documents were screened initially by title and abstract and then by a comprehensive reading to determine if they met the inclusion criteria.

Systematic Review Results

Our combined search of Web of Science, CAB Abstracts, and BIOSIS Citation Index yielded 688 results. Our search of Utah State University's Aspen Bibliography produced 517 results, and our search of ProQuest Dissertations and Theses produced 77 results. An additional 126 documents were identified through citations in those results, 34 documents were identified via Google Scholar alerts, and 55 documents were included from our personal archive, recommendations from colleagues, and hard copies as described above. Although the systematic searches conducted via Web of Science, the Aspen Bibliography, etc. yielded overlapping results, we estimate that upwards of 800 unique documents were considered.

Of these ~800 documents, 307 passed the initial title and abstract screening for a full-text review. After full-text review, 63 papers met the inclusion criteria. Of these, 51 studies met inclusion criterion #1 by quantifying aspen regeneration, recruitment, and/or overstory survival responses to climate, fire, ungulates, insects, and/or diseases (Table 1.1). Some of these studies also met inclusion criterion #2, resulting in 26 total papers that met criterion #2: 23 studies quantifying aspen regeneration, recruitment, and/or overstory survival responses to management and three papers providing specific guidelines for aspen management (Table 1.2). Most studies that met our inclusion criterion were conducted in Arizona. Only four studies were conducted in New Mexico in addition to the three papers that provided specific management guidelines for New Mexico and Arizona. Notably, no studies from Texas or Mexico met our inclusion criteria, except for Worrall et al. (2013) who modeled climate suitability across aspen's entire range including Mexico.

Factors Influencing Aspen Forest Dynamics

In the following sections, we assess how climate, fire, ungulates, insects, and diseases influence aspen regeneration, recruitment, and overstory survival in the Southwest based on our systematic review of the literature (Fig. 1.2).

Regeneration

Forty studies that met our inclusion criteria quantified influences of climate (n=7), fire (n=27), ungulates (n=19), and/or insects and diseases (n=6) on aspen regeneration (Table 1.1). We included studies that assessed biotic and abiotic influences on both asexual reproduction via root suckering and sexual reproduction via seed because both forms of regeneration occur in the Southwest. Until recently, the ability of aspen to regenerate via seed has been underestimated (Mock et al. 2008; Long and Mock 2012; Fairweather et al. 2014; Kreider and Yocom 2021b), as demonstrated by the fact that only three of the 40 regeneration studies included in our review examined seedlings specifically. The historical lack of recognition of aspen seedling establishment might be driven by lack of knowledge on how to identify seedlings versus suckers (Kreider et al. 2020). Kreider et al. (2020) demonstrated that aspen seedlings can be easily distinguished from suckers in the first year after establishment, but after three years differentiation becomes nearly impossible. Although aspen seedling establishment is now thought to be a common occurrence after wildfire in the western US (Kreider and Yocom 2021b), vegetative regeneration is more prevalent. Vegetative regeneration via suckering is triggered by an interruption of two hormones, auxin and cytokinin, flowing between roots and shoots. This hormonal interruption occurs when a stem dies or is otherwise separated from its root system (Schier et al. 1985). Aspen regeneration does not always require hormonal interruption, though, as continuous, low-level suckering is common in undisturbed populations (Schier et al. 1985).

Fire strongly influences regeneration of aspen seedlings and suckers. Aspen seedlings are dependent on the favorable conditions, namely lack of competition for light and water, created after high-severity fire (Landhäusser et al. 2019). Nine post-fire seedling establishment events have been documented in the Southwest (Quinn and Wu 2001; Fairweather et al. 2014; Kreider and Yocom 2021b). Fire also creates a favorable environment for vegetative aspen regeneration by stimulating the hormonal suckering response, increasing understory light transmittance, and warming the soil via blackening (Covington et al. 1983; Schier et al. 1985; Frey et al. 2003; Shepperd 2004). Myriad studies in the Southwest have documented vegetative reproduction after wildfire (Pearson 1914; Jones and Trujillo 1975; Whittaker and Niering 1975; Rolf 2001; Bailey and Whitham 2002; Haire and McGarigal 2008; Stoddard et al. 2018), managed fire (Higgins et al. 2015), and prescribed fire (Covington et al. 1983; Shepperd 2004;

Higgins et al. 2015). Although even low-severity fire can promote aspen suckering (Covington et al. 1983; Stoddard et al. 2018), regeneration is most dense following high-severity fire (Bailey and Whitham 2002; Higgins et al. 2015). Numerous demographic studies have documented a pulse of aspen regeneration before fire suppression and exclusion began in the late 19th century (Fulé et al. 2002, 2003; Mast and Wolf 2004, 2006; Cocke et al. 2005; Heinlein et al. 2005; Binkley et al. 2006; Kaye 2011; Margolis et al. 2011), perhaps due to Indigenous- or settler-initiated burning in association with logging activities and an arid climate (Kulakowski et al. 2004; Kaye 2011). Cocke et al. (2005) highlighted the negative impact that fire exclusion and ensuing succession to conifers has had on aspen establishment. This negative effect of conifers on aspen regeneration is supported by Zegler et al. (2012), who found that conifer regeneration density was positively associated with aspen regeneration mortality.

Not all aspen in the Southwest seems to have regenerated following fire, though, and frequent fire might negatively affect aspen regeneration. Three demographic studies documented regeneration that was not associated with fire (Fulé et al. 2003; Moore and Huffman 2004; Margolis et al. 2011). Two other studies found no difference in aspen regeneration density between burned and unburned areas (Fulé and Laughlin 2007) or less regeneration in burned areas compared to unburned ones (Fulé et al 2004). However, both studies classified regeneration as stems less than 2.5 cm dbh, which includes both regenerating and recruiting stems, making it impossible to assess regeneration- versus recruitment-specific results. Frequently recurring fire might also be detrimental to aspen regeneration (Binkley et al. 2006; Higgins et al. 2015). Conifer density reductions to meet restoration objectives in ponderosa pine and dry mixed-conifer forests are designed to facilitate more low-severity surface fire (Fulé et al. 2012). These forest types often contain small aspen patches and scattered aspen individuals (Jones 1974; Zegler et al. 2012). O'Donnell et al. (2018) modelled the shift in forest conditions following such treatments and found decreased aspen regeneration opportunities in a future with more frequent, low-severity fire and less high-severity fire. Rather than preventing regeneration entirely, it seems more likely that frequent fire, at least when mean fire return intervals exceed ~5 years, would produce thickets of small-diameter aspen that are top-killed and regenerate after each fire (Margolis et al. 2011). Indeed, research from Colorado suggests that compound disturbances promote aspen thickets (Kulakowski et al. 2013; Andrus et al. 2021).

Aspen regeneration potential is limited by intense ungulate browse in many areas of the Southwest. Browsing is initially an issue of recruitment, not regeneration, because intense ungulate browse prevents regenerating stems from growing into overstory trees. If intense ungulate browse continues for 3–5 years, aspen root systems will exhaust their energy supply and stop regenerating, leading to regeneration failure (Rolf et al. 2001). For example, Fairweather et al. (2008) monitored regeneration after acute overstory aspen mortality and found that suckers were most abundant within the first few years after mortality. However, chronic browse prevented these suckers from recruiting and, after several years, aspen root systems stopped regenerating entirely. Some of earliest studies of aspen in the Southwest documented the negative impact of ungulate browse on regeneration (Pearson 1914; Rasmussen 1941). For the first half of the 20th century, livestock were the primary browsers inhibiting aspen regeneration in northern Arizona (Pearson 1914; Larson 1959), whereas mule deer (*Odocoileus hemionus* Rafinesque) were the primary culprit on the Kaibab Plateau

(Rasmussen 1941; Merkle 1954, 1962). Since the mid-20th century, wild ungulates, especially Rocky Mountain elk, have become the primary browsers impacting aspen (Beschta and Ripple 2010; Fairweather et al. 2014). Zegler et al. (2012) found that 58% of regenerating stems across 48 aspen sites had been browsed by ungulates and that browse was significantly associated with increased regeneration mortality. Studies of aspen exclosures in Arizona have documented the lack of suckers outside fenced areas (Shepperd and Fairweather 1994; Binkley et al. 2006) and the failure of new suckers to appear after recruiting stems have been killed by browsing (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Rolf 2001; Shepperd 2004). Two studies highlighted the importance of rocky outcrops in protecting aspen regeneration from browse. Beschta and Ripple (2010) documented aspen regeneration on a rocky outcrop inaccessible to elk in an area otherwise lacking regeneration. Cantor and Whitham (1989) documented a negative influence of pocket gopher (*Thomomys bottae* Eydoux & Gervais) browsing on aspen regeneration and hypothesized that gopher browse limits aspen to rocky outcrops. However, browse pressure from ungulates and reduced fire frequency due to lack of fuels on outcrops could also explain why aspen populations are often limited to rocky outcrop refugia (Beschta and Ripple 2010).

Ungulate impacts have important interactions with fire severity and aspen regeneration type. Bailey and Whitham (2002) found that high-severity fire resulted in more aspen regeneration by an order of magnitude than intermediate-severity fire. However, elk browsed 85% of regenerating stems in high-severity areas compared to 34% in intermediate-severity areas. Because of this intense, selective browsing in areas of high-severity fire, the intermediate-severity stands ultimately produced more aspen regeneration. Similarly, Rolf

(2001) found that elk made heavy use of post-fire aspen regeneration in northern Arizona even after the elk herd in that management unit was reduced by about 30%. These heavy impacts in post-fire areas from ungulates might be so pronounced because ungulates seem to prefer aspen-dominated stands over mixed-conifer stands in which aspen is a minor component (Reynolds 1969). Fairweather et al. (2014) suggested that ungulate browse may have a disproportionately negative impact on aspen seedlings compared to suckers because seedlings lack an extensive root system to draw resources from. Fairweather et al. (2014) documented a higher occurrence of post-fire aspen seedlings inside exclosures than outside exclosures, leading to the conclusion that aspen seedling establishment and survival in Arizona may be more limited by browsing than by a warming climate. On the other hand, Quinn and Wu (2001) also documented post-fire aspen seedling establishment in Arizona but found no evidence that browsing significantly impacted seedlings. Notably, Quinn and Wu's (2001) study occurred in southern Arizona, where elk are absent, whereas the study by Fairweather et al. (2014) occurred in northern Arizona, where elk are abundant.

The influence of climate on aspen regeneration is less discernable than the largely positive impact of fire and negative impact of ungulate browse. Kaye (2011) determined that the 1970s peak in aspen establishment observed on the Kaibab Plateau and other parts of the western US was likely driven by a shift towards a wetter climate. On the other hand, Binkley et al. (2006) and Beschta and Ripple (2010) found that climate trends did not explain variations in aspen establishment in the 20th century. Similarly, Zegler et al. (2012) did not find that aspen regeneration mortality was influenced by heat load or elevation. Although aspen seedlings are more sensitive to climate than suckers (Kreider and Yocom 2021b), Fairweather et al. (2014)

documented post-fire aspen seedling establishment during a period of record drought. They suggested that seasonal climate patterns and micro-climate are more relevant for aspen seedling establishment than annual climate patterns. For example, 83% of seedlings that Fairweather et al. (2014) found were located at a relatively mesic site, and 63% of seedlings established beneath downed logs, which provided shelter for drought-sensitive seedlings. Coarse woody debris might also promote seedling establishment by trapping seeds as they disperse via wind (Kreider and Yocom 2021a). Quinn and Wu (2001) noted that post-fire aspen seedling establishment coincided with unusually high precipitation in May and June, when aspen seedlings typically germinate. In their review of post-fire aspen seedling events across the western US, Kreider and Yocom (2021b) found that areas with higher precipitation and lower temperatures tended to promote seedling establishment. However, the seedling events they assessed from Arizona tended to have lower precipitation and higher temperatures than average years, a paradoxical finding that lends further support to the hypothesis by Fairweather et al. (2014) that seasonal climate patterns may be more relevant to seedling establishment than annual climate patterns. Looking ahead, O'Donnell et al. (2018) modeled climate change based on representative concentration pathways (RCP) 4.5 and 8.5, finding that loss of mesic conditions conducive to aspen regeneration will lead to the species' decline on the Kaibab Plateau; however, this study did not differentiate between sexual and asexual reproduction.

Although aspen regeneration is susceptible to an array of insects and diseases, studies included in our review identified three insects and diseases that cause notable dieback and/or mortality of regenerating stems: Cytospora canker (caused by *Valsa sordida* Nitschke), shepherd's crook (caused by *Venturia tremulae* var. *grandidentatae* Aderh.), and oystershell scale (*Lepidosaphes ulmi* Linn.). Cytospora canker has been associated with regeneration failure of aspen suckers following clearfelling (Jacobi and Shepperd 1991; Shepperd and Fairweather 1994; Fairweather and Tkacz 1999). In all three of these studies, mortality of aspen regeneration from Cytospora canker was preceded by ungulate browse, indicating that Cytospora likely played a secondary role in killing regeneration. Similarly, Zegler et al. (2012) found that ungulate browse, not insects or diseases, was significantly associated with regeneration mortality. Aside from Cytospora canker, Beschta and Ripple (2010) noted shepherd's crook as a common disease causing dieback of aspen regeneration. Generally, though, shepherd's crook is less common, damaging, and pathogenic than Cytospora canker, which typically results in mortality. The third biotic agent affecting regeneration is oystershell scale, which was recently documented causing dieback and mortality of aspen regeneration in Arizona (Crouch et al. 2021). Potential implications of oystershell scale are explored further in the Aspen Management section below.

Recruitment

Thirty studies that met our inclusion criteria quantified influences of climate (n=7), fire (n=15), ungulates (n=17), and/or insects and diseases (n=7) on aspen recruitment (Table 1.1). In addition to studies that directly quantified abundance or mortality of recruiting stems, we also included studies that identified bottlenecks preventing growth of aspen regeneration, such as studies that documented historical gaps in aspen establishment. Of the three processes we consider, recruitment may be the most relevant to aspen management because recruits represent the aspen forests of the future and are an underrepresented size class in the Southwest (Beschta and Ripple 2010; Zegler et al. 2012).

Fire generally has a positive influence on aspen recruitment. Although fire technically has a negative direct effect on recruiting stems because aspen is susceptible to fire-induced mortality, fire has a strong, positive indirect effect on recruitment by promoting abundant regeneration that may grow into recruiting stems. Higgins et al. (2015) found that density of aspen recruits was significantly greater in mixed-conifer forests that had experienced high-severity fire than in low-severity or unburned 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. On the other hand, Higgins et al. (2015) also studied low-severity prescribed fires in the ponderosa pine forest type and found no difference in density of aspen recruits among areas that were unburned, had experienced one fire, and had experienced two fires. Fulé and Laughlin (2007) found that managed fire had no effect on abundance of aspen recruits, while Fulé et al. (2004) found that a prescribed fire, which escaped and became a high-severity wildfire, reduced abundance of aspen recruits. Aside from these four observational studies, numerous demographic studies point to the importance of fire in promoting aspen recruitment. Nine studies documented historical post-fire pulses of aspen recruitment (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), leaving no doubt about the importance of fire for establishing aspen in the Southwest. Lack of fire, which became increasingly common after fire suppression and exclusion began in the late 19th century, also has important implications for recruitment success. Clement et al. (2019)

found that relative conifer density had a strong negative influence on aspen recruitment abundance, and Zegler et al. (2012) found that relative density of conifer recruits was significantly associated with increased mortality of aspen recruits. Fairweather et al. (2008) suggest that this successional replacement of aspen by conifers is due not only to lack of fire but also to chronic ungulate browse.

The positive influence of fire on aspen recruitment is contingent upon the ensuing negative influence of ungulate browse. Rasmussen (1941) first documented the lack of aspen recruitment due to chronic deer browse on the Kaibab Plateau in the early 20th century. Merkle (1954, 1962) later corroborated Rasmussen's observations and noted that there was still little aspen recruitment in mixed-conifer and spruce-fir forests. More recently, Binkley et al. (2006) used multiple lines of evidence to confirm that it was irrupting deer populations that inhibited aspen recruitment on the Kaibab Plateau in the early to mid-20th century. As in other areas of the western US, browsing by livestock has historically limited aspen recruitment in the Southwest (Larson 1959), but the impact from livestock is now minimal compared to the impacts of wild ungulates, especially elk (Beschta and Ripple 2010; Fairweather et al. 2014). In the 1960s aspen stands began to be clearfelled in northern Arizona for firewood and were fenced to exclude cattle (*Bos taurus* Linn.), but nearly all these areas failed to recruit due to intense browse pressure from elk (Rolf 2001). To this day, recruitment is severely limited outside exclosures in areas where elk are present (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Rolf 2001; Shepperd 2004; Bailey et al. 2007; Fairweather et al. 2008; Martin and Maron 2012; Zegler et al. 2012; Martin 2014).

The only study included in our review that did not report a negative influence of ungulate browse on aspen recruitment was Clement et al. (2019), who concluded that ungulates play a relatively unimportant role in limiting recruitment. However, the ungulate-specific results of their study deserve scrutiny for two reasons. First, Clement et al. (2019) indirectly assessed ungulate impacts by counting pellet piles, rather than directly assessing damage to stems. Second, 25% of the study sites sampled by Clement et al. (2019) either lacked elk (e.g., the Kaibab Plateau in northern Arizona and Sky Islands of southern Arizona) or were located in the Wallow Fire, which was an unusually large (~218,000 ha) and severe (17% high soil burn severity) wildfire that may have saturated browse pressure, as has occurred following large, high-severity wildfires in other areas of aspen's range (Smith et al. 2011; Wan et al. 2014). Ungulates do not negatively impact every aspen population in the Southwest (e.g., Quinn and Wu 2001; Fulé et al. 2003; Clement et al. 2019), but the multitude of studies documenting low recruitment due to chronic browse indicates that ungulate browse is a serious concern, especially in areas where elk are abundant.

Climate's influence on aspen recruitment has not been studied as thoroughly as fire or ungulates, but a warming climate seems to negatively influence recruitment. Two studies conducted in Arizona directly evaluated climatic influences on recruitment, and both found that a warmer, drier climate was associated with reduced aspen recruitment (Zegler et al. 2012; Clement et al. 2019). Zegler et al. (2012) found that mortality of recruits increased with heat load and decreased with elevation, and Clement et al. (2019) found that drought was associated with reduced density of recruits. Two studies along the Mogollon Rim in northern Arizona found that declining snowfall was strongly correlated with decreases in aspen stem density, which could be due to reduced water available to plants or to increased ungulate browse in low snow years (Martin 2007; Martin and Maron 2012). These two studies did not consider fire as a covariate, and lack of recent fire in older aspen populations on the Mogollon Rim could also explain low levels of recruitment. Three demographic studies indirectly assessed the influence of climate on aspen recruitment. Kaye (2011) determined that the 1970s peak in aspen recruitment observed on the Kaibab Plateau was likely driven by a shift towards a wetter climate, whereas Binkley et al. (2006) and Beschta and Ripple (2010) concluded that climate trends did not explain variations in aspen establishment in the 20th century. However, these demographic studies assessed success or failure of recruitment, whereas the observational studies by Zegler et al. (2012) and Clement et al. (2019) directly quantified recruitment mortality and abundance, respectively. These observational studies were conducted more recently in the era of prolonged, climate change-driven drought (Breshears et al. 2005), and they provide stronger direct evidence of climate's influence on recruitment. Therefore, we conclude that warm, dry conditions negatively affect aspen recruitment in the Southwest, a finding consistent with aspen in other regions (Kaye 2011; Shinneman and McIlroy 2019; McIlroy and Shinneman 2020).

Drought stress likely predisposes aspen recruits to mortality, whereas insects and diseases likely play an inciting or contributing role in killing recruits (Marchetti et al. 2011; Worrall et al. 2013). Two agents are of particular concern for recruits: Cytospora canker and oystershell scale. Zegler et al. (2012) found that Cytospora canker was the second most common damaging agent affecting aspen recruits in northern Arizona, behind only ungulate damage. Four other studies also identified Cytospora canker as a significant agent contributing to mortality of aspen recruits that were browsed or suppressed (Martin 1965; Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Shepperd 2004). The fungus that causes Cytospora canker, *Valsa sordida*, remains latent in healthy aspen bark until the tree experiences stress, at which point the fungus begins to rapidly cause disease by killing the tree's phloem and cambium (Marchetti et al. 2011). Thus, Cytospora's role as an agent of aspen mortality is limited to trees that have already been stressed or damaged (Hinds 1985; Marchetti et al. 2011). In contrast, oystershell scale is an invasive insect that may function as an inciting factor of aspen mortality (Crouch et al. 2021). Oystershell scale poses a particular threat to recruiting stems, which had higher infestation and mortality levels than aspen regeneration or overstory trees (Crouch et al. 2021). The mechanism underlying oystershell scale's apparent preference for aspen recruits is unknown but represents a major threat to aspen resilience.

Overstory Survival

Sixteen studies that met our inclusion criteria quantified influences of climate (n=9), fire (n=7), and/or insects and diseases (n=4) on overstory aspen survival (Table 1.1). There were no studies that quantified ungulate influences on overstory survival. Although there is likely a connection between ungulate barking and increased susceptibility to diseases (Krebill 1972), animal damage typically does not kill larger stems (DeByle 1985). Our review indicates that both advancing succession and acute mortality events are contributing to overstory aspen mortality in the Southwest.

Climate, particularly drought, is an important driver of acute overstory mortality in the Southwest. Climate's impact is most apparent from the high levels of overstory mortality that have occurred at lower elevations, which tend to be warmer and drier (Gitlin et al. 2006; Fairweather et al. 2008; Zegler et al. 2012; Ireland et al. 2014). Although one study included in our review (Kane et al. 2014) did not find a significant relationship between overstory mortality and elevation, the authors speculate that this is because their study sites were limited to higher elevations (> 2300 m). Two studies (Kane et al. 2014; Ireland et al. 2020) included in our review directly quantified overstory mortality responses to climate, and in both studies, warmer temperatures and lower precipitation were associated with increased mortality. These observational studies corroborate the bleak future that modeling studies indicate aspen will face in a warming climate. Two such modeling studies were included in our review (Rehfeldt et al. 2009; Worrall et al. 2013), and both found that aspen's extent will decline significantly in the Southwest due to higher temperatures and lower precipitation. Drought-induced overstory mortality could be caused directly by increasing the risk of cavitation fatigue (Anderegg et al. 2013; Kane et al. 2014) or indirectly by reducing growth (Ireland et al. 2020), which in turn increases mortality risk (Ireland et al. 2014; Kane and Kolb 2014).

The indirect effect of drought on overstory mortality, mediated through reduced growth, suggests that drought is also contributing to the slower, successional decline of aspen in the Southwest. The primary driver for advancing succession is thought to be lack of fire or other stand-replacing disturbance, resulting in competition with and replacement by conifers (Jones and DeByle 1985). In support of this hypothesis, Zegler et al. (2012) found that overstory mortality increased with increasing relative conifer basal area. Drought might accelerate succession by reducing aspen growth (Ireland et al. 2020), resulting in more rapid conifer encroachment and increased overstory mortality risk (Ireland et al. 2014; Kane and Kolb 2014).

Ireland et al. (2014) suggested that two different pathways of aspen mortality may be occurring in different forest types. Successional loss of aspen may predominate in higher elevation, mixed-conifer forests, whereas acute overstory mortality may be the dominant process in lower elevation ponderosa pine forests (Ireland et al. 2014). In addition to drought, other extreme weather events might also contribute to aspen mortality. For example, a severe early summer frost was likely an inciting factor of acute aspen mortality observed in northern Arizona in the early 21st century (Fairweather et al. 2008). Moreover, research from Utah suggests that frost damage reduces aspen growth (Birch et al. 2022), so frost damage might also contribute to the slower, successional decline of aspen. Concerningly, severe growing season frosts may become more common under climate change, especially for species like aspen that are phenologically sensitive (Ma et al. 2019).

Although drought and successional replacement by conifers are the primary drivers of overstory mortality in the Southwest, fire and biotic agents also play a role. Four studies (Fulé et al. 2004; Fulé and Laughlin 2007; Higgins et al. 2015; Stoddard et al. 2018) quantified fire-induced overstory mortality, which can occur even at low fire severities (Stoddard et al. 2018) and affects even the largest aspen trees (Fulé et al. 2004). Fire does not always result in overstory mortality, though, as three studies documented survival of overstory aspen after low-severity fire (Covington et al. 1983; Quinn and Wu 2001; Margolis et al. 2011). In addition to fire, an array of insects and diseases are known to cause overstory mortality in the Southwest. Some insects, such as western tent caterpillar (*Malacosoma californicum* Packard) and oystershell scale, function as inciting factors of mortality by further weakening trees already stressed by drought (Fairweather et al. 2008; Crouch et al. 2021). These agents could kill trees directly or facilitate mortality from secondary, contributing agents, such as Cytospora canker and bronze poplar borer (*Agrilus liragus* Barter & Brown) (Fairweather et al. 2008; Zegler et al. 2012; Kane et al. 2014). Both fire and biotic agents have the potential to see increased impacts in a warming climate, as we discuss below.

Aspen Management

Understanding a species' ecology informs sound stewardship, and our preceding review of factors influencing aspen forest dynamics sets the stage for a discussion of aspen management. We begin with a brief history of aspen management in the Southwest before proposing three management objectives that will increase aspen resilience and adaptive capacity. We consider how various management strategies could meet these objectives using evidence from studies that quantified aspen responses to management. We also highlight potential threats to aspen forest health and resilience and their associated management challenges.

History

Aspen ecosystems were likely managed for centuries by Indigenous burning prior to Euro-American settlement (Kay 1997; Kimmerer and Lake 2001). Due to a lack of documented information on Indigenous Peoples' management of aspen, we focus here on the post-settlement era of the Southwest for which documentation exists. For most of the 20th century, aspen was a relatively low priority for forest scientists and managers, perhaps because aspen occupies less than 2% of Southwestern forests (Johnson 1994; Rolf 2001; Gitlin et al. 2006; Halbritter and Bender 2011; Zegler et al. 2012) and has low wood products value compared to its conifer associates (Gottfried 1983; Dahms and Geils 1997). Early in the 20th century, scientists acknowledged aspen's propensity to regenerate prolifically by suckering after fire (Pearson 1914), and by the middle of the century, scientists began to recognize the negative impacts of chronic ungulate browse on aspen recruitment (Rasmussen 1941; Merkle 1954, 1962). However, it was not until Jones (1974) reviewed "the status of our knowledge" about mixed-conifer and aspen forests that a formal summary of aspen ecology and management in the Southwest was published. A decade later, DeByle and Winokur (1985) published a comprehensive review of aspen ecology and management in the western US, which arguably marked the beginning of modern aspen science and, to this day, remains a valuable resource. Active aspen management began in the mid-20th century with experimental partial cutting of aspen stands, a technique that removes some but not all overstory aspen, and construction of exclosures to protect regeneration from ungulate browse (Larson 1959; Reynolds 1969; Binkley et al. 2006). From the 1950s to the 1980s, aspen research and management focused heavily on silviculture, with small clearfelling and partial cutting operations in pure aspen stands and various partial harvesting operations in mixed-conifer stands (Jones 1975; Gottfried 1983; Ffolliott and Gottfried 1991). Foresters believed that a market for aspen wood products would develop in the Southwest (Spencer 1966), but such endeavors never materialized. Over the last half century, aspen management priorities have shifted from timber-oriented to conservation objectives, recognizing the array of ecosystem services aspen provides (Patton and Jones 1977; Dahms and Geils 1997). As a result, contemporary aspen management is focused on promoting regeneration and recruitment, particularly in areas where aspen already exists. Common practices include selectively removing conifers in and around existing aspen stands, building exclosures around existing aspen, and clearfelling declining overstory aspen to regenerate a new, healthy cohort of aspen suckers.

Managing for Aspen Resilience and Adaptive Capacity

Aspen faces a singular collection of threats along the southwestern edge of its range, from a warming climate and increased fire activity to chronic ungulate browse and outbreaks of oystershell scale. Managing for aspen ecosystem resilience and adaptive capacity is critical to confront this array of threats and prepare for an increasingly uncertain future. Arguably the most imminent and intractable threat to aspen is a warming climate (Rehfeldt et al. 2009). Given aspen's projected migration into higher elevations under climate change (Rehfeldt et al. 2009), we argue that the contemporary management paradigm of conserving existing aspen populations at all costs must shift to promoting aspen population flexibility across the landscape. To accomplish this goal and increase aspen resilience and adaptive capacity, we propose that aspen management in the Southwest should seek to (1) promote diversity in age structure across the landscape, particularly by enhancing regeneration and recruitment, (2) mitigate negative impacts of ungulate browse on recruitment, and (3) enhance structural, adaptive, and functional complexity (Fahey et al. 2018) (Fig. 1.3). In this section, we discuss strategies for meeting these objectives by synthesizing the 26 studies that met inclusion criterion #2 by quantifying aspen responses to management or providing specific guidelines for aspen management in the Southwest (Table 1.2). Although the studies we discuss below were not implemented with the goal of promoting resilience or adaptability, we can consider them in a modern lens and assess their potential for meeting contemporary management objectives (Fahey et al. 2018).

1. Promoting Diversity in Age Structure

Diverse age structures with ample regeneration and recruitment at the landscape level facilitate resilience to biotic and abiotic disturbance agents, maximize aspen's adaptive capacity, and promote aspen population flexibility across the landscape. At the stand level, natural diversity in age structure will vary based on whether a given aspen population is stable or seral (Harniss and Harper 1982). Stable populations, which remain aspen through several ecological rotations with minimal succession to conifers, are typically uneven-aged, whereas seral populations, which depend on fire and other stand-replacing disturbance to favor aspen over conifers, are typically even-aged (Rogers et al. 2014). In theory, managers should only promote stand-level age class diversity in stable populations. However, debate on whether aspen in the Southwest is stable or seral, or which populations fall into which category, is active and largely unresolved. To determine a given population's status, one needs long-term (> 100 years or > 1 ecological rotation) data on the population's structure and composition (Rogers et al. 2014). In the Southwest, most aspen populations have recently regenerated following high-severity fire, are chronically browsed by ungulates, or have recently been fenced to exclude ungulates. As a result, few aspen populations have had the opportunity to recruit another aspen cohort or succeed to conifers without fire or ungulates interrupting stand dynamics. Further discussion of aspen stable versus seral status is beyond the scope of this review, except to note that research is needed to untie the status of aspen populations and their relative frequency in the Southwest (Box 1.1). To do this, ungulate impacts need to be minimized for stable populations to establish new cohorts and for seral populations to recruit after disturbance.

Silvicultural techniques are well-suited for increasing stand- and landscape-scale diversity in age structure via increased regeneration and recruitment (Fig. 1.3). Clearfelling has been the traditional regeneration method for aspen in the western US (Shepperd 2004). Although clearfelling is not appropriate in stable aspen populations (Rogers et al. 2014; Rogers 2017), clearfelling seral aspen populations can stimulate aspen regeneration in the absence of a stand-replacing disturbance such as fire. Clearfelling promotes abundant aspen regeneration (Jones 1975; Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Rolf 2001; Shepperd 2004), with post-treatment regeneration densities as high as 34,000-50,000 stems/ha in healthy stands (Jones 1975; Shepperd and Fairweather 1994; Rolf 2001) and as low as 4,000-9,000 stems/ha in stands with regeneration mortality from browse and disease (Fairweather and Tkacz 1999). Even the low end of this range meets the self-replacement threshold of 2,500 regenerating stems/ha suggested by O'Brien et al. (2010). Aspen also regenerates after partial cutting, a technique that removes some but not all overstory aspen and can facilitate establishment of a second age cohort (Larson 1959; Reynolds 1969). Larson (1959) studied a 50% removal of basal area and documented almost 10,000 regenerating stems/ha, while Reynolds (1969) studied a thinning treatment, which removed 25% of basal area, and reported only 370 regenerating stems/ha. In an average healthy stand in Arizona, approximately 40 regenerating stems will translate into a single overstory tree over time (C. Crouch, unpublished data), so the regeneration levels documented by Reynolds (1969) would translate to less than

10 overstory trees. Reynolds (1969) did not explain why such low levels of regeneration were observed, but we speculate that residual overstory aspen limited suckering, suggesting a 50% removal of basal area is more effective for establishing a second cohort in thinned aspen stands. The long-term trajectory of aspen regeneration after partial cutting is unclear because the overstory is expected to interfere with development of suckers by limiting their access to light (Box 1.1) (Larson 1959; Jones 1974, 1975; Patton and Jones 1977).

Aspen in the Southwest commonly occurs in mixed stands with conifers, which can also be treated silviculturally to promote aspen regeneration and establish additional aspen cohorts. Partial cutting was a common harvesting technique of mixed-conifer forests in eastern Arizona in the 1970s and 1980s, although the primary regeneration objective of these harvests was to promote regeneration of conifers, not aspen (Patton 1969, 1976; Gottfried and Jones 1975; Gottfried 1983, 1987; Ffolliott and Gottfried 1991). These studies all documented increases in aspen regeneration after partial cutting of mixed-conifer forests. More intense harvesting with larger openings generally promoted more aspen regeneration (Patton 1969, 1976; Gottfried and Jones 1975; Gottfried 1983, 1987; Ffolliott and Gottfried 1991; Beschta and Ripple 2010). For example, a diameter-limit cut, which removed trees greater than 25.4 cm dbh and mimicked overstory removal, resulted in more abundant aspen regeneration (~3250 stems/ha) than an adjacent unit where single-tree and group selection were implemented (aspen regeneration ~2450 stems/ha) (Gottfried and Jones 1975; Gottfried 1983). Partial cuts in mixed-conifer forests resulted in less aspen regeneration than clearfelling of pure aspen stands by 1-2 orders of magnitude, with post-partial cut regeneration ranging from 250-3250 stems/ha. This is not surprising because pure aspen stands have more light available and a more extensive root system to regenerate from than aspen in mixed stands. However, clearfelling does not increase stand-level diversity of structure, composition, and age classes, whereas partial cutting in mixed-conifer forests can be implemented to meet those objectives (Fig. 1.3).

While harvesting conifers for timber is now less common in the Southwest, conifer removal is a strategy commonly proposed for promoting aspen in late successional stands. Shepperd (2004) outlined two case studies from Arizona in which aspen regeneration increased after removal of ponderosa pine, and Binkley et al. (2006) found that aspen regeneration was an order of magnitude above the long-term trend during a period of increased logging from 1963-1992 on the Kaibab Plateau. In addition, ecological studies have suggested that conifer removal should reduce risk of overstory aspen mortality (Kane and Kolb 2014; Ireland et al. 2014; Ireland et al. 2020). Given that drought reduces aspen growth and results in more rapid conifer encroachment (Kane and Kolb 2014; Ireland et al. 2014, 2020), perhaps the current and historical lack of a focus on managing for aspen productivity should be reconsidered. Mechanical root stimulation is another strategy for promoting aspen regeneration by severing lateral roots and initiating the hormonal suckering response (Shepperd 2004). In two case studies, Shepperd (2004) found that using a tractor with a ripper attachment promoted aspen regeneration. Similarly, Reynolds (1969) incidentally observed that aspen regeneration was most abundant after a partial cut where root systems were severed by soil disturbance. A potential advantage of mechanical root stimulation is that, if conducted at shallow depths (~20 cm) and away from overstory trees (~8-10 m), it does not kill overstory aspen (Shepperd 2004). This makes mechanical root stimulation a valuable technique for expanding existing aspen clones or introducing new size classes into a stand while maintaining the living overstory (Shepperd 2004).

Climate change is a critical consideration when deciding how and where regeneration treatments should occur. For example, promoting post-fire aspen seedling establishment, which can occur greater than 1 km away from the nearest seed source (Fairweather et al. 2014; Kreider and Yocom 2021b), is a more promising strategy for aspen migration than promoting expansion by vegetative regeneration, which is limited to where aspen root systems already exist. Strategies to directly promote post-fire seedling establishment include actively surveying recently burned areas for aspen seedlings and building fenced exclosures around these areas or preemptively building exclosures in post-fire sites that are suitable for seedling establishment, such as those that are mesic, have abundant coarse woody debris, and are near an aspen seed source (Fairweather et al. 2014; Kreider and Yocom 2021b). Managers could also actively assist aspen migration by planting seedlings, but aspen seedlings' intolerance to competition and drought may require extensive site preparation (Fisher and Neumann 1986) and watering (M. Nabel, USDA Forest Service, pers. comm.) for successful establishment. Even in the most xeric portions of its range, aspen is likely to persist in refugia that are buffered against a warming climate (Yang et al. 2015). For example, refugia sites in Arizona could include mid-elevation aspen populations (~2500 m) on north-facing aspects. Climate-buffered refugia could even include lower elevation populations located near springs that provide consistent groundwater availability. In addition to promoting population flexibility into higher elevations, managers should identify potential refugia and actively manage for aspen regeneration and recruitment at such sites. Attempts to maintain aspen on lower elevation sites are also challenged by recent outbreaks of the invasive insect oystershell scale, which is pervasive in low elevation (< 2500 m) exclosures in northern Arizona (Crouch et al. 2021). Managers may need to proactively promote aspen at higher elevations rather than continue to invest resources in conserving low-elevation populations. For example, the Coconino National Forest in northern Arizona has stopped building new aspen exclosures below ~2300 m given their likelihood of future failure (M. Nabel, USDA Forest Service, pers. comm.).

As the climate continues to warm, so too does the likelihood of increased wildfire size, frequency, and severity (Singleton et al. 2019). These changes may facilitate increased dominance of aspen, a species that is extremely well-adapted to recovery after fire (see Factors Influencing Aspen Forest Dynamics section) and repeated, overlapping disturbances of various types (e.g., Kulakowski et al. 2013; Andrus at el. 2020, 2021). Fire has high potential for increasing aspen's adaptive capacity because it not only promotes vegetative regeneration in existing stands but also creates opportunities for aspen to establish in new areas via seedlings (Fairweather et al. 2014; Kreider and Yocom 2021b). Although aspen regeneration after prescribed fire has been studied less thoroughly than regeneration after wildfire, prescribed fire successfully promotes vegetative regeneration (Covington et al. 1983; Shepperd 2004; Higgins et al. 2015). Prescribed fire can be difficult to implement in aspen ecosystems due to moist understory fuels, so opportunities to burn aspen in the Southwest may be limited to late fall when fuels have dried out after the summer monsoon season (Shepperd 2004). A potential alternative scenario for aspen in a future with abundant fire is that more frequent fire might negatively impact aspen resilience because aspen is killed by low severity fires that conifers are able to tolerate (Binkley et al. 2006; Higgins et al. 2015; O'Donnell et al. 2018). As a result, more frequent fire, especially in the presence of chronic ungulate browse, might reduce aspen's footprint. Although forest managers are unlikely to actively promote high-severity fire for the sake of aspen regeneration, such fire can be capitalized on as an opportunity for aspen to increase its footprint, provided ungulate impacts are adequately addressed. Aspen does have potential value for improving overall forest resilience following high-severity fire because it is one of the few species in the Southwest that can regenerate following the loss of overstory seed sources (Falk et al. 2022).

2. Mitigating Ungulate Impacts

Chronic ungulate browse poses a significant threat to aspen ecosystem resilience and adaptive capacity by inhibiting recruitment (Fig. 1.4). Ungulate impacts are especially intense in the Southwest because Rocky Mountain elk, one of aspen's primary browsers, is not native to the region (Bailey et al. 2007; Beschta and Ripple 2010). Rocky Mountain elk were first introduced into Arizona in 1913 following the extinction of the native Merriam's elk (*Cervus canadensis merriami* Nelson) (Beschta and Ripple 2010). Merriam's elk occurred in limited populations in a few isolated mountainous areas, whereas Rocky Mountain elk now occur in large populations throughout higher elevation areas of the Colorado Plateau (Beschta and Ripple 2010). Browsing is also more severe in the Southwest because ungulates browse aspen during the growing season, when entire stems can be consumed (Fairweather and Tkacz 1999; Halbritter and Bender 2011). Ungulate browsing could grow even more intense with climate change because, as snowpacks decrease, elk may be able to browse year-round (Beschta and Ripple 2010; Martin and Maron 2012).

The primary management strategy for mitigating ungulate impacts has been construction of fenced exclosures, which are typically built 2 m tall to exclude all ungulates and range in size from 0.02 ha to 15 ha. Variations on the traditional 2 m fence include barriers built using harvested overstory trees and 2 m fences with a gap at the bottom to allow some mammals to pass beneath (VerCauteren et al. 2007). Studies in the Southwest have invariably found that exclosures promote aspen vegetative regeneration and recruitment by protecting suckers from intense browsing by livestock (Pearson 1914; Larson 1959), deer (Binkley et al. 2006), and elk (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Rolf 2001; Bailey and Whitham 2002; Shepperd 2004; Bailey et al. 2007; Beschta and Ripple 2010; Martin and Maron 2012; Martin 2014). Fairweather et al. (2014) also found that exclosures were important for promoting establishment of aspen seedlings. Initially, it was thought that exclosures could be removed after aspen crowns grew tall enough to escape browse, but removal of fencing after about 5 years when most stems were 2.5–3.5 m tall still resulted in heavy elk browse and failure of some clones to recruit (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999; Rolf 2001; Bailey et al. 2007). Today, exclosures are maintained for at least 10–15 years, allowing stems to exceed 4 cm dbh and 4–5 m tall, and some are maintained permanently (Box 1.1) (Shepperd and Fairweather 1994; Rolf 2001; Shepperd 2004). Exclosures have three major drawbacks. First, they are expensive to install and maintain (Shepperd 2004; Fairweather et al. 2008). Second, they confine aspen regeneration and recruitment to the specific spatial footprint of each exclosure, limiting aspen's adaptive capacity in a warming climate. Third, the future success of exclosures is threatened by oystershell scale, which is pervasive in lower elevation exclosures and on recruiting stems in northern Arizona (Crouch et al. 2021).

Although less common than exclosures, alternative strategies for mitigating ungulate impacts do exist. One such strategy is jackstrawing, which creates large piles of woody debris in or around areas of aspen regeneration to limit ungulate access and impacts. Jackstrawing reduced browsing by elk, deer, and cattle in recently thinned aspen stands in northern Arizona (Reynolds 1969), but it is uncertain whether this result would hold up today with the larger population sizes of elk living in the area (Box 1.1) (Beschta and Ripple 2010; Fairweather et al. 2014). For example, a case study from northern Arizona indicated that jackstrawing after the 2010 Schultz Fire did not decrease ungulate browse of aspen regeneration (Gonzales 2017). A variation on jackstrawing is "hinging" of conifers or aspen, which entails leaving cut trees on 1–1.5 m stumps to prevent easy passage by ungulates (Kota and Bartos 2010). However, anecdotal experience in northern Arizona suggests that many trees must be cut and hinged to successfully inhibit ungulate movement (M. Sedgeman and J. Ouzts, USDA Forest Service, pers. comm.). Another creative strategy to reduce browse impacts could be the use of hunting dogs to ward off wild ungulates. Binkley et al. (2006) found that aspen successfully recruited for two decades in a small area on the Kaibab Plateau where cougar-hunting dogs were kept, despite large deer populations preventing recruitment elsewhere on the plateau. A third potential strategy for mitigating ungulate impacts is treating large enough areas with fire or silvicultural treatment to saturate ungulate browse with abundant aspen regeneration. Although this strategy was recommended by multiple studies included in our review (Jones 1974, 1975; Covington 1983; Shepperd 2004; Clement et al. 2019), it has never been directly tested, except for incidentally in large wildfires, such as the Wallow and Schultz Fires in Arizona that seem to have saturated ungulate browse. These incidental examples are not definitive proof, though, and exact proportions of post-fire aspen regenerating stems to elk on the landscape are needed (Box 1.1).

Exclosures, jackstraws, treating large areas, and even hunting dogs are a band-aid on a larger ecosystem problem. One solution to treat the underlying cause of large ungulate population sizes may be to re-introduce predators. Mexican gray wolves were introduced into the White Mountains of eastern Arizona and western New Mexico in the late 1990s (Beschta and Ripple 2010). However, the introduced wolves have so far failed to reach an ecologically effective density (Beschta and Ripple 2010). Two likely explanations for this failure are human-caused wolf mortality and the fact that non-native Rocky Mountain elk are considerably larger than Cous white-tailed deer (*Odocoileus virginianus couesi* Coues & Yarrow), which were historically the primary prey of Mexican grey wolves (Beschta and Ripple 2010). Instead of re-introducing predators, a more effective strategy might be to directly reduce ungulate populations, especially of non-native elk. Rolf (2001) found that a 30% reduction of the elk herd in one management unit did not mitigate impacts of elk browse on post-fire aspen regeneration. However, a more recent increase in hunting tags around the San Francisco Peaks after the 2010 Schultz Fire in northern Arizona seems to have facilitated post-fire recruitment, either by reducing the number of elk on the landscape or by making them move around to avoid hunters (Gonzales 2017). Permanently reducing elk densities state-wide, despite being an obvious solution, faces significant political and social resistance (Fairweather et al. 2014). The agencies that manage aspen and recognize the negative impacts of chronic ungulate browse do not have direct control over ungulate population sizes. Instead, game management agencies that have such control benefit from maintaining large ungulate population sizes (Rolf 2001).

Until social, political, or legal pressure (see Hunt v. United States 1928) forces these agencies to reduce ungulate populations, especially of non-native elk, aspen management will be limited to superficial solutions that attempt to fix an underlying ecosystem problem (Shepperd and Fairweather 1994).

3. Enhancing Complexity

Management of aspen ecosystems should seek to enhance adaptive, structural, and functional complexity wherever possible. Managing for complexity is important for maximizing potential success in an uncertain future (Puettmann et al. 2013; Fahey et al. 2018). In addition to uncertainties surrounding aspen's responses to future fire regimes and climate change, one of the most uncertain threats to aspen in the Southwest is the recent emergence of oystershell scale and the potential emergence of other novel, biotic threats. Oystershell scale is an invasive insect that has recently begun causing dieback and mortality of aspen in Arizona and other western states and threatens aspen adaptive capacity by contributing to acute mortality, especially of recruiting stems (Crouch et al. 2021). In addition to oystershell scale, two other high-impact invasive species, cheatgrass (*Bromus tectorum* L.) and spongy moth (*Lymantria dispar* Linn.), have the potential to migrate into aspen ecosystems in the Southwest in the future (Logan et al. 2007; Yang et al. 2015; Reikowski et al. 2022). It is impossible to know how best to prepare for these uncertain threats, which is why managing for complexity is important.

Perhaps the easiest starting place for managers is to consider how strategies for meeting objectives 1 and 2 might also impact complexity at different spatial scales (Fig. 1.3). For example, clearfelling reduces stand-level complexity by resetting the stand's successional trajectory, whereas partial cutting increases stand-level complexity by promoting a second age cohort. Similarly, mechanical root stimulation can be implemented to expand existing aspen clones or introduce new age cohorts into a stand while maintaining the living overstory (Shepperd 2004). As mentioned previously, management to promote new age cohorts should ideally occur only in aspen populations known to be stable because seral populations naturally are even-aged (Rogers et al. 2014). Research in other regions supports findings from the Southwest that partial cutting leads to undesirable rates of regeneration mortality or lower than acceptable rates of stocking due to soil compaction and negative interactions with the residual overstory (Perala 1977; David et al. 2001). Additionally, uneven-aged aspen stands in Colorado were found to have high rates of disease in younger cohorts (Betters and Woods 1981). Given the current state of aspen in the Southwest, we do not recommend widespread partial cutting unless future research finds it to be an acceptable pathway for increasing aspen resilience and adaptive capacity across scales (Box 1.1). At the landscape scale, all three of these strategies could increase complexity and adaptive capacity by promoting a diversity of age classes, especially in areas where most aspen populations are mature and lack regeneration and recruitment.

In addition to promoting a diversity of structures and age classes, managers must also consider how interventions may impact genetic diversity (Goessen et al. 2022). Although we know little about the influence of genetics on aspen forest dynamics, there is evidence that certain genotypes are more susceptible to ungulate browse (Shepperd and Fairweather 1994; Rolf 2001) and dieback and acute mortality (Dixon and DeWald 2015). Research from Colorado has also found that ploidy level has significant interactions with environmental conditions and influences aspen demography and mortality (Blonder et al. 2021, 2022). More research must be conducted before specific management recommendations can be made regarding aspen genetics (Box 1.1), but promoting genetic diversity by facilitating successful seedling establishment and maximizing aspen's footprint on the landscape are two good starting places.

Conclusion

We systematically reviewed literature from the southwestern edge of aspen's range to determine how biotic and abiotic factors influence aspen forest dynamics. We found that fire and silvicultural treatments promote aspen regeneration, but chronic ungulate browse inhibits recruitment. We also found that drought is a driver of overstory mortality and has a negative influence on recruitment. Although understanding the influence and relative importance of these drivers is an important first step in determining how to promote healthy aspen ecosystems, it is also critical to consider how future changes, such a warming climate, novel biotic and abiotic disturbances, and continued chronic ungulate browse, may challenge aspen management. To address these potential challenges and increase aspen ecosystem resilience and adaptive capacity, we proposed three management objectives: (1) promote diversity in age structure, (2) mitigate ungulate impacts, and (3) enhance complexity. After reviewing the existing literature on aspen responses to management and considering how various management strategies could meet these objectives, we conclude that ungulate population reduction and increased application of fire are the most effective tools for meeting the three management objectives we proposed. Finally, our systematic review highlighted important gaps in our knowledge about aspen ecosystems, such as a need for experimental research on aspen management strategies, opportunities for remote sensing and social scientific investigations, and other questions outlined in Box 1.1. Perhaps the largest gap identified by our review was the lack of research on aspen in Mexico. Because of the potential importance of aspen in Mexico as a genetic resource for climate adaptation (Quinn and Wu 2001; Callahan et al. 2013) and because understanding the state and dynamics of aspen in Mexico may help us better understand the species in more northerly parts of its range, research on aspen populations at the true southern limit of the species' range is critically needed.

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Tables

Table 1.1. Summary of the 51 papers from the southwestern edge of aspen's range that met inclusion criterion #1 by evaluating the influence of climate, fire, ungulate browse, insects, and/or diseases on aspen regeneration (regen), recruitment (recruit), and/or overstory survival.

Author(s)	**Year**	**Geographic scope**	**Influencing factor(s) studied**	**Aspen dynamic(s) studied**
Crouch et al.	2021	northern & southern AZ	insect (oystershell scale)	regen, recruit, survival
Kreider & Yocom	2021b	AZ [western US]	climate, fire	regen (seedling)
Ireland et al.	2020	northern AZ	climate	survival
Clement et al.	2019	AZ	climate, fire, ungulates, insects/diseases	recruit
O'Donnell et al.	2018	Kaibab Plateau AZ	climate, fire	regen
Stoddard et al.	2018	northern AZ	fire	regen, survival
Higgins et al.	2015	Kaibab Plateau AZ	fire	regen, recruit, survival
Fairweather et al.	2014	northern AZ	climate, fire, ungulates	regen (seedling)
Ireland et al.	2014	northern AZ	climate	survival
Kane & Kolb	2014	northern AZ	climate	survival
Kane et al.	2014	northern AZ	climate, insects/diseases	survival
Martin	2014	northern AZ	ungulates	recruit
Worrall et al.	2013	AZ, NM, Mexico [North America]	climate	survival
Martin & Maron	2012	northern AZ	climate, ungulates	recruit
Zegler et al.	2012	northern AZ	climate, fire (conifers), ungulates, insects/diseases	regen, recruit, survival
Kaye	2011	Kaibab Plateau AZ [western US]	climate, fire	regen, recruit
Margolis et al.	2011	northern & southern AZ, NM	fire	regen, recruit, survival
Beschta & Ripple	2010	northern AZ	climate, ungulates, disease (shepherd's crook)	regen, recruit
Rehfeldt et al.	2009	AZ, NM [western US]	climate	survival
Fairweather et al.	2008	central AZ	climate (site factors), ungulates, insects/diseases	regen, recruit, survival
Haire & McGarigal	2008	Kaibab Plateau AZ [& northern NM]	fire	regen
Bailey et al.	2007	northern AZ	ungulates	regen, recruit
Fulé & Laughlin	2007	Kaibab Plateau AZ	fire	regen, recruit, survival
Martin	2007	northern AZ	climate, ungulates	recruit
Binkley et al.	2006	Kaibab Plateau AZ	climate, fire, ungulates	regen, recruit
Gitlin et al.	2006	northern AZ	climate (site factors)	survival
Mast & Wolf	2006	Kaibab Plateau AZ	fire	regen, recruit
Cocke et al.	2005	northern AZ	fire (conifers)	regen, recruit, survival
Heinlein et al.	2005	northern AZ	fire	regen, recruit
Fulé et al.	2004	Kaibab Plateau AZ	fire	regen, recruit, survival
Mast & Wolf	2004	Kaibab Plateau AZ	fire	regen, recruit

Author(s)	**Year**	**Geographic scope**	**Influencing factor(s) studied**	**Aspen dynamic(s) studied**
Moore & Huffman	2004	Kaibab Plateau AZ	fire (meadow encroachment)	regen, recruit
Shepperd	2004	northern AZ [western US]	fire, ungulates, disease (Cytospora canker)	regen, recruit
Fulé et al.	2003	Kaibab Plateau AZ	fire	regen, recruit
Bailey & Whitham	2002	northern AZ	fire, ungulates	regen
Fulé et al.	2002	Kaibab Plateau AZ	fire	regen, recruit
Quinn & Wu	2001	southern AZ	fire, ungulates	regen (seedling)
Rolf	2001	northern AZ	fire, ungulates	regen, recruit
Fairweather & Tkacz	1998	northern AZ	ungulates, disease (Cytospora canker)	regen, recruit
Shepperd & Fairweather	1994	northern AZ	ungulates, disease (Cytospora canker)	regen, recruit
Jacobi & Shepperd	1991	northern AZ [& CO]	disease (Cytospora canker)	regen
Cantor & Whitham	1989	northern AZ	browse (pocket gophers)	regen
Covington et al.	1983	northern AZ	fire	regen
Jones & Trujillo	1975	northern AZ	fire	regen
Whittaker & Niering	1975	southern AZ	fire	regen, recruit
Martin	1965	northern AZ	disease (Cytospora canker)	recruit
Merkle	1962	Kaibab Plateau AZ	ungulates	regen, recruit
Larson	1959	northern AZ	ungulates	regen, recruit
Merkle	1954	Kaibab Plateau AZ	ungulates	regen, recruit
Rasmussen	1941	Kaibab Plateau AZ	ungulates	regen, recruit
Pearson	1914	northern AZ	fire, ungulates	regen

State abbreviations are AZ (Arizona), NM (New Mexico), CO (Colorado). Arizona regions are defined as follows:
northern Arizona is north of the Mogollon Rim; southern Arizona is south of the Mogollon Rim; Kaibab Plateau is part of northern AZ but is distinguished separately because elk only occur in small population sizes on the Plateau. See Fig. 1.1 for a map of where these areas occur. Brackets in the geographic scope column indicate a larger study area with results specific to the area outside brackets.

Table 1.2. Summary of the 26 papers from the southwestern edge of aspen's range that met inclusion criterion #2 by evaluating management influences on aspen regeneration, recruitment, and/or overstory survival or by providing specific guidelines for aspen management.

Author(s)	**Year**	**Geographic scope**	**Management approach(es) studied**
O'Donnell et al.	2018	Kaibab Plateau AZ	conifer thinning
Fairweather et al.	2014	northern AZ	exclosures
Martin	2014	northern AZ	exclosures
Martin & Maron	2012	northern AZ	exclosures
Beschta & Ripple	2010	northern AZ	exclosures, conifer thinning, wolf re-introduction
Bailey et al.	2007	northern AZ	exclosures
Binkley et al.	2006	Kaibab Plateau AZ	exclosures, hunting dogs
Shepperd	2004	northern AZ [western US]	exclosures, clearfelling pure aspen, conifer removal, mechanical root stimulation
Bailey & Whitham	2002	northern AZ	exclosures
Rolf	2001	northern AZ	exclosures, clearfelling pure aspen
Fairweather & Tkacz	1998	northern AZ	exclosures, clearfelling pure aspen
Dahms & Geils	1997	AZ & NM	guidelines: exclosures, clearfelling and partial cutting of pure aspen and mixed-conifer-aspen, fire
Shepperd & Fairweather	1994	northern AZ	exclosures, clearfelling pure aspen
Ffolliott & Gottfried	1991	northern AZ	partial cutting mixed-conifer-aspen
Gottfried	1987	northern AZ	partial cutting mixed-conifer-aspen
Fisher & Neumann	1986	NM [& northern NM]	site preparation for seedlings
Gottfried	1987	northern AZ	partial cutting mixed-conifer-aspen
Patton & Jones	1977	AZ & NM	guidelines: clearfelling and partial cutting of pure aspen and mixed-conifer-aspen
Patton	1976	northern AZ	partial cutting mixed-conifer-aspen
Gottfried & Jones	1975	northern AZ	partial cutting mixed-conifer-aspen
Jones	1975	northern AZ	clearfelling pure aspen
Jones	1974	AZ & NM	guidelines: clearfelling and partial cutting of pure aspen and mixed-conifer-aspen, fire
Reynolds	1969	northern AZ	partial cutting pure aspen
Patton	1969	northern AZ	partial cutting mixed-conifer-aspen
Larson	1959	northern AZ	exclosures (livestock only), partial cutting pure aspen
Pearson	1914	northern AZ	exclosures (livestock only)

State abbreviations are AZ (Arizona) and NM (New Mexico). Arizona regions are defined as follows: northern Arizona is north of the Mogollon Rim; southern Arizona is south of the Mogollon Rim; Kaibab Plateau is part of northern AZ but is distinguished separately because elk only occur in small population sizes on the Plateau. See Fig. 1.1 for a map of where these areas occur. Brackets in the geographic scope column indicate a larger study area with results specific to the area outside brackets. Exclosures are tall fences built around aspen to exclude ungulates from browsing aspen.

Box 1.1. Research needs and questions identified by our systematic review of aspen ecology and management in the Southwest.

1. **Interactions among factors influencing aspen regeneration, recruitment, and mortality.** Although the individual factors influencing aspen forest dynamics have been well studied, there is a need to better understand their interactions, particularly in light of rapidly changing climates.
    a. *Is there a certain fire size or area of aspen treated that will saturate ungulate browse and allow aspen to recruit without exclosures or reduced ungulate population sizes?*
    b. *How will interactions between drought and warmer temperatures (i.e., hotter droughts) affect aspen regeneration, recruitment, and susceptibility to insects and diseases?*
    c. *Will aspen be able to capitalize on increased opportunities for post-fire regeneration in an increasingly arid climate?*
    d. *Will more frequent fire in a warming climate have a positive or negative influence on aspen abundance at the landscape scale?*
2. **Experimental research on management strategies**. Ample research on aspen responses to management was conducted in the 20th century, but it is unclear if and how those results hold up in an increasingly arid climate and in the face of novel disturbance regimes.
    a. *What silvicultural systems are appropriate for promoting aspen resilience and adaptability?*
    b. *What are the appropriate prescribed fire parameters (e.g., return interval, intensity) for promoting aspen resilience and adaptability?*
    c. *What are the impacts of harvesting equipment on soil compaction and subsequent aspen regeneration?*
    d. *When is the optimal time to remove fenced exclosures?*
    e. *At what point has a declining aspen stand's root system died back enough that overstory removal or fire will no longer result in successful regeneration?*
    f. *Most studies on aspen regeneration only monitor short-term responses to management or disturbance. What is the long-term trajectory of aspen following fire, fencing, and silvicultural management, especially in mixed stands and after partial cutting?*
3. **Aspen forest dynamics in Mexico.** A major knowledge gap identified in our systematic review is the lack of information on aspen in Mexico. Aspen in Mexico represents a potentially important genetic resource because the genotypes in this region may have novel adaptations for withstanding drought (Quinn and Wu 2001; Callahan et al. 2013). These genotypes could be useful for assisted migration of aspen into more northerly latitudes (Callahan et al. 2013; Goessen et al. 2022).
    a. *How does aspen function ecologically and physiologically in Mexico? Does this differ from aspen in more northerly latitudes, and if not, what can this teach us about aspen's ability to adapt to a warming climate?*
    b. *Is aspen in Mexico declining as it appears to be in the Southwest? If so, which factors are driving this decline, and if not, what can we learn from aspen's resilience at the very southern limit of its range?*
4. **Remote sensing.** There is ample opportunity to use remote sensing for answering urgent questions about aspen forest dynamics and to guide aspen management at landscape scales (Achim et al. 2020).
    a. *Can remote sensing be used to assess the state of aspen in Mexico?*
    b. *Can we detect real time increases and decreases in aspen's landscape-level footprint?*
    c. *Can remote sensing technologies be leveraged to detect emerging outbreaks of oystershell scale and other biotic agents?*

5. **Aspen seedling establishment.** We now know that aspen seedling establishment is common after wildfires in the western US (Kreider and Yocom 2021b), but questions remain about the frequency of such establishment events, the long-term trajectory of seedlings, and their role in facilitating adaptation to stressors such as climate change.
    a. *How prevalent are aspen seedling establishment events in the Southwest?*
    b. *What is the long-term trajectory of seedlings after establishment, and what factors influence development of individual seedlings into clones?*
    c. *What role does aspen sexual reproduction play in facilitating adaptation to climate change, ungulate browse, and novel biotic and abiotic disturbance regimes?*
6. **Genetics.** Many questions remain about aspen genetics, especially regarding the influence of genetics on aspen forest dynamics and the role that management can play in influencing genetic diversity and adaptation.
    a. *How do genetics influence aspen's capacity to regenerate and recruit?*
    b. *Are certain genotypes more susceptible to diseases and insects, such as oystershell scale?*
    c. *How do management strategies, such as exclosures and fire, influence aspen genetic diversity at the stand- and landscape-scales?*
7. **Aspen ecosystems as fire breaks.** Our review highlighted how it can be difficult to implement prescribed fire in aspen ecosystems due to moist understory fuels (Shepperd 2004), and an emerging topic for research is the potential for aspen to inhibit spread of wildfires.
    a. *Do aspen ecosystems act as a fire break by inhibiting wildfire spread and/or reducing extreme fire behavior, even in the Southwest where aspen patches are small?*
    b. *How can management influence the capacity of aspen ecosystems to burn, either positively to more effectively implement prescribed fire or negatively to make aspen more resistant to high-severity wildfire?*
8. **Social scientific investigations.** Aspen's tenuous position in the Southwest was caused by anthropogenic actions, from climate change and introduction of invasive species to fire exclusion and unnaturally large ungulate populations. For better or worse, aspen's future is in human hands, and social scientific investigations are critical for informing future aspen management.
    a. *How can we more effectively advocate for and implement aspen conservation policies and management strategies?*
    b. *What are current and historical Indigenous uses and values of aspen? What do these uses and values have to teach us about managing aspen ecosystems?*
    c. *Why we should care about aspen ecosystems and what we stand to lose, socially and culturally, without them?*

Figures

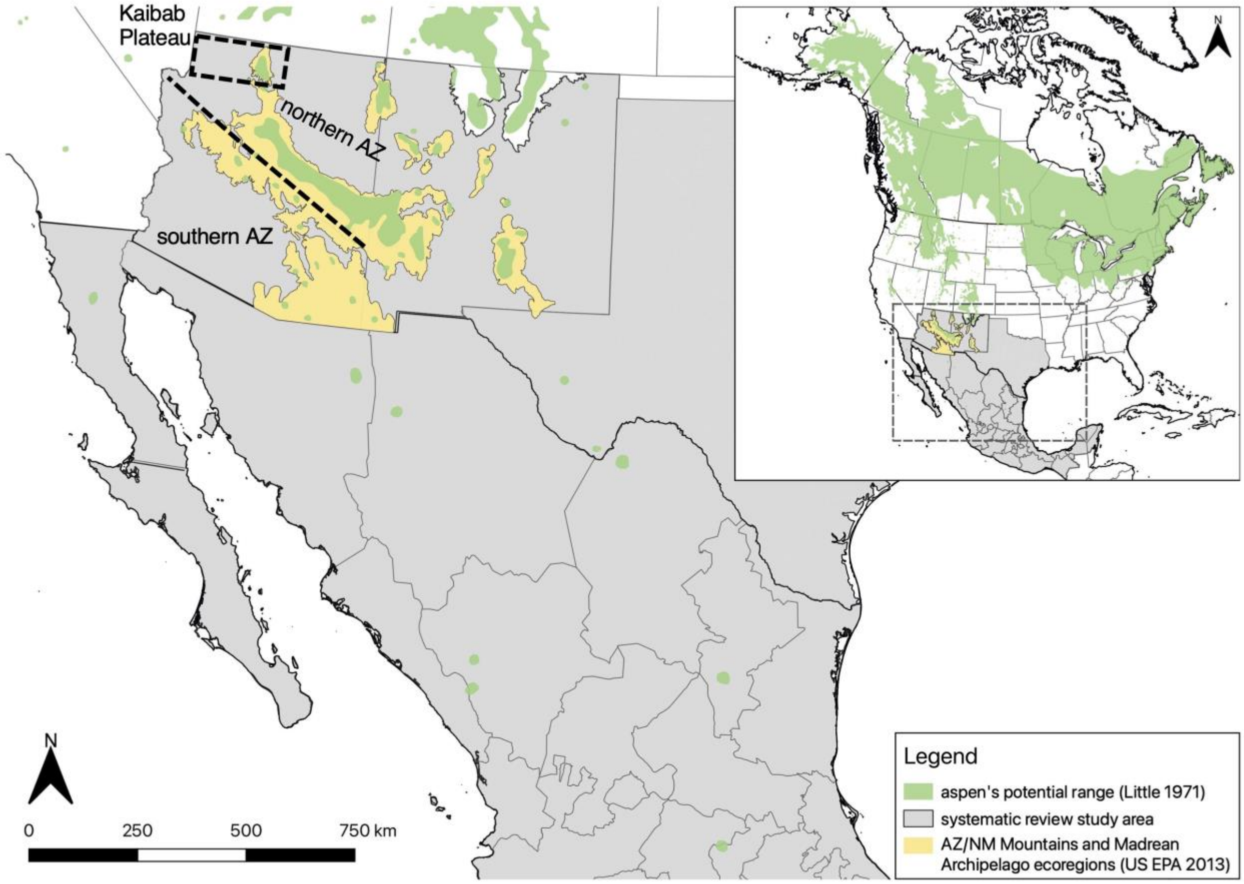

Figure 1.1. Map of our systematic review's study area on the southwestern edge of aspen's range (see inset for aspen's expansive range in North America). We included studies conducted in Arizona, New Mexico (excluding where the Rocky Mountains extend into northern New Mexico), Texas, and Mexico. Aspen in this region is limited to higher elevation areas, and almost all aspen in the southwestern US occurs in two Level III Ecoregions: Arizona/New Mexico Mountains and the Madrean Archipelago (US EPA 2013). The map also shows regions within Arizona that we refer to throughout the manuscript. We use northern Arizona and southern Arizona to refer to the areas north and south of Mogollon Rim, respectively, and we use Kaibab Plateau to distinguish the area north of the Grand Canyon from the rest of northern Arizona.

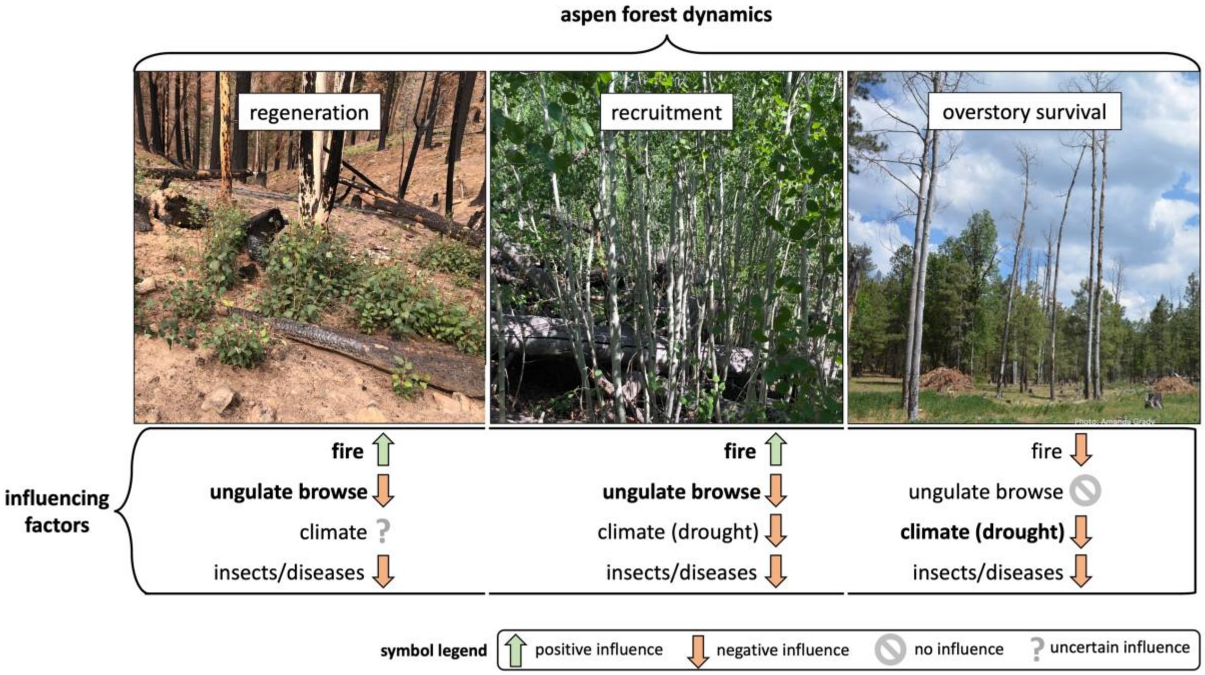

Figure 1.2. Summary of the main findings from our systematic review of how biotic and abiotic factors influence aspen forest dynamics in the Southwest. Factors highlighted in bold indicate particularly strong influences as indicated by our review. Fire had a strong positive influence on regeneration and recruitment, while ungulate browse had a strong negative influence. Climate was the most important factor influencing overstory survival, with drought associated with increased mortality.

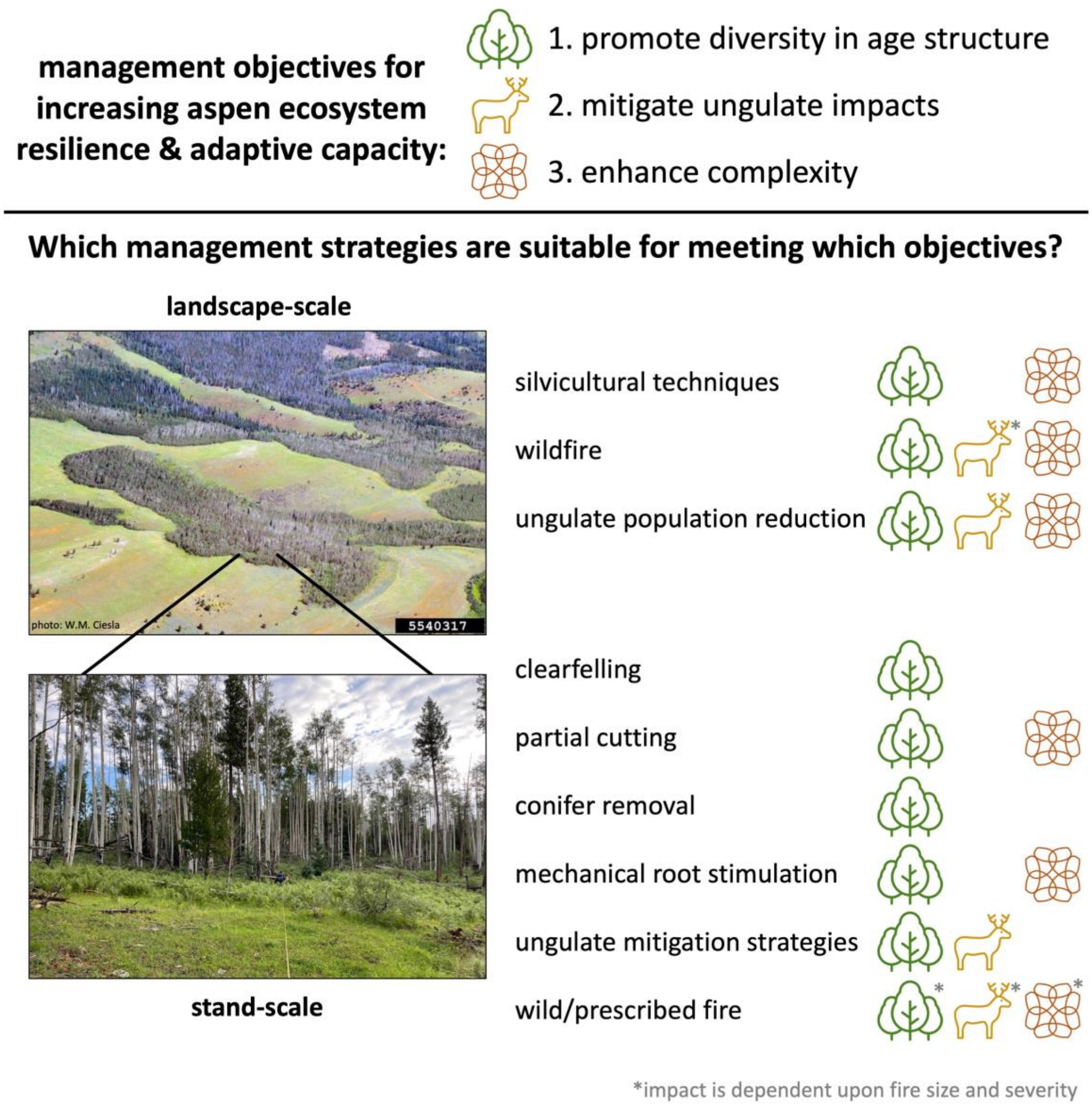

Figure 1.3. Conceptual diagram showing how various aspen management strategies may or may not be suitable for meeting three objectives designed to increase aspen ecosystem resilience and adaptive capacity. Landscape-level strategies that promote aspen regeneration and recruitment, such as wildfire and ungulate population reduction, meet all three objectives. Ungulate mitigation strategies refer to tactics that reduce local ungulate impacts, such as fenced exclosures, jackstrawing, and hinging.

Figure 1.4. Aspen suckering is typically abundant after (a) high-severity fire and (b) clearfelling. However, aspen recruitment is sorely limited in the Southwest by chronic ungulate browse, especially of non-native Rocky Mountain elk. Recruiting stems are uncommon outside of large, high-severity fires and (c) ungulate exclosures because (d) aspen suckers are browsed heavily.

Chapter 2: Sustainability and drivers of aspen regeneration and recruitment near the southwestern edge of its range

Abstract

Quaking aspen (*Populus tremuloides*) 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, USA 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: (1) 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, drier 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 limiting factors for aspen recruitment were ungulate browse, especially by non-native Rocky Mountain elk (*Cervus canadensis*), 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: Arizona, climate change, fire, exclosures, oystershell scale, *Populus tremuloides*, structural equation modeling, ungulate browse

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. 2012; Senf et al. 2018; Stanke et al. 2021). A notable example of a tree species that has experienced widespread mortality in the western US is quaking aspen (*Populus tremuloides*; 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 general public and to local communities that benefit from aspen-driven tourism and recreation (Dahms and Geils 1997; McCool 2001; Assal 2020). Aspen mortality events across western North America have been thoroughly studied, revealing two pathways of stand-scale mortality: (1) long-term successional replacement of aspen by conifers in the absence of stand-replacing disturbance (Kay 1997) and (2) 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 *Valsa sordida*] 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, overstory mortality should not be a major concern when there is adequate regeneration and recruitment (i.e., juvenile aspen) to replace dying trees.

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 events, we understand how individual factors influence juvenile aspen (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). Similarly, conifer encroachment inhibits aspen juveniles (Zegler et al. 2012; Clement et al.

2019), and certain insects and diseases contribute to mortality of regenerating and recruiting stems (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, USA and other western states (Crouch et al. 2021). 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 best 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 (Holling and Meffe 1996; Millar et al. 2007; 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 could 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). 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 to assess the direct and indirect influence of these factors on aspen juveniles. Specifically, we addressed two questions: (1) Is aspen sustainably regenerating and recruiting in Arizona? (2) Which biotic and abiotic factors significantly influence aspen regeneration and recruitment in Arizona?

Methods

Study Area

Our study area encompassed aspen ecosystems throughout Arizona, USA (Fig. 2.1a, 2.1b) (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 2,000 m in elevation in the ponderosa pine (*Pinus ponderosa* var. *scopulorum*) 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* var. *glauca*) at lower elevations, white pine (*Pinus strobiformis* or *Pinus flexilis* var. *reflexa*) and white fir (*Abies concolor*) at mid elevations, and subalpine fir (*Abies lasiocarpa* var. *arizonica*) and Engelmann spruce (*Picea engelmannii*) 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. 2.1b). 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. 2.1b). All data were collected during the 2020, 2021, and 2022 growing seasons (June – October), when aspen trees had leaves. Most of our sampling occurred around Flagstaff because of the wide range of sites that aspen occupies in this area (Fig. 2.1c).

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 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 on the Coconino National Forest; Williams Ranger District on 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 of our strata. 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 2.1). 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 our plots occurring in ungulate management treatments (Table 2.1).

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. We established the remaining 139 plots by identifying aspen stands that filled target strata, standing on the edge of selected stands, laying out a transect longways through those stands, 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 m to 300 m. In contrast, Zegler et al. (2012) established sites at randomly located points within known aspen stands and sampled plots in each of the four cardinal directions 20 m from those points.

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 (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. 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. In the 8 m overstory plot, all trees with diameter at breast height (dbh; height = 1.37 m) > 12.7 cm were measured. In the 4 m regeneration plot, all trees > 0.02 cm in height and < 12.7 cm dbh were measured. In the regeneration plot, 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 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). For all live aspen, we recorded height and dbh (except for regeneration and recruits that were < 1 cm dbh). 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 to native insect species and less pathogenic diseases (Hinds 1985; Zegler et al. 2012; Crouch et al. 2021, 2023). 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, drought scorch on leaves, and chlorosis of leaves. We assessed animal damage to aspen stems, including browse, ungulate barking (i.e., elk chewing aspen bark), and other animal damage. In addition to directly quantifying ungulate impacts on aspen stems, we counted ungulate scat piles within the 8 m overstory plot. We identified scat piles by species (i.e., elk [*Cervus canadensis*], deer [*Odocoileus hemionus* or *O. 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 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 2.2). We used height and diameter data to calculate basal area of stems > 5.1 cm dbh for live aspen, dead aspen, live tree species other than aspen, and live conifers (Table 2.2). 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 2.2).

Using the GPS coordinates we collected at each plot's center, we calculated elevation, aspect, and slope using a 30 m^2 digital elevation model (Table 2.2). We transformed raw aspect into a continuous variable ranging from 0–2 with 0 representing southwest (225°) and 2 representing northeast (45°) (Beers et al. 1966). We also calculated heat load and potential annual direct radiation, two indices that assess site-level temperature based on slope, aspect, and latitude (McCune and Keon 2002). 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 2.2). 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 2.2).

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 2.2). SoilGrids provides data up to 2 m below the surface; however, 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 1985). We obtained climate data for each plot from ClimateNA (https://climatena.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 for the five years preceding when we sampled each plot (Table 2.2). We chose five 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). Because these thresholds were developed for aspen in more northerly parts of its range, we wanted to develop 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 overstory (201.9 trees ha^{-1}), recruiting (4411.9 trees ha^{-1}), and regenerating stems (8575.1 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. 2.1b).

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 2.2). We conducted two analyses – random forests and structural equation modeling (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 help us 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 towards 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 assess 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. 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. 2.2) applied to all three response variables and accounted for all 69 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 (i.e., replacing heat load with radiation) affected the model, although only one such swap resulted in both improved model fit and explanatory power (spring climate moisture index [CMI] swapped in to replace winter CMI in the live aspen regeneration SEM). We used the *piecewiseSEM* package to build our SEMs because this package accommodates 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 our plots (i.e., plots [n=220] within study sites [n=87] within minor areas [n=19] 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, and to do so, we fit six simple linear regression models with each of the three species' scat counts as predictors and 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).

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 our study plots, and observed recruitment density exceeded the WNA self-replacement threshold of 1250 recruiting stems ha^{-1} in 35.9% of plots (Table 2.3). 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 our study plots, while recruitment was absent from 40.0% of plots. Concerningly, 25.0% of our plots had unsustainable levels of both regeneration and recruitment based on the WNA thresholds, compared to 53.2% of plots with unsustainable regeneration and recruitment using the AZ thresholds (Table 2.3).

There were substantial differences in sustainability of juvenile aspen across the seven major areas where aspen occurs in Arizona (Fig. 2.3; Table 2.3). Across all areas, proportion of plots with sustainable regeneration and recruitment was typically higher when using the WNA thresholds compared to the more conservative, site-specific AZ thresholds (Table 2.3). The proportion of plots with sustainable regeneration was highest on the Coronado (85.7% for both thresholds) and Mogollon Rim (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 2.3). 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 (Appendix 2.1).

The only areas where we sampled plots inside of areas treated for ungulate management were the 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 be much lower outside of treated areas (Table 2.4). In fact, in all three areas, no plot outside of exclosures or jackstraw treatments was sustainably recruiting using the AZ threshold (Fig. 2.3b; Table 2.4), while the sustainability rate was less than 10% for these areas using the WNA threshold (Table 2.4).

Factors Influencing Regeneration

The most important variables influencing density of live aspen regeneration (trees ha^{-1}) based on random forests were major area and heat load (Table 2.5). The optimal SEM for live regeneration (AIC = -1351; Fisher's C = 6.425 with p = 0.983 [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, heat load, fire strata, proportion of stems with abiotic damage, and proportion of stems with sooty bark canker (Fig. 2.4a). 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 ($p < 0.05$) predictor of live regeneration density was sooty bark canker (effect size = -0.13; $p = 0.018$), with higher levels of sooty bark canker being associated with less aspen regeneration. Spring CMI had the largest effect size (0.14; $p = 0.233$) on regeneration, indicating less arid conditions (i.e., higher spring CMI) were associated with increased regeneration. Variables with smaller effect sizes included autumn precipitation (0.12; $p = 0.302$), abiotic damage (0.10; $p = 0.090$), heat load (-0.09; $p = 0.200$), and fire strata (-0.12; $p = 0.316$). Increased aspen regeneration was associated with more autumn precipitation, a greater proportion of stems with abiotic damage, lower heat load, and recent fire. Although their direct effects on regeneration were not significant, autumn precipitation (-0.51; $p < 0.001$) and heat load (0.20; $p < 0.001$) had significant influences on fire strata. More precipitation in autumn and lower heat load were associated with more recent fire. Thus, autumn precipitation indirectly increased live aspen regeneration density through its effect on fire strata, while heat load indirectly decreased live regeneration density through its effect on fire strata. Both indirect effects were consistent with the direct effects of autumn precipitation and heat load on live regeneration density.

Factors Influencing Recruitment

The most important variables influencing 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 2.5). The optimal SEM for live recruitment (AIC = 1178; Fisher's C = 18.786 with $p = 0.845$; response marginal $R^2 = 0.43$, conditional $R^2 = 0.76$) included eight influencing factors: snowfall, mean winter temperature, heat load, fire severity, fire strata, proportion of stems browsed, ungulate management, and proportion of stems with Cytospora canker (Fig. 2.4b). More severe fire (effect size = 0.52; $p < 0.001$), less recent fire (0.32; $p = 0.004$), presence of ungulate management (0.35; $p < 0.001$), higher levels of Cytospora canker (0.12; $p = 0.009$), and lower levels of browse (-0.34; $p < 0.001$) resulted in significantly greater density of live recruitment. Although not significant, snowfall (-0.33; $p = 0.069$) and winter temperature (-0.32; $p = 0.232$) had relatively strong negative effects on live recruitment, indicating less snowfall and cooler winter temperatures were more favorable for live aspen recruits. The influence of heat load (0.01; $p = 0.862$) was negligible. Looking at indirect effects, ungulate management significantly decreased browse (-0.59; $p < 0.001$), meaning 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; $p = 0.082$). Fire strata had a negative effect on browse that approached significance (-0.16; $p = 0.090$), meaning more recent fire was associated with more browse. Finally, both heat load and winter temperature had significant influences on fire severity and strata. Higher winter temperatures were associated with more severe fire (0.23; $p < 0.001$) and more recent fire (-0.26; $p < 0.001$), whereas higher heat load was associated with lower fire severity (-0.28; $p < 0.001$) and less recent fire (0.23; $p < 0.001$).

The most important variables influencing density of dead aspen recruitment (trees ha^{-1}) based on random forests were major area, fire severity, snowfall, and dead aspen basal area (Table 2.5). The optimal SEM for dead recruitment (AIC = 637; Fisher's C = 2.219 with $p = 0.898$;

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. 2.4c). The only significant predictor of dead recruitment density was oystershell scale (effect size = 0.24; $p = 0.028$), which was associated with increased density of dead recruits. Although insignificant, snowfall (-0.25; $p = 0.172$) and browse (-0.14; $p = 0.079$) were associated with less dead recruitment, while elevation (0.19; $p = 0.341$) and ungulate management (0.20; $p = 0.066$) were positively associated with dead recruitment, indicating 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; $p = 0.021$), resulting in higher elevations being indirectly associated with less dead recruits. Oystershell scale was significantly more abundant in areas of ungulate management (0.23; $p = 0.002$), whereas browse was significantly reduced in areas of ungulate management (-0.55; $p < 0.001$).

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 density of live ($p < 0.001$) and dead recruits ($p = 0.006$). In contrast, deer and cattle did not have significant relationships with either response ($p \geq 0.105$).

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, whereas 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 issues with sustainability 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; Zegler 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 US (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 Zegler 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, we sampled inside exclosures, whereas Zegler et al. (2012) did not, and our levels of sustainable recruitment outside exclosures in the South Kaibab area (7.1%) are more consistent with those reported in Zegler et al. (2012). 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 are 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 will not translate to successful self-replacement. This is especially true for aspen, which is a species that regenerates reliably after fire, other disturbances, and management tactics that trigger aspen's sprout response (Crouch et al. 2023) but that 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 tended to observe higher levels of sustainability for regeneration than for recruitment (Table 2.3), indicating that recruitment bottlenecks are 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 5.1-10.1 cm dbh. Comparing these earlier studies to ours, the sustainability of recruitment has not improved. 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 a higher bar to meet 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, 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, heat load, and climate. No single driver seemed to dominate. 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. 2.4a). 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 aspen stands might produce less regeneration. On the other hand, proportion of stems with abiotic damage had a positive influence on regeneration. The two most common abiotic damages in our study were fire damage, which was found on larger stems that survived fire, and foliar drought scorch, which typically occurred on smaller stems. Therefore, more aspen regeneration associated with abiotic damage could be due to prolific regeneration after fire or could simply be an artifact of our observational sampling approach, in which plots with drought scorch happened to be plots with dense regeneration. In support of the former, we found more aspen regeneration in areas of recent fire, which is consistent with our understanding that aspen regenerates abundantly after fire and that aspen density tends to decline with time since fire (Jones and Trujillo 1975; Covington et al. 1983; Bailey and Whitham 2002; Shepperd 2004; Haire and McGarigal 2008; Higgins et al. 2015; Stoddard et al. 2018). However, interpreting the effects of sooty bark canker and abiotic damage should be done with care because of the infrequency with which they occurred. Abiotic damage was observed on 1.0% of the 9965 live aspen stems we sampled, and sooty bark occurred on only 0.06% of live aspen stems.

A novel finding from our study was the influence of heat load and climate on aspen regeneration. Heat load had a negative influence on aspen regeneration density, whereas spring CMI and autumn precipitation had positive influences (Fig. 2.4a). Together, these findings indicate that aspen regeneration is less abundant on hotter sites and in warmer, drier climates. Before our study, the influence of climate on aspen regeneration 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 US (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 heat load in the South Kaibab area. However, our survey of aspen populations across Arizona indicated that climate has a strong influence on regeneration density, perhaps because our study had a larger spatial scale and included a wider range of climates than previous studies (Appendix 2.2). This finding has important implications for aspen sustainability in a warming climate. Warmer, drier sites are already less suitable for aspen regeneration, and as Arizona’s climate continues to become more arid (Seager et al. 2007), we expect that aspen’s regeneration potential will 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 further in the Management Implications section below.

Factors Influencing Recruitment

Interpreting drivers of aspen recruitment is more 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. Density of living aspen recruits was strongly influenced by climate, fire, heat load, browse, ungulate management, and Cytospora canker (Fig. 2.4b), whereas density of dead recruits was driven by climate, elevation, browse, ungulate management, and oystershell scale (Fig. 2.4c). The drivers of living and dead recruitment density were relatively consistent, with the exceptions of fire influencing density of living but not dead recruits and of different damaging agents and site factors influencing the two responses. Unlike for regeneration, the relative strength of factors driving aspen recruitment were much clearer. Fire and ungulate management were the most important positive influences on recruitment, whereas browse and oystershell scale were the primary factors limiting recruitment. Because the status of recruitment is not only more complex but also more dire than that of regeneration, we go into detail on each of the factors that influenced aspen recruitment in the following paragraphs.

Fire had a strong positive influence on 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 to plots that burned < 2 and > 20 years ago. This indicates that less than two years is not enough time for most aspen regeneration to grow taller than 1.37 m but that recent fire in the past 20 years is clearly important for promoting aspen recruitment. Similar to regeneration, the importance of fire in promoting aspen recruitment is well established in the literature (Higgins et al. 2015; Clement et al. 2019), although the majority of such evidence from Arizona is from demographic studies (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). The importance of fire severity in promoting recruitment is also supported in the literature. Higgins et al. (2015) found that 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. Interestingly, fire severity was also an important influence on density of dead aspen recruits based on random forests, but the optimal SEM for dead recruits did not include fire severity as a factor. We would expect more dead aspen recruits in areas of high-severity fire simply because there are more recruits after high-severity fire, in general, and because stem exclusion in high-density, post-fire stands would result in many dead recruits (David et al. 2001). However, the strength of that signal was not strong enough to improve fit or explanatory power of the dead recruitment SEM.

Ungulate browse had a strong negative influence on aspen recruitment, while local management tactics to reduce impacts of ungulate browse had a strong positive influence. Both browse and ungulate management were strong influencing factors of live recruitment based on random forests, and these two factors were included in the optimal live and dead recruitment SEMs. Higher levels of browse resulted in significantly less live aspen recruitment, whereas ungulate management significantly reduced browse and increased 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, and our study indicates that non-native Rocky Mountain elk have an outsized negative influence compared to deer or cattle. Species-specific scat counts were not included in either of the optimal recruitment SEMs, nor were they considered especially important predictors of live or dead recruitment by random forests. Elk scat count was ranked as the 42nd most important variable influencing live recruitment and as the 53rd most important variable for dead recruitment, whereas deer scat count was ranked 57th for live recruitment and 60th for dead recruitment. Cattle scat count was considered an unimportant predictor for both response variables. We found that elk scat count had a significant negative relationship with 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 non-native elk are present (Table 2.3; Appendix 2.2). Alarmingly, no plots outside of exclosures or jackstraw treatments had sustainable recruitment in the South Kaibab, Flagstaff, and Mogollon Rim major areas (Fig. 2.3b; Table 2.4), highlighting the dire threat to aspen sustainability posed by non-native elk in Arizona.

Two biotic agents – Cytospora canker and oystershell scale – were important factors influencing 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 readily kills stressed or damaged stems (Hinds 1985; Fairweather et al. 2008; Marchetti et al. 2011; Zegler et al. 2012). We hypothesize that the positive influence of Cytospora on live recruitment density 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. 2.4b). Alternatively, intraspecific competition in stands with dense recruitment might increase tree stress and, thereby, increase 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 (R. Davis, USDA Forest Service, personal communication). 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. 2.4c). 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 host availability inside exclosures.

Climate and site factors also influenced 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 density of living and dead recruits. These seemingly contradictory influences suggest that less aspen recruits, in general, occur in areas with less 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 on the Mogollon Rim (Martin 2007; Martin and Maron 2012). We also found 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 surprising finding 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 indicate that higher elevation aspen populations may be experiencing recruitment challenges, which is a concern for aspen sustainability under climate change.

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 along the southwestern edge of its range and beyond.

To sustain aspen in the future, management must 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 promoting 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 1985; Johnson 1994; Cocke et al. 2005; Binkley et al. 2006). As a result, many seral 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 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, 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 McIroy 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 heat load 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 to 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 thereby reducing 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: (1) directly reduce ungulate population sizes, particularly of non-native elk, to facilitate landscape-level recruitment, (2) manage for aspen at higher elevations, which should be more suitable for aspen in a changing climate and less susceptible to oystershell scale, and (3) 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.

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Tables

Table 2.1. Proportion of aspen observed, based on area, compared to proportion of aspen sampled, 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 on the Flagstaff, Mogollon Rim, and Williams Ranger Districts of the Coconino and Kaibab National Forests (DePinte 2018).

Table 2.2. List of 69 variables considered as potential influencing factors of aspen regeneration and recruitment. 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	0–1,194
Dead aspen overstory density	67	0–846
Live non-aspen density	1,769	0–34,268
Live conifer density	1,057	0–34,268
Live non-aspen regeneration density	1,648	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 (*Cervus canadensis*) scat	1.3	0–23
Deer (*Odocoileus hemionus* & *O. virginianus couesi*) scat	1.1	0–29
Cattle (*Bos taurus*) scat	0.3	0–20
Damaging agents[c]		
Oystershell scale (*Lepidosaphes ulmi*)	0.15	0–1
Sucking & 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 *Valsa sordida*)	0.02	0–0.34
Hypoxylon canker (caused by *Entoleuca mammatum*)	0.002	0–0.10
Ceratocystis canker (caused by *Ceratocystis* spp.)	0.02	0–0.42
Sooty bark canker (caused by *Encoelia pruinosa*)	0.001	0–0.05
All cankers	0.33	0–1
Foliar & 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 & 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%)	

Influencing factor	Mean	Range
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/yr)	0.98	0.71–1.08
Radiation (MJ/cm^2/yr)	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	453804	358542–674303
UTM northing	3880092	3589116–4052723
Soils		
Soil order[l]	1 (2.7%), 2 (14.1%), 3 (13.2%), 4 (70.0%)	
Soil pH in H_2O (pHx10)	63.4	55.4–71.4
Cation exchange capacity (CEC) (mmol(c)/kg at pH 7)	232.9	176.3–272.2
Nitrogen (cg/kg)	110.0	80.0–188.3
Soil organic carbon content (dg/kg)	135.2	93.8–193.9
Bulk density (cg/cm^3)	147.5	130.1–157.8
Sand content (g/kg)	321.7	187.5–592
Clay content (g/kg)	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
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 climate moisture index (CMI)	-5.2	-15.2–8.4
Summer climate moisture index (CMI)	-24.7	-38.8–3.7
Autumn climate moisture index (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

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[a] basal area = m^2 ha^{-1}
[b] density = trees ha^{-1}
[c] proportion of aspen stems affected by damaging agent
[d] scat = pellet piles/plot
[e] categorical: 1 (0-2 yrs since fire), 2 (2-20 yrs since fire), 3 (> 20 yrs since fire)
[f] categorical: 1 (unburned in past 20 yrs), 2 (unburned/low), 3 (low), 4 (moderate), 5 (high)
[g] categorical: 0 (burned < 2 times in past 20 yrs), 1 (burned twice in past 20 yrs)
[h] categorical: 0 (no ungulate management), 1 (exclosure or jackstraw)
[i] categorical: 0 (no treatment), 1 (conifer removal)
[j] 0–2 (0 = 225°, 1 = 135° or 315°, 2 = 45°)
[k] categorical: 1 (Coronado), 2 (Flagstaff), 3 (Mogollon Rim), 4 (North Kaibab), 5 (Prescott), 6 (South Kaibab), 7 (White Mountains)
[l] categorical: 1 (Inceptisols), 2 (Mollisols – Borolls), 3 (Mollisols – Ustolls), 4 (Alfisols)
[m] precipitation = mm
[n] temperature = °C
[o] CMI = mm
[p] see methods for equation

Seasons for climate variables are winter (December – February), spring (March – May), summer (June – August), autumn (September – November). See Appendix 2.2 for means and standard errors of the 62 continuous variables across each of the seven major areas where aspen occurs in Arizona. See Appendix 2.3 for the percentage of plots occurring in each level of the seven categorical variables we considered, along with their standard errors.

Table 2.3. 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). Cell color is scaled numerically, with dark green = 100% and white = 0%.

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 Mntns*	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 non-native 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 Methods section for additional details on these self-replacement thresholds.

Table 2.4. 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). Cell color is scaled numerically, with dark green = 100% and white = 0%.

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 Methods section for additional details on these self-replacement thresholds.

Table 2.5. 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. 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.

Rank	Live aspen regeneration	Live aspen recruitment	Dead aspen recruitment
1	**major area**	**fire severity**	**major area**
2	**heat load**	**fire strata**	**fire severity**
3	fire strata	**major area**	**snow**
4	sooty bark canker	**ungulate management**	**dead aspen basal area**
5	slope	**snow**	oystershell scale
6	radiation	**winter temp (mean)**	coarse fragments
7	abiotic damage	**browse**	browse
8	UTM easting	winter temp (min)	elevation
9	winter CMI	heat load	summer precip
10	autumn precip	summer precip	soil organic carbon
11	spring CMI	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	ungulate management
20	winter precip	soil pH	defoliating insects
21	summer precip	Cytospora canker	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)

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.

Figures

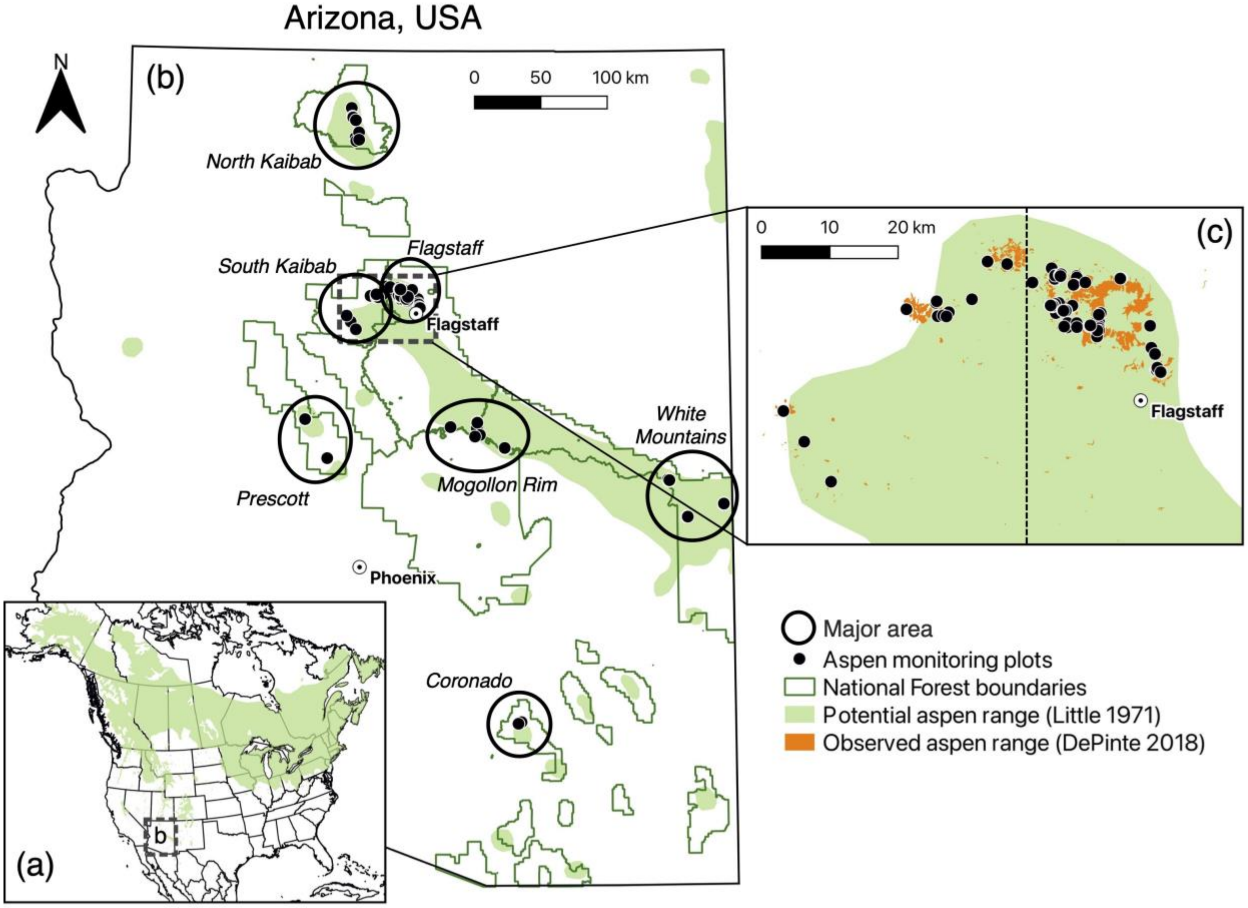


Figure 2.1. Maps showing (a) the location of our study area on the southwestern edge of aspen's range in North America, (b) the locations of our 220 aspen study plots across seven major areas (*in italics*) where aspen occurs in Arizona, USA, and (c) locations of our plots surrounding Flagstaff, Arizona, 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).

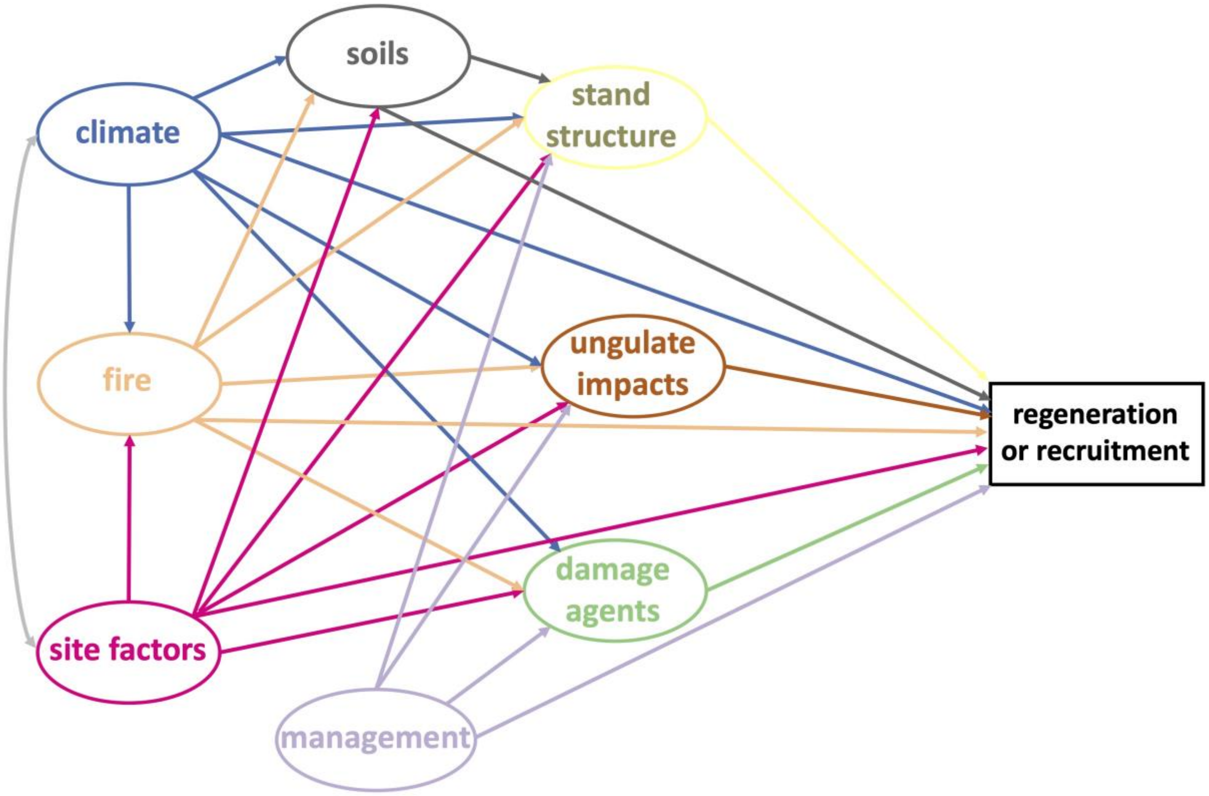


Figure 2.2. *A priori* structural equation model (SEM) illustrating hypothesized directional relationships among influencing factors and aspen regeneration or recruitment. Arrows indicate causal relationships, and colors correspond to each of the eight categories of influencing factors. See Table 2.2 for complete list of measured variables included in each of these eight categories.

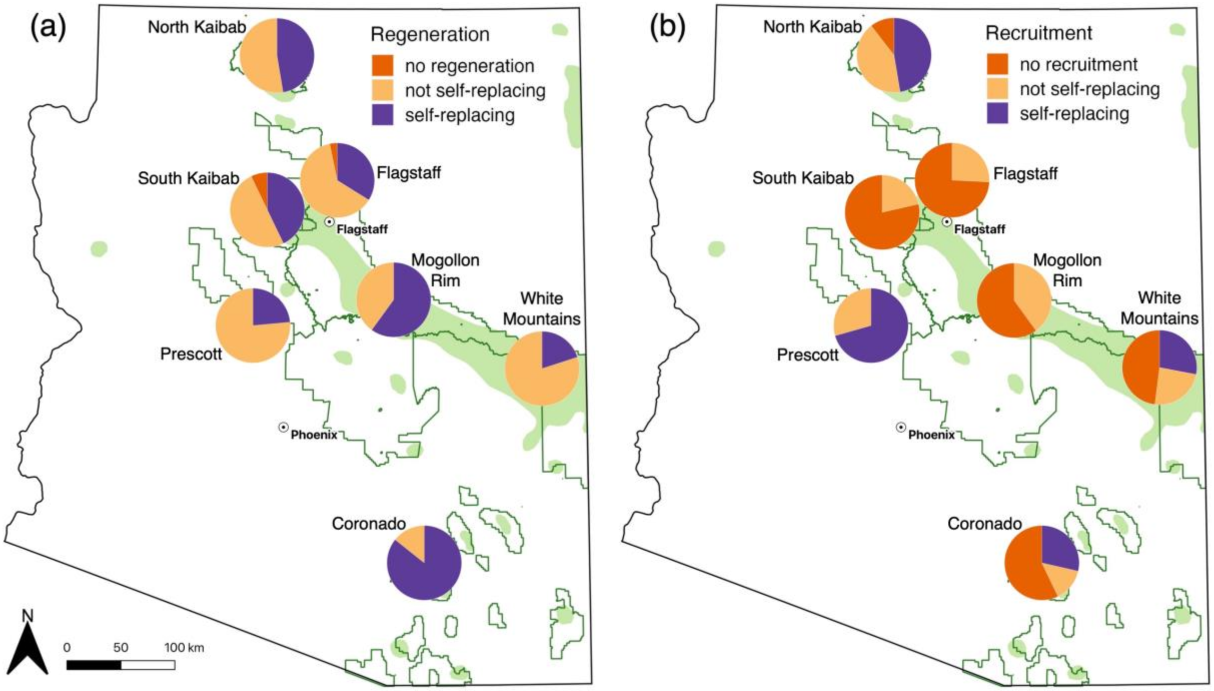


Figure 2.3. Maps showing sustainability status of (a) regenerating and (b) recruiting stems across seven major areas where aspen occurs in Arizona, USA. Data shown here do not include the 71 study plots inside of exclosures or jackstraw treatments, and sustainability status is based on the site-specific AZ thresholds for self-replacement.

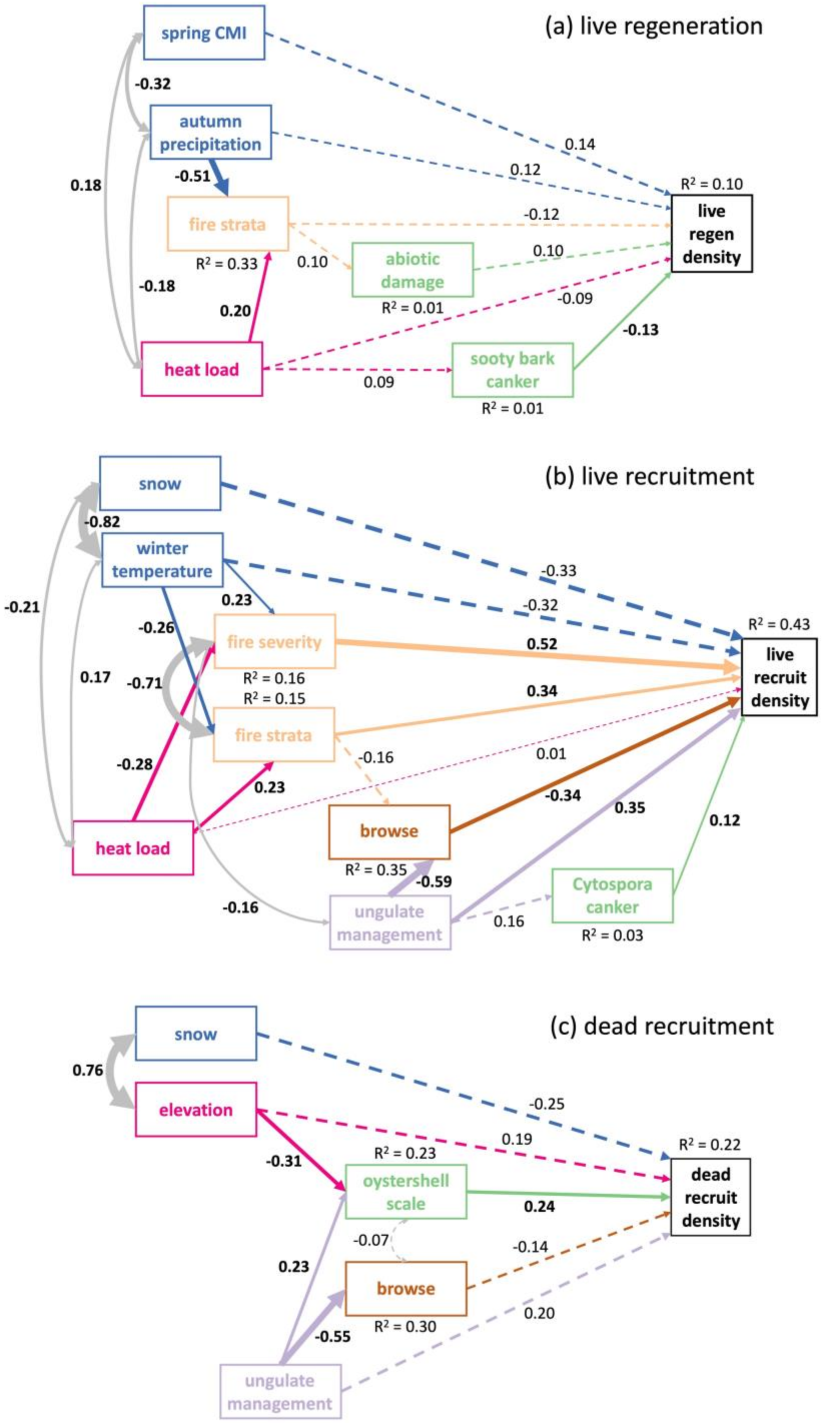
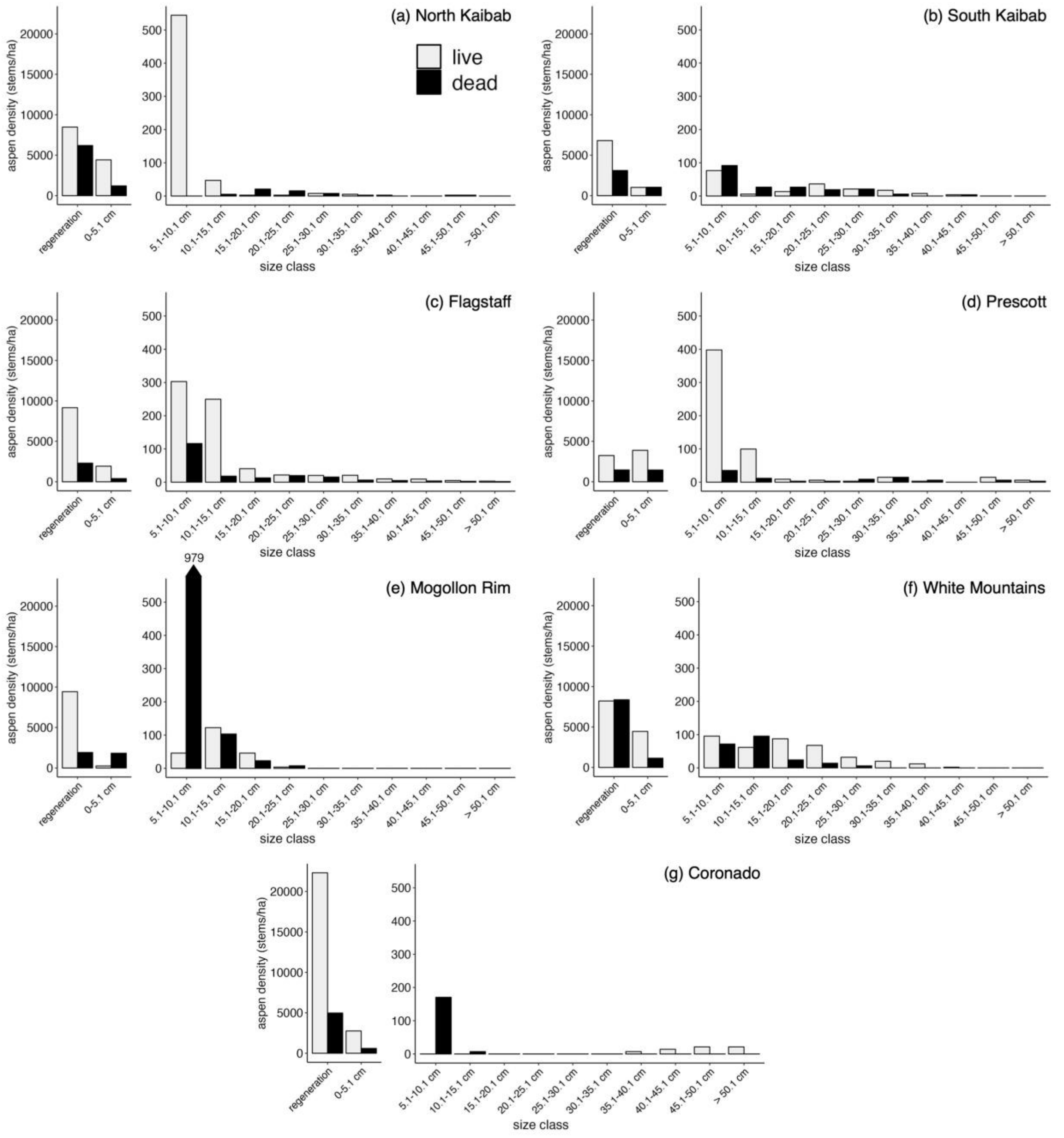


Figure 2.4. Optimal SEMs for density (trees ha^{-1}) of (a) live aspen regeneration, (b) live aspen recruitment, and (c) dead aspen recruitment. Significant ($p < 0.05$) path coefficients are shown in bold, and their corresponding paths are depicted as solid lines. In contrast, insignificant coefficients are not bolded, and their corresponding paths are shown as dashed lines. Path thickness indicates strength of its coefficient, with wider paths indicating stronger relationships. See Table 2.2 for descriptions and summary statistics of influencing factors.

Supplementary Materials



Appendix 2.1. Size class distributions for live (light grey) and dead (black) aspen stems from all study plots, split apart by the seven major areas shown in Fig. 2.1 and Fig. 2.3. Note that density scales differ for regenerating and smaller recruiting stems (< 5.1 cm dbh) compared to larger stems (> 5.1 cm dbh).

Appendix 2.2. Means and standard errors for the 62 continuous variables considered as potential influencing factors of aspen regeneration and recruitment, summarized across each of the seven major areas in our study.

	Mean (standard error)						
Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Stand structure							
Live aspen basal area[a]	4.2 (4.2)	6.4 (9.7)	13.0 (13.5)	8.8 (11.6)	3.0 (7.2)	11.1 (10.7)	11.4 (20.2)
Dead aspen basal area	2.3 (4.7)	4.3 (7.4)	5.1 (7.8)	4.5 (6.7)	5.4 (6.2)	2.9 (5.4)	0.6 (1.0)
Live non-aspen basal area	12.0 (14.2)	7.6 (9.1)	9.8 (15.5)	4.6 (4.6)	12.5 (10.8)	13.5 (17.0)	19.7 (25.9)
Live conifer basal area	12.0 (14.2)	7.3 (9.1)	9.8 (15.5)	4.1 (4.7)	9.9 (12.1)	13.5 (17.0)	19.7 (25.9)
Live aspen overstory density[b]	28.8 (41.7)	105.2 (167.2)	213.9 (275.6)	73.1 (98.1)	126.3 (303.6)	282.5 (304.5)	63.9 (110.1)
Dead aspen overstory density	52.4 (102.8)	88.0 (138.1)	71.7 (138.1)	44.9 (63.1)	57.4 (90.5)	75.6 (153.4)	7.1 (18.8)
Live non-aspen density	4,607 (8,665)	1,567 (2,777)	687 (1,515)	4,342 (4,961)	3,409 (4,920)	712 (1,127)	6,579 (8,874)
Live conifer density	4,607 (8,665)	1,069 (1,654)	676 (1,511)	170 (164)	1,255 (2,892)	712 (1,127)	355 (619)
Live non-aspen regen density	4,419 (8,573)	1,492 (2,728)	576 (1,475)	4,283 (4,975)	3,290 (4,926)	565 (996)	6,423 (8,990)
Live conifer regen density	4,419 (8,573)	1,002 (1,619)	565 (1,472)	117 (158)	1,163 (2,890)	565 (996)	199 (445)
Ungulate impacts							
Browse[c]	0.37 (0.28)	0.32 (0.35)	0.30 (0.34)	0.25 (0.20)	0.25 (0.26)	0.33 (0.24)	0.28 (0.30)
Ungulate barking[c]	0.00 (0.01)	0.06 (0.17)	0.03 (0.10)	0.00 (0.00)	0.06 (0.15)	0.00 (0.02)	0.00 (0.00)
Total ungulate scat[d]	8.4 (9.6)	3.0 (5.5)	1.1 (3.0)	0.4 (0.7)	3.1 (5.0)	6.0 (3.6)	3.0 (3.9)
Elk scat	0.0 (0.0)	2.8 (5.5)	0.4 (1.0)	0.0 (0.0)	3.1 (5.0)	5.0 (3.7)	0.0 (0.0)
Deer scat	8.0 (8.7)	0.2 (0.5)	0.3 (0.8)	0.4 (0.7)	0.0 (0.0)	0.6 (1.0)	3.0 (3.9)
Cattle scat	0.4 (1.4)	0.0 (0.0)	0.4 (2.3)	0.0 (0.0)	0.0 (0.0)	0.3 (0.7)	0.0 (0.0)
Damaging agents[c]							
Oystershell scale	0.00 (0.00)	0.24 (0.26)	0.15 (0.33)	0.54 (0.26)	0.15 (0.23)	0.00 (0.00)	0.00 (0.00)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Sucking & gall-forming insects	0.16 (0.14)	0.05 (0.08)	0.07 (0.13)	0.09 (0.09)	0.16 (0.26)	0.11 (0.20)	0.08 (0.10)
Bark beetles	0.00 (0.01)	0.00 (0.01)	0.01 (0.03)	0.00 (0.00)	0.00 (0.00)	0.02 (0.05)	0.00 (0.00)
Wood-boring insects	0.48 (0.24)	0.24 (0.21)	0.17 (0.19)	0.30 (0.17)	0.16 (0.20)	0.24 (0.19)	0.03 (0.04)
Defoliating insects	0.60 (0.19)	0.56 (0.21)	0.55 (0.31)	0.61 (0.24)	0.68 (0.15)	0.75 (0.17)	0.85 (0.15)
Cytospora canker	0.01 (0.02)	0.03 (0.07)	0.02 (0.04)	0.03 (0.04)	0.02 (0.04)	0.03 (0.07)	0.00 (0.00)
Hypoxylon canker	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.00)	0.01 (0.02)	0.00 (0.00)
Ceratocystis canker	0.04 (0.05)	0.00 (0.02)	0.01 (0.03)	0.02 (0.02)	0.01 (0.03)	0.08 (0.10)	0.00 (0.01)
Sooty bark canker	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)
All cankers	0.53 (0.14)	0.32 (0.24)	0.34 (0.26)	0.09 (0.11)	0.11 (0.16)	0.54 (0.19)	0.03 (0.05)
Foliar & shoot diseases	0.18 (0.14)	0.24 (0.19)	0.18 (0.27)	0.06 (0.08)	0.19 (0.13)	0.14 (0.13)	0.74 (0.18)
Decay diseases	0.01 (0.04)	0.02 (0.04)	0.05 (0.11)	0.05 (0.06)	0.00 (0.00)	0.03 (0.05)	0.00 (0.01)
Abiotic damage	0.00 (0.01)	0.01 (0.03)	0.02 (0.07)	0.02 (0.04)	0.01 (0.01)	0.00 (0.01)	0.00 (0.01)
Other animal damage	0.01 (0.04)	0.01 (0.02)	0.01 (0.02)	0.00 (0.00)	0.00 (0.00)	0.01 (0.02)	0.00 (0.00)
Site factors							
Elevation (m above sea level)	2697 (67)	2393 (139)	2582 (159)	2059 (46)	2305 (51)	2853 (119)	2582 (159)
Aspect[e]	0.75 (0.66)	1.21 (0.65)	0.87 (0.71)	1.71 (0.35)	0.77 (0.74)	0.78 (0.76)	1.79 (0.20)
Slope (°)	4.9 (4.5)	11.6 (10.0)	8.0 (7.2)	7.1 (4.3)	2.7 (3.0)	7.0 (2.5)	16.3 (7.4)
Heat load (MJ/cm^2/yr)	0.99 (0.02)	0.96 (0.07)	0.98 (0.08)	0.95 (0.03)	1.00 (0.03)	1.00 (0.05)	0.87 (0.10)
Radiation (MJ/cm^2/yr)	0.99 (0.04)	0.92 (0.12)	0.96 (0.08)	0.94 (0.05)	1.00 (0.01)	1.00 (0.04)	0.84 (0.09)
UTM easting	396422 (1886)	410677 (8727)	434335 (5411)	364491 (8218)	494638 (13092)	650996 (18608)	520833 (1262)
UTM northing	4039131 (8562)	3909453 (7935)	3910738 (4513)	3807999 (14347)	3805194 (7929)	3759419 (11454)	3589789 (621)
Soils							
Soil pH in H_2O (pHx10)	65.6 (4.3)	65.3 (2.6)	63.0 (1.7)	63.2 (2.1)	62.4 (1.7)	64.0 (1.1)	57.0 (1.7)
CEC (mmol(c)/kg at pH 7)	205.9 (9.7)	241.2 (12.1)	235.1 (7.5)	178.7 (2.6)	254.0 (9.4)	263.3 (6.0)	223.5 (20.7)
Nitrogen (cg/kg)	97.4 (12.2)	96.6 (16.3)	105.3 (13.8)	133.6 (36.8)	108.7 (14.3)	123.6 (16.7)	166.0 (21.2)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Soil organic carbon (dg/kg)	126.9 (6.8)	125.8 (20.6)	138.2 (21.5)	118.8 (28.5)	115.9 (15.1)	156.0 (18.8)	144.0 (12.4)
Bulk density (cg/cm^3)	149.0 (3.2)	151.7 (4.0)	148.0 (4.1)	150.0 (6.1)	151.7 (5.2)	140.3 (2.9)	132.1 (2.0)
Sand content (g/kg)	413.0 (9.2)	240.2 (28.8)	298.2 (57.8)	407.0 (66.7)	253.9 (25.6)	352.0 (68.2)	565.6 (25.7)
Clay content (g/kg)	265.1 (10.8)	336.7 (27.3)	255.7 (24.1)	302.1 (51.4)	357.1 (32.4)	226.6 (36.6)	153.8 (22.6)
Coarse fragments (cm^3/dm^3)	170.2 (38.2)	146.0 (60.9)	166.0 (63.1)	188.4 (30.9)	188.4 (36.3)	247.0 (19.5)	258.3 (20.3)
Climate							
Precipitation as snow (annual)[f]	152.7 (24.5)	93.6 (20.3)	151.6 (73.0)	29.0 (7.6)	66.8 (3.5)	131.3 (53.3)	83.2 (29.9)
Winter temperature (mean)[g]	-1.1 (0.2)	0.1 (0.7)	-1.3 (0.9)	4.0 (0.0)	2.3 (0.5)	-0.9 (0.7)	2.3 (0.7)
Spring temperature (mean)	5.9 (0.3)	6.8 (0.7)	5.6 (0.8)	10.5 (0.1)	9.1 (0.3)	5.5 (0.7)	8.5 (0.9)
Summer temperature (mean)	18.2 (0.4)	17.7 (0.7)	16.2 (0.9)	21.0 (0.1)	19.7 (0.2)	14.9 (0.5)	17.6 (1.0)
Autumn temperature (mean)	8.6 (0.3)	9.2 (0.7)	7.7 (0.8)	12.8 (0.1)	11.5 (0.4)	7.8 (0.6)	11.2 (0.9)
Summer temperature (max)	25.5 (0.3)	26.7 (0.8)	24.7 (1.3)	28.2 (0.1)	26.2 (0.3)	22.2 (0.7)	23.6 (1.2)
Winter temperature (min)	-7.3 (0.3)	-7.3 (0.7)	-8.4 (0.6)	-2.2 (0.4)	-2.8 (1.1)	-7.9 (1.2)	-3.2 (0.6)
Winter precipitation[f]	208.7 (24.9)	211.2 (26.0)	226.8 (50.5)	274.0 (76.3)	357.7 (52.2)	228.6 (44.1)	397.4 (20.7)
Spring precipitation	165.1 (7.0)	122.0 (11.9)	135.4 (23.8)	123.0 (14.4)	134.7 (19.4)	97.1 (26.4)	104.1 (5.5)
Summer precipitation	111.1 (4.5)	160.6 (11.0)	175.2 (13.9)	259.6 (13.9)	261.9 (32.7)	230.7 (25.4)	345.9 (27.2)
Autumn precipitation	84.6 (2.7)	113.3 (12.9)	111.2 (20.6)	188.4 (21.7)	228.3 (55.3)	153.9 (13.6)	232.9 (12.3)
Winter CMI[h]	17.4 (2.6)	15.6 (2.2)	18.7 (5.5)	17.8 (8.0)	29.0 (5.5)	18.3 (4.8)	31.9 (3.1)
Spring CMI	0.2 (1.0)	-8.2 (1.9)	-3.4 (4.3)	-13.1 (2.1)	-7.0 (2.5)	-6.4 (3.7)	-10.9 (2.7)
Summer CMI	-33.0 (0.7)	-33.2 (2.3)	-26.5 (4.0)	-21.4 (1.0)	-16.0 (4.8)	-14.1 (3.7)	-1.7 (5.0)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Autumn CMI	-14.0 (0.6)	-15.3 (1.8)	-11.4 (3.9)	-9.6 (2.8)	-1.2 (6.6)	-5.5 (2.1)	-0.1 (3.1)
Annual dryness index[i]	0.08 (0.01)	0.07 (0.01)	0.06 (0.01)	0.06 (0.01)	0.05 (0.01)	0.06 (0.01)	0.04 (0.01)
Monsoon index[i]	0.20 (0.02)	0.27 (0.02)	0.27 (0.03)	0.31 (0.05)	0.27 (0.01)	0.33 (0.03)	0.32 (0.01)

[a] basal area = m^{2} ha^{-1}

[b] density = trees ha^{-1}

[c] proportion of aspen stems affected by damaging agent

[d] scat = pellet piles/plot

[e] 0–2 (0 = 225°, 1 = 135° or 315°, 2 = 45°)

[f] precipitation = mm

[g] temperature = °C

[h] CMI = mm

[i] see methods for equation

Seasons for climate variables are winter (December – February), spring (March – May), summer (June – August), autumn (September – November).

Appendix 2.3. The percentage of plots in each level of the seven categorical variables, along with their standard errors, that were considered as potential influencing factors of aspen regeneration and recruitment.

Influencing factor	Mean (%)	Standard error
Fire strata		
0-2 yrs since fire	14.1	2.3
2-20 yrs since fire	22.7	2.8
> 20 yrs since fire	63.2	3.3
Fire severity		
Unburned in past 20 yrs	65.5	3.2
Unburned/low	9.1	1.9
Low	11.4	2.1
Moderate	8.2	1.8
High	5.9	1.6
Burned twice		
Burned < 2 times in past 20 yrs	95.0	1.5
Burned twice in past 20 yrs	5.0	1.5
Ungulate management		
No ungulate management	67.7	3.2
Exclosure or jackstraw	32.3	3.2
Conifer removal		
No treatment	87.7	2.2
Conifer removal	12.3	2.2
Major area		
Coronado	3.2	1.2
Flagstaff	51.4	3.4
Mogollon Rim	5.9	1.6
North Kaibab	8.6	1.9
Prescott	7.7	1.8
South Kaibab	11.8	2.2
White Mountains	11.4	2.1
Soil order		
Inceptisols	2.7	1.1
Mollisols – Borolls	14.1	2.3
Mollisols – Ustolls	13.2	2.3
Alfisolls	70.0	3.1

Chapter 3: Extent, impacts, and drivers of oystershell scale invasions in aspen ecosystems

Abstract

Invasive herbivores that kill foundation tree species pose a major threat to forest ecosystem sustainability. One important foundation tree species in the western United States is quaking aspen (*Populus tremuloides*), which is threatened by recent outbreaks of an invasive insect, oystershell scale (*Lepidosaphes ulmi*; OSS). OSS outbreaks were first reported in 2016, when OSS began causing dieback and mortality of aspen in northern Arizona. Previous studies of OSS in Arizona have highlighted the threat that OSS poses to aspen sustainability, warranting a comprehensive survey of OSS invasions and their impacts on aspen ecosystems. We sampled aspen populations across Arizona and addressed three questions: (1) Where does OSS occur? (2) What impacts does OSS have on aspen? (3) Which biotic and abiotic factors influence OSS abundance? We found that OSS was widespread in Arizona and had a negative impact on aspen forest health. OSS was associated with crown damage and tree mortality, especially of intermediate-sized, recruiting stems. Climate was the most important driver of plot-level OSS abundance, with warmer, drier conditions resulting in significantly more OSS. OSS abundance was also associated with less recent fire, presence of ungulate management strategies such as fenced exclosures, and stands with a greater density of aspen saplings. We conclude that active management is required to suppress OSS populations and mitigate damage to aspen ecosystems, and we provide OSS monitoring and management recommendations based on our findings.

Keywords: climate change, invasion ecology, *Lepidosaphes ulmi*, *Populus tremuloides*, sleeper species

Introduction

Invasive species pose a major threat to sustainability of forest ecosystems (Chornesky et al. 2005). Of particularly high concern are invasive species that kill foundation tree species, resulting in reductions to biodiversity and other ecosystem services (Ellison et al. 2005; Ellison 2019). Unlike keystone species, which are low in abundance but have an outsized influence on ecosystem dynamics, foundation species are common at the landscape scale and often abundant at smaller spatial scales (Ellison et al. 2005; Ellison 2019). An important foundation tree species in the western United States is quaking aspen (*Populus tremuloides*; hereafter aspen), which has the widest distribution of any tree species in North America (Little 1971; Perala 1990). Despite its continental abundance, aspen has high conservation value in the western US because it is one of the only hardwood species that forms pure, single-species stands (Rogers et al. 2020). As such, aspen ecosystems make disproportionately large contributions to biodiversity and other ecosystem services compared to neighboring conifer-dominated stands (DeByle 1985; Kay 1997; Chong et al. 2001; LaMalfa and Ryle 2008; Kuhn et al. 2011; Rogers et al. 2020). The conservation value of aspen is especially pronounced along the southwestern edge of its range, which includes Arizona, because aspen occupies less than 2% of forested land (Johnson 1994; Rolf 2001; Gitlin et al. 2006; Halbritter and Bender 2011; Zegler et al. 2012; Crouch et al. 2023). Concerningly, aspen in the Southwest is threatened by recent outbreaks of an invasive insect, oystershell scale (*Lepidosaphes ulmi*; hereafter OSS) (Crouch et al. 2021) (Fig. 3.1).

OSS is an armored scale (Hemiptera: Diaspididae) that feeds by inserting its stylet through the bark of woody host plants to feed on the fluid of non-vascular cells (Griswold 1925; Beardsley and Gonzalez 1975). This feeding damages host cells, resulting in cell death and cracking of the host's bark under heavy infestations (Beardsley and Gonzalez 1975). Mortality of heavily infested branches and stems may also occur (Griswold 1925; Beardsley and Gonzalez 1975). OSS is polyphagous, with around 100 host genera globally (Miller and Davidson 2005). Twelve host genera (*Acer*, *Alnus*, *Ceanothus*, *Cornus*, *Frangula*, *Fraxinus*, *Juglans*, *Lupinus*, *Populus*, *Ribes*, *Salix*, and *Symphoricarpos*) have been documented in the western US (Crouch et al. 2021). OSS is most common on woody, deciduous plants, especially those with relatively thin bark (Miller and Davidson 2005). As an obligate parasite, OSS completes its entire life cycle on woody tissue of living hosts (Samarasinghe 1965). Questions remain about the timing of OSS's life cycle on aspen and other hosts in Arizona (Crouch et al. 2021), but OSS is known to overwinter in the egg stage (Beardsley and Gonzalez 1975). All OSS life stages are sessile, except for first-instar crawlers, which actively disperse along the host's stem or branches in search of a suitable feeding site (Miller and Davidson 2005). Once a feeding site is found, OSS will remain there through adulthood (Griswold 1925). In bisexual populations, males shed their tests and fly to mate with females; however, female-only populations occur and reproduce via parthenogenesis (Beardsley and Gonzalez 1975; Miller and Davidson 2005). Questions also remain about OSS dispersal mechanisms and distances, but long-distance crawler dispersal is likely driven by human movement of infested plants, whereas short- and intermediate-distance dispersal are likely driven by wind, potentially with animal assistance (Griswold 1925; Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010). Crawlers do not actively move more than 1 m due to limited energy reserves and susceptibility to adverse climatic conditions (Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010).

Although the native range and introduction history of OSS are uncertain, the species was likely transported to North America by European settlers on infested plant material (Griswold 1925; Beardsley and Gonzalez 1975). OSS was first reported as a pest of apple trees (*Malus* spp.) in the 1700s and is now present throughout much of North America, especially in urban and ornamental settings (Griswold 1925; Miller and Davidson 2005). Despite the species' polyphagous nature, its pervasiveness in North America, and its long invasion history, OSS has rarely been a major pest in wildland forest settings (but see Sterrett 1915; DeGroot 1967; Houston 2001). OSS was first reported on aspen in wildland forest settings in Arizona, USA by Fairweather (1992) and Zegler et al. (2012), but in both cases OSS abundance was low, and impacts were minimal. However, in 2016 OSS was observed causing dieback and mortality of aspen in wildland forest settings (Grady 2017), and severe outbreaks have since been observed in both areas where Fairweather (1992) and Zegler et al. (2012) first observed OSS. Based on this invasion history, Crouch et al. (2021) suggested that OSS may be a sleeper species, which is defined as a non-native species that establishes successfully but experiences slow population growth before suddenly awakening when conditions become favorable and experiencing rapid population growth (Groves 1999; Bradley et al. 2018; Frank and Just 2020). It is unclear what led to the awakening of OSS, but recent climatic changes, namely warmer and drier conditions (Williams et al. 2022), are a likely explanation (Crouch et al. 2021). A warming climate may have improved conditions for OSS by increasing the species' fitness and abundance and/or by increasing susceptibility of aspen to infestation and mortality (Frank 2020; Crouch et al. 2021). OSS's role as a sleeper species and its potential interactions with climate change are concerning because continued climate warming may trigger OSS invasions in other areas of aspen's range (Crouch et al. 2021).

Critical to managing any invasive species is baseline information on its occurrence and impacts. The first peer-reviewed report on OSS outbreaks in Arizona indicated that the species is already widespread in northern Arizona (Crouch et al. 2021). Crouch et al. (2021) also observed that OSS only occurred in the lower half of aspen's elevation range (< 2500 m) and that OSS seemed to be particularly pervasive on, and damaging to, smaller recruiting stems. In a study focused on aspen across Arizona, Crouch (2023) corroborated those early results by finding that there was significantly less OSS at higher elevations and that OSS contributed to mortality of aspen recruits (stems > 1.37 m tall and < 12.7 cm diameter at breast height [dbh; height = 1.37 m]). Both studies also found that OSS was more common in fenced ungulate exclosures (2 m tall fences built to exclude ungulates from browsing on aspen) than outside of them. Because recruitment is critical for self-replacement, these early findings highlight the threat that OSS poses to aspen resilience and sustainability (DeRose and Long 2014; Crouch et al. 2023), warranting a comprehensive survey of OSS and its impacts on aspen across Arizona. We have much to learn about which factors influence OSS's presence across the landscape and what specific impacts OSS has on aspen ecosystems. Obtaining this information is critical for informing management of OSS and mitigating damage caused by this high-impact invasive species. To fill these critical knowledge gaps, we sampled aspen populations across Arizona and addressed three questions: (1) Where does OSS occur in Arizona? (2) What impacts does OSS have on aspen? (3) Which biotic and abiotic factors influence OSS abundance in aspen ecosystems?

Methods

Study Area

Our study area encompassed aspen ecosystems across Arizona, USA. Although OSS has been observed on numerous hosts in Arizona (Crouch et al. 2021), our study is focused on aspen because the first OSS outbreaks were observed in aspen ecosystems and because of aspen's importance as a foundation species. Aspen ecosystems in Arizona tend to be small (0.1–25 ha in size), especially compared to more northerly latitudes of aspen's range (Zegler et al. 2012). Aspen is limited to relatively high elevations (2000–3000 m), where lower temperatures and higher precipitation allow the drought-intolerant species to survive (Perala 1990; Rehfeldt et al. 2009). At lower elevations, small pockets of aspen occur on north-facing slopes or in drainages with increased water availability, and as elevation increases, the aspen component tends to be more abundant and less aspect-limited (Rasmussen 1941; Covington et al. 1983; Merkle 1962; Fairweather et al. 2008; Zegler et al. 2012). In addition to occurring alone in small single-species stands, aspen commonly co-occurs with conifers, including ponderosa pine (*Pinus ponderosa* var. *scopulorum*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) at lower elevations, white pine (*Pinus strobiformis* or *Pinus flexilis* var. *reflexa*) and white fir (*Abies concolor*) at mid elevations, and subalpine fir (*Abies lasiocarpa* var. *arizonica*) and Engelmann spruce (*Picea engelmannii*) at the highest elevations.

Site Selection

We sampled 220 aspen plots that represent the range of conditions under which aspen exists in Arizona (Fig. 3.2a). 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. 3.2a). All data were collected during the 2020, 2021, and 2022 growing seasons (June – October), when aspen trees had leaves.

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 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) – 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 occurs in each stratum. We assessed aspen's actual occurrence in each stratum using an observed GIS layer of aspen's range on three national forest ranger districts surrounding Flagstaff (Flagstaff and Mogollon Rim Ranger Districts on the Coconino National Forest; Williams Ranger District on 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 of our strata. 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 (Crouch 2023).

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. Specifically, 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. We established the remaining 139 plots by identifying aspen stands that filled target strata, standing on the edge of selected stands, laying out a transect longways through those stands, 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 m to 300 m. In contrast, Zegler et al. (2012) established sites at randomly located points within known aspen stands and sampled plots in each of the four cardinal directions 20 m from those points.

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 (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. 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. In the 8 m overstory plot, all trees with dbh > 12.7 cm were measured. In the 4 m regeneration plot, all trees > 0.02 cm in height and < 12.7 cm dbh were measured. In the regeneration plot, we classified stems into three size classes adapted from Zegler et al. (2012): short regeneration (< 1.37 m tall), tall regeneration (> 1.37 m tall and < 5.1 cm dbh), and saplings (5.1–12.7 cm dbh). We considered both tall regeneration and saplings to be recruiting stems (Crouch 2023) and chose a 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). For all live aspen, we measured height, dbh (except for regeneration and recruits that were < 1 cm dbh), crown dieback ([percentage of dead branches above the bottom of the tree's live crown] 0%, 1–33%, 34–67%, > 67%), crown ratio (percentage of total height occupied by the tree's live crown), and OSS presence and severity. We assessed OSS severity using the system devised by Crouch et al. (2021), which rates OSS severity on each tree from ground level to 6 m. Each tree's stem up to 6 m is divided into thirds, and severity is rated for each 2 m section (or shorter for trees < 6 m tall) on both the north and south sides of the tree. Severity is rated 0–3: 0 = no OSS present (light), 1 = only a handful of OSS present (trace), 2 = OSS covers < 50% of section (light), 3 = OSS covers > 50% of section (severe). For every dead aspen and live tree species other than aspen, we recorded size class and dbh.

For all live aspen in our study plots, 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 OSS), 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 certain cankers individually because of their potential to have outsized impacts on aspen tree health compared to less pathogenic diseases (Hinds 1985; Zegler et al. 2012; Crouch et al. 2023). The cankers we assessed individually were Cytospora canker (caused by *Valsa sordida*), 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, drought scorch on leaves, and chlorosis of leaves. We also assessed animal damage to aspen stems, including browse, ungulate barking (i.e., elk chewing aspen bark), and other animal damage. In addition to directly quantifying ungulate impacts via browse and barking on individual aspen stems, we counted ungulate scat piles within the 8 m overstory plot. We identified scat piles by species (i.e., elk [*Cervus canadensis*], deer [*Odocoileus hemionus* or *O. 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).

OSS Extent

We used OSS observations across the 220 study plots to assess where OSS occurs in Arizona. Specifically, we assessed presence, absence, and abundance of OSS in each plot. OSS abundance, which we also refer to as plot-level abundance, was calculated by assessing the proportion of stems in each plot that were infested by OSS at any level of severity. We also used descriptive statistics to quantify OSS presence and severity across the study plots. At the tree level, we assessed OSS infestation severity across the four aspen size classes (i.e., short regeneration, tall regeneration, saplings, and overstory trees) to determine if there were differences in susceptibility to OSS. 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.

OSS Impacts

We assessed OSS impacts on aspen at both the tree and stand levels. At the tree level, we built univariate regressions to quantify the influence of OSS presence and severity on aspen dieback and crown ratio, which are metrics that capture individual stem health (Schomaker et al. 2007). Tree-level OSS severity was calculated by taking the mean percentage of each category in the rating system (i.e., 1% for 1, 25% for 2, and 75% for 3) and calculating the mean for the six ratings recorded for each tree. We used the *nlme* package (Pinheiro et al. 2022) to fit four linear mixed-effects models with crown dieback and crown ratio as responses, OSS presence and severity as fixed effects, and the hierarchical, nested structure of our plots (i.e., plots [n=220] within study sites [n=87] within minor areas [n=19] within major areas [n=7]) 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). To assess OSS impacts at the stand level, we built univariate regressions between plot-level OSS abundance (i.e., proportion of stems infested by OSS) and aspen mortality. We used the *nlme* package (Pinheiro et al. 2022) to fit six linear mixed-effects models with dead aspen basal area, dead aspen density, and density of dead aspen in each of the four size classes individually as the six response variables. For these stand-level regressions, we fit OSS abundance as the fixed effect and the hierarchical, nested structure of our plots (i.e., plots [n=64] within study sites [n=23] within minor areas [n=9] within major areas [n=4]) as a random effect. Sample sizes differ for these stand-level models compared to the tree-level models because we used only the 64 plots in which OSS occurred for these stand-level models.

Factors Influencing OSS Abundance

To assess drivers of OSS invasions in aspen ecosystems, we collected data representing an array of biotic and abiotic factors that may influence plot-level OSS abundance (Table 3.1). In total, we considered 99 variables across eight categories of potential influencing factors: stand structure, ungulates, other damaging agents, fire, management, site factors, soils, and climate. Although some of these factors (e.g., ungulates) are unlikely drivers of OSS invasions, we included as many potential influencing factors as possible because we have no prior data on which factors drive OSS invasions. Using tree height and diameter data, we calculated basal area of stems > 5.1 cm dbh for live aspen, all OSS host species, and non-host species (Table 3.1).

We calculated stem densities (trees ha^{-1}) for live aspen, all host species, and non-host species across each of four stem size classes (i.e., short regeneration, tall regeneration, saplings, and overstory trees). 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 3.1).

Using the GPS coordinates we collected at each plot's center, we calculated elevation, aspect, and slope using a 30 m^2 digital elevation model (Table 3.1). We transformed raw aspect into a continuous variable ranging from 0–2 with 0 representing southwest (225°) and 2 representing northeast (45°) (Beers et al. 1966). We also calculated heat load and potential annual direct radiation, two indices that assess site-level temperature based on slope, aspect, and latitude (McCune and Keon 2002). We assessed fire occurrence in each plot for the past 20 years using wildland fire perimeters obtained from the USDA Forest Service Region 3 GIS database (https://www.fs.usda.gov/detail/r3/landmanagement/gis) and prescribed fire perimeters from national forest staff. We assessed fire severity 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 3.1). 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 3.1).

We obtained soils data from SoilGrids (https://www.isric.org/explore/soilgrids), which provides global soil mapping data 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 3.1). SoilGrids provides data up to 2 m below the surface; however, 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 1985). We obtained climate data from ClimateNA (https://climatena.ca/), which downscales PRISM data (Daly et al. 2008) at 800 m resolution (Wang et al. 2016). Because we expected climate to be an important driver of OSS abundance but had no prior data on which aspects of climate are the most important, we included as many climate variables as possible. Specifically, we obtained variables representing annual and, when available, seasonal degree-days, temperature, precipitation, humidity, evaporation, and drought for the two years preceding when we sampled each plot (Table 3.1). We chose two years because, based on our many years of observing OSS in the field, we assumed that most OSS we observed on trees accumulated in the preceding two years. Although dead OSS are likely capable of lasting even longer on host trees, more recent climate data captures the most recent trends in OSS population abundance.

We used random forests, structural equation modeling (SEM), and stand- and tree-level regressions to determine which biotic and abiotic factors drive OSS invasions. First, we used random forests to determine which of the 99 predictor variables had the strongest influence on plot-level OSS abundance. 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 tree. We used this ranked list of variables when building SEMs and assessing univariate relationships between influencing factors and OSS abundance. We also used the climate variables in this list to search for climatic thresholds beyond which OSS does not occur in Arizona.

Once we obtained a list of the most important variables influencing OSS abundance, we used SEM to assess how those variables and their interactions affect OSS abundance. SEM is an insightful tool for ecological research because it allows 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). Our first step in building an SEM was to construct an *a priori* model based on our theoretical understanding of how biotic and abiotic factors might influence OSS. This *a priori* model (Fig. 3.3) accounted for all 99 variables that potentially influence OSS abundance using the eight categories of influencing factors (i.e., stand structure, ungulates, other damaging agents, fire, management, site factors, soils, and climate). We then built a “full” SEM, which included the highest ranked variable based on random forests from each of the eight categories of influencing factors (Table 3.1). We used a combination of backward and forward selection to optimize model fit (using AIC and Fisher’s C statistic) and maximize 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 (i.e., replacing fire severity with fire strata) affected the model. We used the *piecewiseSEM* package to build our SEMs because this package accommodates use of mixed-effects models (Lefcheck 2016). 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 our plots modeled as random effects.

We also fit stand- and tree-level regressions to assess how various factors influence OSS presence and severity. At the stand level, we took the top 25 factors influencing OSS abundance based on random forests and built univariate regressions to quantify relationship direction, strength, and significance. For these models, we used the *nlme* package (Pinheiro et al. 2022) to fit linear mixed-effects models with plot-level OSS abundance as the response, the 25 individual influencing factors as fixed effects, and the hierarchical, nested structure of our plots as random effects. At the tree level, we built univariate regressions to determine the influence of aspen tree size on OSS presence and severity. We used the *nlme* package (Pinheiro et al. 2022) to fit eight linear mixed-effects models with OSS presence and severity as responses, with dbh, height, height-to-diameter ratio, and size class as fixed effects, and with the hierarchical, nested structure of our plots as random effects. Because size class is a categorical variable with four levels, we also used the “anova” function in R (R Core Team, 2022) to conduct one-way analysis of variance (ANOVA), allowing us to test for significant differences in OSS presence and severity among the four size classes. When ANOVA found a significant ($\alpha = 0.05$) difference between size classes, we used the *emmeans* (Lenth, 2022), *multcomp* (Hothorn et al. 2008), and *multcompView* (Graves et al. 2019) packages to conduct post-hoc Tukey-adjusted pairwise comparisons and determine which size classes significantly differed. We used these same ANOVA procedures to compare height-to-diameter ratios inside versus outside areas of ungulate management to assess how these treatments influence aspen growth.

Results

Aspen Condition

Mean basal area of all aspen, including living and standing dead trees, in our 220 study plots was 14.6 m^2 ha^{-1}, of which dead trees made up 29.5% (Table 3.2). Mean aspen density was 16,069 trees ha^{-1}, 27.7% of which were dead. Looking at individual stem size classes, our study plots contained an average of 239 overstory aspen ha^{-1} (28.2% of which were dead), 519 saplings ha^{-1} (31.9% dead), 3,196 tall regeneration stems ha^{-1} (24.9% dead), and 12,115 short regeneration stems ha^{-1} (28.2% dead). Of the 9965 live aspen stems we sampled, 34.2% of stems had no crown dieback, 44.5% of stems had 1–33% dieback, 13.9% of stems had 34–67% dieback, and 7.5% of stems had 67–99% dieback (Table 3.2). Mean crown ratio of live aspen was 52.0%.

OSS Extent

OSS was present in 29% of our study plots and occurred in four of seven major areas where aspen occurs in Arizona: South Kaibab, Flagstaff, Prescott, and Mogollon Rim (Fig. 3.2a). OSS was not found in the North Kaibab, White Mountains, or Coronado major areas. The area around Prescott had the highest plot-level rate of infestation, with OSS present in all 17 plots. The South Kaibab had 65.4% of plots infested (Fig. 3.2b), the Mogollon Rim had 53.4% of plots infested (Fig. 3.2c), and Flagstaff had 20.4% of plots infested (Fig. 3.2b). Of the 9965 live aspen stems we sampled, 10.7% were infested with OSS. Tree-level rates of infestation across major areas were consistent with plot-level rates of infestation. When looking at all plots, not just those in which OSS occurred, Prescott had the highest proportion of trees infested (60.3%), followed by South Kaibab (20.8%), Mogollon Rim (16.2%), and Flagstaff (7.6%).

OSS infested aspen stems of all sizes, although there was a clear preference for trees taller than 1.37 m (i.e., tall regeneration stems and larger) (Fig. 3.4). Using the OSS severity rating, 6.9% of all live aspen stems we sampled had a mean rating of trace, 2.3% were light, and 1.4% were severely infested. In the 64 plots where OSS was present, mean severity ratings were 34.5% trace, 11.6% light, and 7.2% severe. Patterns of OSS severity across stem size classes generally followed those of OSS presence, with more severe infestations occurring as rate of presence increased (Fig. 3.4).

OSS Impacts

OSS presence at the tree level was significantly ($p < 0.001$) associated with reduced aspen crown ratio and increased crown dieback based on univariate regression (Table 3.3). Trees infested with OSS were associated with a 9.8% reduction in crown ratio and a 0.5 unit increase in dieback compared to trees without OSS. Because dieback was assessed on a categorical scale from 0 to 3 (0 = 0% dieback, 1 = 1–33% dieback, 2 = 34–67% dieback, 3 = 67–99% dieback), a 0.5

unit increase on the categorical scale equates to a roughly a 16% increase in dieback. Tree-level OSS severity was also significantly ($p < 0.001$) associated with reduced crown ratio and increased dieback (Table 3.3). Tree-level OSS severity ranged from 0 to 0.75, with 0 indicating a tree without OSS and 0.75 indicating a tree with the highest possible severity rating (OSS covering > 50% of all six stem sections rated). Thus, an increase in OSS severity of 0.1 equates to a 10% increase in OSS infestation of the tree's stem up to 6 m in height. A 0.1 unit increase in OSS severity was associated with a 3.9% reduction in crown ratio and a 0.2 unit increase in dieback, which equates to roughly 6.6% dieback. Despite the high degree of significance for all four of these univariate relationships, OSS presence and severity explained a low proportion of the variance observed in aspen crown ratio and dieback ($R^2 \leq 0.03$), indicating that OSS is one of many factors influencing aspen stem health.

For the 64 study plots in which OSS was present, plot-level OSS abundance was significantly ($p = 0.019$) associated with increased dead aspen basal area (Table 3.4). An increase in OSS abundance of 1, which represents the difference between no stems infested by OSS and all stems infested by OSS, was associated with an increase in dead aspen basal area of 5.7 m^2 ha^{-1}. For context, mean basal area of living aspen in these 64 plots was 11.4 m^2 ha^{-}1 and in all 220 study plots was 10.3 m^2 ha^{-1}. We also assessed the influence of OSS abundance on five measures of dead aspen density: total dead aspen and density of the each of the four size classes. None of these univariate relationships were significant, although the tall regeneration ($p = 0.054$) and sapling ($p = 0.061$) models approached significance (Table 3.4). An increase in OSS abundance of 1 was associated with 1,654 more dead tall regeneration stems ha^{-1} and 532 more dead saplings ha^{-1}. For context, there were 1,579 living tall regeneration stems ha^{-1} and

867 living saplings ha^{-1} on average in the 64 plots where OSS occurred and 2,399 tall regeneration stems ha^{-1} and 354 living saplings ha^{-1} across all study plots. The models for total dead aspen density, density of dead short regeneration, and density of dead overstory trees were insignificant ($p \geq 0.350$).

Factors Influencing OSS Abundance

Of the 99 potential influencing factors considered in our study, the five most important influences on plot-level OSS abundance based on random forests were reference evaporation in autumn, elevation, degree-days between 10°C and 40°C, winter climate moisture index (CMI), and autumn precipitation (Table 3.5). Based on univariate relationships between the top 25 most important influencing factors and OSS abundance, the five strongest influencing factors were maximum winter temperature ($R^2 = 0.43$; $p < 0.001$), winter evaporation ($R^2 = 0.41$; $p < 0.001$), maximum spring temperature ($R^2 = 0.30$; $p < 0.001$), elevation ($R^2 = 0.26$; $p < 0.001$), and minimum spring temperature ($R^2 = 0.21$; $p = 0.004$).

The optimal SEM for plot-level OSS abundance (AIC = 861.6; Fisher's C = 1.018 with $p = 0.907$ [high p value indicates better fit]; response marginal $R^2 = 0.53$, conditional $R^2 = 0.88$ [marginal includes only fixed effects, conditional includes both fixed and random effects]) included seven influencing factors: autumn evaporation, winter CMI, maximum winter temperature, elevation, fire strata, live aspen sapling density, and presence of ungulate management (Fig. 3.5). Based on this SEM, all influencing factors except for winter CMI and elevation had a significant ($p < 0.05$) direct effect on OSS abundance. Autumn evaporation had a negative direct effect (effect size = -0.33; $p = 0.011$) on OSS abundance, whereas maximum winter temperature (0.60; $p = 0.011$), fire strata (0.30; $p < 0.001$), live aspen sapling density (0.13; $p = 0.001$), and presence of ungulate management (0.26; $p < 0.001$) had positive direct effects. Fire strata and ungulate management were categorical variables (Table 3.1), and SEM indicated that less recent fire and presence of ungulate management resulted in greater OSS abundance. All three climate variables had significant ($p \leq 0.003$) influences on fire strata, with recent fire being driven by less autumn precipitation, higher winter CMI, and higher maximum temperatures in winter. Thus, more autumn evaporation indirectly led to more OSS, while higher winter CMI and maximum winter temperatures indirectly led to less OSS. More autumn evaporation and higher winter CMI also resulted in significantly ($p \leq 0.003$) fewer aspen saplings, resulting in both climate variables having an additional negative indirect effect on OSS abundance. Finally, aspen sapling density was significantly ($p < 0.001$) lower at higher elevation, resulting in a negative indirect effect of elevation on OSS abundance.

To further assess the relationship between climate and OSS, we search for thresholds using the climate variables that random forests, univariate regressions, and SEM indicated were the most important drivers of plot-level OSS abundance. We identified clear elevational and climatic thresholds beyond which OSS does not occur in Arizona (Fig. 3.6). According to these thresholds, OSS was not observed in plots that exceeded 2545 m in elevation, received greater than 152 mm of snow annually, experienced maximum winter temperatures below 5.25°C, experienced maximum spring temperatures below 13.25°C, and had fewer than 825 degree-days between 10°C and 40°C (calculated as accumulated temperature difference from the degree-day threshold, rather than a true accumulation of degree-days [Wang et al. 2006]). In addition, OSS was not observed in plots with less than 218 mm of autumn reference evaporation, except for one plot which had 202.5 mm of evaporation and a single aspen stem infested with OSS.

We also assessed univariate relationships between tree-level OSS presence and severity and four measures of aspen stem size: size class, height, dbh, and height-to-diameter ratio. One-way ANOVA indicated that there were significant differences ($p < 0.001$) in OSS presence and severity among the four stem size classes (Table 3.6). OSS presence was significantly greater on overstory trees and saplings compared to tall and short regeneration, and OSS presence was significantly greater on tall regeneration than short regeneration. Saplings and tall regeneration had significantly greater OSS severity than overstory trees and short regeneration, while overstory trees had significantly greater OSS severity than short regeneration. OSS presence and severity significantly ($p < 0.001$) increased with increasing height and decreasing dbh (Table 3.6). In addition, OSS presence and severity significantly ($p \leq 0.042$) increased with increasing aspen height-to-diameter ratio, and one-way ANOVA indicated that height-to-diameter ratios were significantly ($p < 0.001$) greater inside areas of ungulate management than outside these areas. Similar to the tree-level crown ratio and dieback results, aspen stem size explained a low proportion of the variance observed in OSS presence and severity (marginal $R^2 \leq 0.02$) (Table 3.6).

Discussion

OSS Extent

OSS is widely distributed throughout aspen ecosystems in Arizona (Fig. 3.2a), confirming the initial report of OSS outbreaks in the region (Crouch et al. 2021). This study added plots in three areas not originally surveyed by Crouch et al. (2021) – the North Kaibab, White Mountains, and Coronado – none of which had OSS. We also added plots in the South Kaibab, Flagstaff, Prescott, and Mogollon Rim major areas, with mixed results in terms of OSS presence and absence. Aspen ecosystems on the North Rim and in the White Mountains may be free of OSS because the wetter, colder climates in those areas (Appendix 3.1) may be unsuitable for OSS, as we discuss later. Alternatively, these areas may have evaded OSS invasions for a different, unknown reason. For example, OSS spread at the landscape level is likely facilitated by its ability to infest a wide array of hosts in addition to aspen (Crouch et al. 2021) and perhaps even by historical transportation of infested apple stock by Euro-American settlers. However, our ability to determine how other host species may facilitate OSS invasions of aspen ecosystems is limited due to the lack of fine-scale mapping of where apples were historically planted and of where other OSS host species occur, particularly understory hosts such as *Ceanothus* spp. In contrast to the North Rim and White Mountains, aspen ecosystems on the Coronado tend to occur on relatively warmer, drier sites (Appendix 3.1), but OSS may have been absent in our Coronado study plots because all the plots we sampled were in areas burned the previous year by the 2020 Bighorn Fire. Importantly, our sampling was not exhaustive, so OSS may occur in the North Kaibab, White Mountains, and Coronado. More extensive monitoring in these areas, including on hosts other than aspen, is required to determine whether or not OSS is present. However, even if OSS is present in these areas, it is unlikely that their population sizes are large because forest managers in these areas have not yet reported seeing OSS to USDA Forest Health Protection (A. Grady, USDA Forest Service, personal communication).

OSS Impacts

OSS had a negative influence on aspen health at both the tree and stand levels. Aspen trees infested with OSS had significantly lower crown ratios and higher dieback, indicating reduced stem health. As OSS infestations became more severe, crown ratio significantly decreased, and dieback significantly increased (Table 3.3). This crown damage was likely caused by OSS's feeding, which sucks fluid from the host plant's non-vascular cells (Griswold 1925; Beardsley and Gonzalez 1975), but the exact mechanism that causes damage remains unknown and represents an important research need. For example, aspen bark is photosynthetic (Jones and DeByle 1985), so OSS feeding might reduce the tree's photosynthetic capacity. Alternatively, OSS feeding may compromise stem health by causing trees to allocate resources from growth to defense (Cope et al. 2021). At the stand level, aspen plots with more stems infested by OSS had significantly greater dead aspen basal area, with a 10% increase in OSS abundance equating to an increase of 0.57 m^2 ha^{-1} in dead aspen basal area (Table 3.4). Although density of total dead aspen stems and density of dead stems in each of the four size classes had insignificant relationships with OSS abundance, the models for dead tall regeneration and saplings approached significance, suggesting that OSS may have an outsized influence on these intermediate-sized, recruiting stems (Crouch 2023).

Intermediate-sized stems seem to be the most susceptible to OSS infestation. Density of aspen saplings and saplings of all host species were significantly associated with increased plot-level OSS abundance (Table 3.5). We would expect that OSS would be more abundant in stands where more hosts are available, but it is notable that, of all size classes, saplings were most significantly associated with OSS abundance. At the tree level, OSS infestations were more severe on tall regeneration and saplings and were associated with taller and thinner stems (Table 3.6). We hypothesize short regeneration had such low infestation rates because these stems remain shorter than 1.37 m for only a few years, which reduces the likelihood of OSS finding them before they grow into taller size classes. Short regeneration may also be more likely to evade OSS because they are smaller targets. We hypothesize that overstory trees may resist OSS because, as aspen trees grow larger, their bark tends to thicken, possibly making them less susceptible to OSS. On the other hand, overstory trees may have had lower OSS severity than tall regeneration and saplings because the OSS severity rating system does not assess OSS above 6 m in height. The mechanisms underlying OSS's outsized impacts on intermediate-sized, recruiting stems merit further research, but the potential impacts of this finding are clear. Recruiting stems are critical indicators of aspen community resilience (Rogers and Mittanck 2014; Rogers 2017), and increased mortality of these stems from OSS poses a major threat to sustainability of aspen ecosystems (Crouch 2023).

Factors Influencing OSS Abundance

Climate was the most important factor driving OSS invasions of aspen ecosystems in Arizona. According to random forests, seven of the top 10 and 15 of the top 25 factors influencing OSS abundance were climate variables. Moreover, SEM indicated that climate variables, namely autumn evaporation and maximum winter temperature, had the strongest direct effect on OSS abundance. Generally, warmer and drier conditions were associated with increased OSS abundance. For example, greater OSS abundance was significantly associated with fewer degree-days below 0°C and more degree-days between 10°C and 40°C, with warmer temperatures in winter, spring, and summer, with less winter precipitation and annual snowfall, and with greater spring climate moisture deficit (CMD) and winter evaporation (Table 3.5). The strong relationship between climate and OSS abundance is not surprising because of the well-established influence of climate on development of armored scale insects (Beardsley and Gonzalez 1975). Alternatively, the relationship between climate and OSS might be mediated through host stress (Crouch et al. 2021). Based on the plant stress hypothesis, drought might not only weaken aspen defenses but also increase nutritional quality, leading to increased OSS fitness and abundance (White 1984; Dale and Frank 2017). In support of this hypothesis, the optimal host for sap-feeding herbivores is one that has experienced long-term, intermediate drought stress punctuated by temporary releases from that stress (Kolb et al. 2016). Notably, we found that wetter conditions in autumn (e.g., reduced autumn evaporation and precipitation) were associated with increased OSS abundance, which contradicts the overarching pattern of more arid conditions being associated with more OSS. Therefore, we hypothesize that OSS thrives when conditions are arid throughout the year with temporary releases from drought in autumn. Further research is needed to assess this hypothesis and elucidate the mechanisms underlying climate's influence on OSS.

Previous research has indicated that elevation is an important limiting factor for OSS (Crouch et al. 2021; Crouch 2023), but our study found that climate drives this relationship. Based on SEM, elevation did not have a significant direct effect on plot-level OSS abundance when climate was accounted for. Instead, climate variables had significant direct effects on OSS abundance and were significantly correlated with elevation. A clear elevation threshold was observed in our study, in which no OSS was found above 2545 m (Fig. 3.6a). However, thresholds were also observed for climate variables (Fig. 3.6b–f), indicating that there are clearly cooler, wetter climatic conditions which are currently unsuitable for OSS, and these conditions happen to coincide with elevation. We suspect that these thresholds, particularly the elevation threshold, will change as the climate continues to warm (Seager et al. 2007); however, repeated measurements of our study plots will be required to confirm this.

Given OSS's hypothesized role as a sleeper species and the strong influence of climate on OSS abundance, our study suggests that climate change most likely caused OSS population sizes to rapidly increase and to transition from an innocuous pest to a high-impact invasive species. We have shown that OSS is associated with more arid conditions, so we hypothesize that record drought over the past 10–20 years (Williams et al. 2022) caused OSS populations in Arizona to awaken. Climate is generally considered the most common cause of sleeper species awakenings (Bradley et al. 2018; Frank and Just 2020), although other possible explanations exist, such as completion of a mutualism, a food web change, evolution, or introduction of a new genetic strain (Lockwood et al. 2005; Borden and Flory 2021; Spear et al. 2021). Completion of a mutualism is unlikely because there are no documented mutualists associated with OSS (Griswold 1925; Miller and Davidson 2005), whereas the other three explanations are conceivable and represent fruitful areas for future research. For example, armored scale populations are susceptible to suppression by natural enemies (Edmunds 1973; Raupp et al. 2010; Frank 2020), so release from one or more natural enemies could have led to OSS population growth. Interestingly, climate change can cause such a release by creating asynchrony between phenology of scale insects and their natural enemies (Frank 2020). Research on OSS genetics is needed to determine whether evolution or introduction of a new genetic strain of OSS may have influenced awakening of OSS populations. Because of the strong relationship between climate and OSS, we have serious concerns that OSS populations in other areas will continue awakening with continued climate warming (Seager et al. 2007), as has recently been observed in Utah, Nevada, and Idaho (R. Davis, USDA Forest Service, personal communication).

In addition to climate, presence of recent fire also had a strong influence on OSS abundance. Fire strata was the third most important direct influence on OSS abundance based on SEM. Less recent fire resulted in significantly more OSS, suggesting that fire may be an important strategy for managing OSS. Of the 31 study plots that experienced fire in the two years prior to sampling, only two plots were infested with OSS, and in these plots rates of OSS infestation were low: 1.7% and 7.3%. In contrast, 40 of the 139 plots that had not experienced fire in the preceding 20 years were infested with OSS. Fire may be an important limiting factor for OSS because it kills OSS both directly and indirectly by killing hosts upon which OSS is dependent (Crouch et al. 2021). Aspen has thin bark, making it highly susceptible to fire mortality, so even low severity fire can kill overstory aspen (Jones and DeByle 1985; Stoddard et al. 2018) and, in turn, kill the OSS feeding on aspen. Alternatively, lack of OSS in areas of recent fire might simply be due to timing. It might take two or more years after a fire for stands of recruiting stems, which we know are susceptible to OSS infestation, to develop.

We also found that presence of ungulate management, which primarily consisted of fenced exclosures, resulted in significantly more OSS (Fig. 3.5). Although exclosures are highly effective at promoting aspen recruitment (Crouch 2023), this study supports previous findings that OSS is more common in areas of ungulate management (Crouch et al. 2021; Crouch 2023).

We hypothesize that ungulate exclosures promote OSS by directly increasing aspen density and, potentially, by indirectly reducing host vigor. Aspen stands inside exclosures may be unnaturally dense because no ungulate browse has occurred to reduce densities. Dense aspen stands not only provide more available host material and feeding sites for OSS but might also facilitate OSS spread. Increased stand densities inside exclosures might also reduce host vigor, thereby making aspen more susceptible to OSS. In support of this hypothesis, we found that aspen inside areas of ungulate management had significantly greater height-to-diameter ratios compared to aspen outside these areas. Dense stands produce stems with greater height-to-diameter ratios (i.e., increased slenderness) (Wang et al. 1998; Frey et al. 2004), likely because trees prioritize height growth over diameter growth to compete with their neighbors for light. We expect that this is especially true for shade-intolerant species such as aspen (Perala 1990). Frey et al. (2004) hypothesized that slender aspen in dense stands are more susceptible to stressors because they have more difficulty with hydraulic conductivity and may be more vulnerable to water stress and reduced photosynthesis as the stand naturally thins out. In our study, aspen with greater height-to-diameter ratios (i.e., taller, thinner stems) were significantly associated with increased OSS presence and severity (Table 3.6), indicating that slender stems with reduced vigor may be more susceptible to OSS. Research is needed to determine which of these mechanisms explains why more OSS is found inside ungulate exclosures.

Management Implications

OSS is already widespread in Arizona, so management tactics intended to eradicate this pest are unlikely to succeed. Eradication is further complicated by OSS's ability to infest an array of different host species and by the fact that small populations are exceedingly difficult to detect due to OSS's small size and cryptic coloring, which blends in well with aspen bark (Crouch et al. 2021). Instead of eradication, management should focus on suppressing OSS population sizes and mitigating damage to native ecosystems through integrated pest management. Critical to managing any invasive species is robust monitoring to assess the species' occurrence and impacts. Continued monitoring in areas of Arizona where OSS has not yet been found (e.g., southern Arizona, North Kaibab, and White Mountains) is necessary, as is continued monitoring of areas where OSS already occurs to document potential changes to the species' range (i.e., will OSS migrate to higher elevations in the future?). We also recommend monitoring of OSS in nursery stock of all host species, in urban areas that contain aspen, and in surrounding wildland aspen ecosystems, all of which may harbor sleeper populations of OSS (Frank and Just 2020). Our findings can help managers prioritize which aspen ecosystems to monitor. For example, OSS is most likely to occur on warmer, drier sites, in areas that have not recently experienced fire, and in stands that have dense recruitment, such as those inside fenced ungulate exclosures. Specifically, the climatic and elevation thresholds we identified (Fig. 3.6) can guide monitoring efforts. Although elevation is the easiest metric for managers to consider when searching for OSS, the 2545 m threshold is liable to change across aspen's expansive range. Instead, the climate thresholds are likely to be more consistent outside our study area, though we anticipate such climate-based thresholds will shift as warming continues. These climate data can be easily obtained via ClimateNA (https://climatena.ca/).

Our findings can also be used to guide management that seeks to suppress OSS populations and mitigate damage to aspen ecosystems. Our study indicates that three strategies might help to suppress OSS populations: (1) increasing application of fire at the landscape scale, (2) reducing reliance on ungulate exclosures, and (3) decreasing aspen stand density. Fire has a negative influence on OSS, and although frequency and size of wildfires will likely increase as climate warming continues (Seager et al. 2007; Singleton et al. 2019), managers may consider implementing prescribed fire to suppress OSS infestations in individual aspen stands. Frequent, low-severity fire may be detrimental to aspen stands, especially in the presence of chronic ungulate browse (Crouch et al. 2023), so fire should be implemented with caution and infrequency when managing for OSS. Advantages of fire as an OSS management strategy include low cost of implementation, the ability to kill OSS on multiple host species including understory plants, and the fact that fire is a natural component of aspen ecosystems (Crouch et al. 2021).

Another strategy managers may consider is reducing use of fenced ungulate exclosures. Reducing reliance on exclosures should help reduce OSS population sizes, although this will require finding other ways to overcome chronic ungulate browse that threatens aspen ecosystem resilience, adaptive capacity, and sustainability (Rogers 2017; Crouch 2023; Crouch et al. 2023). We speculate that ungulate exclosures might promote OSS abundance by creating unnaturally dense stands because no browsing has occurred to reduce stand density. These dense stands with abundant recruiting stems are the structure that seems most favorable for OSS population growth. However, it remains unclear whether the relationship between aspen stand density and OSS is due to increased host availability, facilitated spread among densely growing stems, and/or decreased host vigor in more slender stems. Further research is needed to determine how stand density and growth versus defense trade-offs influence aspen susceptibility to OSS at different spatial scales.

A third strategy managers may consider for suppressing OSS populations is reducing aspen stand densities via thinning. Thinning might also promote aspen resistance to drought, as reduced growth rates which occur in dense stands are associated with increased mortality during drought (Kane and Kolb 2014; Ireland et al. 2014, 2020; Crouch et al. 2023). However, thinning must be implemented with care in aspen stands because aspen is sensitive to mechanical damage from logging equipment and susceptible to subsequent infection by canker-causing fungi and decay diseases (Walters et al. 1982; Jones and Shepperd 1985). Another potential drawback to thinning is that sudden, direct exposure of aspen stems to sunlight may cause sunscald (Krasnow et al. 2012), creating potential infection courts for pathogens and leading to mortality. Before we can wholeheartedly recommend use of prescribed fire or silvicultural strategies like thinning to manage OSS, experimental research is needed to assess the efficacy of these strategies for suppressing OSS populations and mitigating damage to aspen ecosystems. Research is also needed to assess the efficacy of other forms of management, such as application of systemic insecticides, that will be critical components of an integrated pest management program for OSS.

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Tables

Table 3.1. List of 99 variables considered as potential influencing factors of plot-level oystershell scale (OSS) abundance. 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		
Aspen basal area[a]	10.3	0–55.9
All hosts basal area	10.3	0–55.9
Non-host basal area	10.2	0–78.1
Aspen overstory density[b]	172	0–1,194
Aspen sapling density	354	0–6,565
Aspen tall regeneration density	2,399	0–89,127
Aspen short regeneration density	8,694	0–136,873
All hosts overstory density	172	0–1,194
All hosts sapling density	356	0–6,565
All hosts tall regeneration density	2,460	0–89,127
All hosts short regeneration density	8,745	0–136,873
Non-host overstory density	115	0–945
Non-host sapling density	65	0–1,592
Non-host tall regeneration density	192	0–9,350
Non-host short regeneration density	1,394	0–33,224
Ungulates		
Browse[c]	0.30	0–1
Ungulate barking[c]	0.03	0–0.85
Total ungulate scat[d]	2.6	0–35
Elk (*Cervus canadensis*) scat	1.3	0–23
Deer (*Odocoileus hemionus* & *O. virginianus couesi*) scat	1.1	0–29
Cattle (*Bos taurus*) scat	0.3	0–20
Damaging agents[c]		
Sucking & gall-forming insects (excluding OSS)	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 *Valsa sordida*)	0.02	0–0.34
Hypoxylon canker (caused by *Entoleuca mammatum*)	0.002	0–0.10
Ceratocystis canker (caused by *Ceratocystis* spp.)	0.02	0–0.42
Sooty bark canker (caused by *Encoelia pruinosa*)	0.001	0–0.05
All cankers	0.33	0–1
Foliar & 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 & barking)	0.01	0–0.15

Influencing factor	Mean	Range
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/yr)	0.98	0.71–1.08
Radiation (MJ/cm^2/yr)	0.96	0.64–1.09
Major area[k]	1 (3.6%), 2 (51.8%), 3 (6.4%), 4 (9.1%), 5 (8.2%), 6 (11.8%), 7 (11.4%)	
UTM easting	453804	358542–674303
UTM northing	3880092	3589116–4052723
Soils		
Soil order[l]	1 (2.7%), 2 (14.1%), 3 (13.2%), 4 (70.0%)	
Soil pH in H_2O (pHx10)	63.4	55.4–71.4
Cation exchange capacity (CEC) (mmol(c)/kg at pH 7)	232.9	176.3–272.15
Nitrogen (cg/kg)	110.0	80.0–188.3
Soil organic carbon content (dg/kg)	135.2	93.8–193.9
Bulk density (cg/cm^3)	147.5	130.1–157.8
Sand content (g/kg)	321.7	187.5–592
Clay content (g/kg)	269.1	129.7–397.7
Volumetric fraction of coarse fragments (cm^3/dm^3)	179.2	75.2–293.0
Climate		
Degree-days below 0°C	323.9	109.0–596.0
Degree-days above 5°C	1883	1215–2819
Degree-days below 18°C	3823	2656–4842
Degree-days above 18°C	137.1	24.5–389.0
Degree-days above 10°C and below 40°C	909.0	464.5–1521.0
Number of frost-free days	181.2	140.5–265.5
Frost-free period	113.4	78.0–185.0
Winter temperature (maximum)[m]	6.0	2.5–10.6
Spring temperature (maximum)	13.8	10.7–17.8
Summer temperature (maximum)	25.3	21.2–29.1
Autumn temperature (maximum)	16.6	13.3–20.3
Winter temperature (minimum)	-7.6	-10.8– -2.2

Influencing factor	Mean	Range
Spring temperature (minimum)	-1.2	-4.4–3.7
Summer temperature (minimum)	9.1	6.5–14.0
Autumn temperature (minimum)	0.8	-1.7–6.2
Winter temperature (mean)	-0.8	-4.2-3.9
Spring temperature (mean)	6.3	3.2–10.4
Summer temperature (mean)	17.2	13.9–21.1
Autumn temperature (mean)	8.7	5.8–12.4
Precipitation as snow (annual)[n]	135.8	29.5–332.0
Winter precipitation[n]	211.3	83.5–516.5
Spring precipitation	148.8	66.5–240.0
Summer precipitation	147.8	64.5–292.5
Autumn precipitation	130.5	62.5–366.0
Winter relative humidity[o]	51.0	44.5–70.5
Spring relative humidity	51.7	47.0–66.0
Summer relative humidity	53.0	47.0–63.0
Autumn relative humidity	50.8	43.0–66.0
Winter Hargreaves reference evaporation[n]	30.0	0–125.5
Spring Hargreaves reference evaporation	272.1	192.5–323.0
Summer Hargreaves reference evaporation	463.1	396.5–535.0
Autumn Hargreaves reference evaporation	224.1	193.5–263.0
Winter climatic moisture deficit (CMD)[n]	6.2	0–26.0
Spring climatic moisture deficit (CMD)	163.6	117.0–216.0
Summer climatic moisture deficit (CMD)	325.6	177.0–461.5
Autumn climatic moisture deficit (CMD)	139.2	57.5–199.0
Winter climate moisture index (CMI)[n]	18.5	5.6–42.7
Spring climate moisture index (CMI)	-3.2	-14.7–9.6
Summer climate moisture index (CMI)	-29.9	-48.3– -7.3
Autumn climate moisture index (CMI)	-11.0	-21.8–15.2
Annual dryness index[p]	0.07	0.04–0.12
Annual heat moisture index[q]	31.8	18.1–49.8
Summer heat moisture index[r]	118.8	45.1–242.4

[a] basal area = m^2 ha^{-1}

[b] density = trees ha^{-1}

[c] proportion of aspen stems affected by damaging agent

[d] scat = pellet piles/plot

[e] categorical: 1 (0-2 yrs since fire), 2 (2-20 yrs since fire), 3 (> 20 yrs since fire)

[f] categorical: 1 (unburned in past 20 yrs), 2 (unburned/low), 3 (low), 4 (moderate), 5 (high)

[g] categorical: 0 (burned < 2 times in past 20 yrs), 1 (burned twice in past 20 yrs)

[h] categorical: 0 (no ungulate management), 1 (exclosure or jackstraw)

[i] categorical: 0 (no treatment), 1 (conifer removal)

[j] 0–2 (0 = 225°, 1 = 135° or 315°, 2 = 45°)

[k] categorical: 1 (Coronado), 2 (Flagstaff), 3 (Mogollon Rim), 4 (North Kaibab), 5 (Prescott), 6 (South Kaibab), 7 (White Mountains)

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[l] categorical: 1 (Inceptisols), 2 (Mollisols – Borolls), 3 (Mollisols – Ustolls), 4 (Alfisols)

[m] temperature = °C

[n] precipitation, evaporation, CMD, CMI = mm

[o] relative humidity = %

[p] annual dryness index = annual degree days above 5°C ÷ annual precipitation

[q] annual heat moisture index = (annual temperature + 10) ÷ (annual precipitation ÷ 1000)

[r] summer heat moisture index = warmest month temperature ÷ (summer precipitation ÷ 1000)

Seasons for climate variables are winter (December – February), spring (March – May), summer (June – August), autumn (September – November).

Table 3.2. Means and standard errors of variables representing dead aspen basal area, dead aspen density in different stem size classes, live aspen crown ratio and dieback, and OSS presence and severity. For categorical variables, percentage of plots in each level are shown.

Variable	**Mean**	**Std error**
Dead aspen basal area (m^2 ha^{-1})	4.3	0.4
Total dead aspen density (trees ha^{-1})	4,450.5	704.2
Dead aspen short regeneration density (trees ha^{-1})	3,420.9	674.6
Dead aspen tall regeneration density (trees ha^{-1})	796.7	126.6
Dead aspen sapling density (trees ha^{-1})	165.5	42.6
Dead aspen overstory density (trees ha^{-1})	67.4	8.6
Aspen crown ratio (%)	52.0	0.5
Aspen crown dieback (categorical)		
0% dieback	34.2	0.5
1–33% dieback	44.5	0.5
34–67% dieback	13.9	0.3
68–99% dieback	7.5	0.3
OSS presence (categorical)		
OSS absent	89.3	0.3
OSS present	10.7	0.3
OSS severity (%)	1.2	< 0.1

Table 3.3. Univariate relationships between two measures of aspen stem health (crown ratio and dieback) and OSS presence and severity at the tree level.

Response	**Predictor**	**Coefficient**	**Std error**	***p* value**	**Marginal R^2**
Aspen crown ratio (%)	OSS presence[a]	-9.83	1.25	< 0.001	0.012
Aspen crown ratio (%)	OSS severity (%)	-38.87	4.33	< 0.001	0.009
Aspen crown dieback[b]	OSS presence[a]	0.52	0.04	< 0.001	0.031
Aspen crown dieback[b]	OSS severity (%)	2.06	0.14	< 0.001	0.024

These relationships are based on linear mixed models. Marginal R^2 is based solely on the model's fixed effects, which were either OSS presence or severity.

[a] 0–1 (0 = OSS absent, 1 = OSS present)

[b] 0–3 (0 = 0% dieback, 1 = 1–33% dieback, 2 = 34–67% dieback, 3 = 68–99% dieback)

Table 3.4. Univariate relationships between six measures of dead aspen density and plot-level OSS abundance (i.e., proportion of stems infested by OSS). These models were fit using data only from the 64 study plots in which OSS was present.

Response	**Predictor**	**Coefficient**	**Std error**	***p* value**	**Marginal R^2**
Dead aspen basal area[a]	OSS (%)	5.74	2.35	0.019	0.108
Total dead aspen[b]	OSS (%)	1029.67	1644.03	0.535	0.005
Dead aspen short regeneration[b]	OSS (%)	-646.59	961.49	0.505	0.005
Dead aspen tall regeneration[b]	OSS (%)	1654.33	834.21	0.054	0.076
Dead aspen saplings[b]	OSS (%)	532.32	275.75	0.061	0.070
Dead overstory aspen[b]	OSS (%)	33.15	35.04	0.350	0.015

These relationships are based on linear mixed models. Marginal R^2 is based solely on the model's fixed effect, which was plot-level OSS abundance.

[a] $m^2\ ha^{-1}$

[b] trees ha^{-1}

Table 3.5. Top 25 most important variables influencing plot-level OSS abundance based on 50 random forest runs, each of which was built using 2000 trees. Univariate relationships between influencing factors and OSS abundance were based on linear mixed models. See Table 3.1 for list of all influencing factors considered.

Random forests		**Univariate regressions**		
Rank	**Influencing factor**	**Coefficient**	**Marginal R^2**	***p* value**
1	autumn evaporation	-0.003	0.014	0.195
2	elevation	< -0.001	0.263	< 0.001
3	degree-days 10–40°C	< 0.001	0.197	0.003
4	winter CMI	0.005	0.015	0.302
5	autumn precipitation	0.002	0.168	0.002
6	winter evaporation	0.006	0.413	< 0.001
7	winter temp (max)	0.120	0.428	< 0.001
8	wood boring insects	0.121	0.007	0.034
9	winter precipitation	< -0.001	0.002	0.755
10	clay	< 0.001	0.003	0.638
11	degree-days < 0°C	-0.001	0.190	0.003
12	snow	-0.002	0.146	0.001
13	spring temp (max)	0.105	0.301	< 0.001
14	spring CMD	0.004	0.109	0.002
15	spring evaporation	0.002	0.037	0.085
16	aspen saplings ha^{-1}	< 0.001	0.018	0.001
17	host saplings ha^{-1}	< 0.001	0.018	0.001
18	degree-days > 5°C	< 0.001	0.198	0.003
19	spring temp (min)	0.071	0.210	0.004
20	host regeneration ha^{-1}	< -0.001	< 0.001	0.455
21	UTM easting	< -0.001	0.088	0.170
22	other animal damage	0.070	< 0.001	0.891
23	summer temp (mean)	0.068	0.174	0.005
24	aspen regeneration ha^{-1}	< -0.001	< 0.001	0.458
25	fire severity	-0.014	0.003	0.463

Marginal R^2 is based solely on the model's fixed effect, which was the influencing factor shown in each row.

Table 3.6. Univariate relationships between tree-level OSS presence and severity and four measures of aspen stem size (size class, height, dbh, and height-to-diameter ratio).

Response	**Predictor**		**Coefficient**	**Std error**	***p* value**	**Marginal R^2**
OSS presence [a]	size class	SR	-12.246 c	1.936	< 0.001	0.014
		TR	1.752 b	0.189	< 0.001	
		S	2.905 a	0.279	< 0.001	
		O	2.904 a	0.280	< 0.001	
OSS severity (%)	size class	SR	0.010 c	0.008	0.239	0.021
		TR	0.027 a	0.002	< 0.001	
		S	0.035 a	0.004	< 0.001	
		O	0.011 b	0.003	< 0.001	
OSS presence[a]	height (m)		0.006	0.001	< 0.001	0.004
OSS severity (%)	height (m)		0.001	< 0.001	< 0.001	0.002
OSS presence[a]	dbh (cm)		-0.003	0.001	< 0.001	0.005
OSS severity (%)	dbh (cm)		-0.001	< 0.001	< 0.001	0.012
OSS presence[a]	height:diameter (m)		0.458	0.166	0.006	0.001
OSS severity (%)	height:diameter (m)		0.114	0.056	0.042	0.001

These relationships are based on linear mixed models. Aspen size class abbreviations: SR (short regeneration, < 1.37 m tall), TR (tall regeneration, > 1.37 m tall and < 5.1 cm dbh), S (saplings, 5.1–12.7 cm dbh), O (overstory trees, > 12.7 cm dbh). Different letters after coefficients indicate significant differences among size classes based on post-hoc Tukey-adjusted pairwise comparisons. Marginal R^2 is based solely on the model's fixed effects, which was aspen size class, height, dbh, or height-to-diameter ratio.

[a] 0–1 (0 = OSS absent, 1 = OSS present)

Figures

Figure 3.1. Photo of young aspen stand inside of an exclosure experiencing high levels of dieback and mortality from oystershell scale (OSS). Photos on the right show close-ups of OSS on aspen.

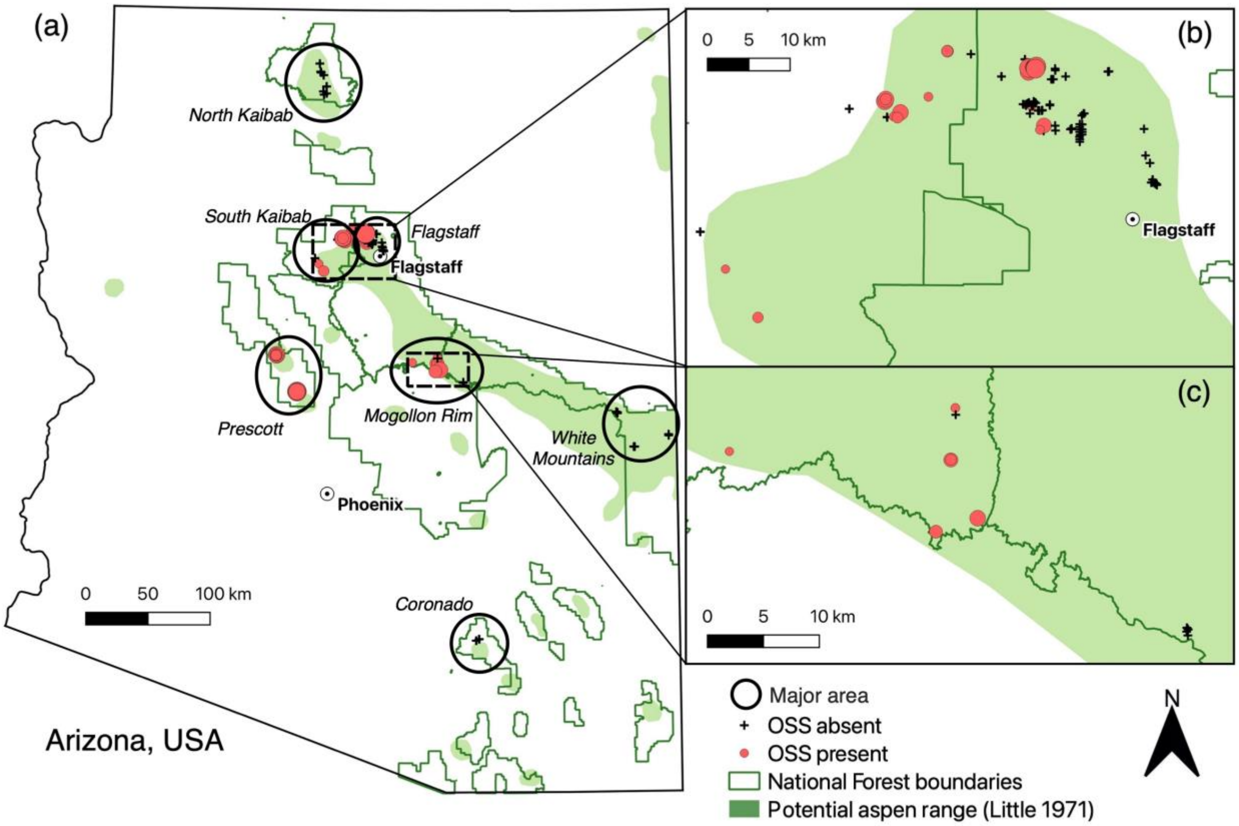

Figure 3.2. Maps showing absence, presence, and abundance of OSS in (a) 220 study plots across seven major areas (*in italics*) where aspen occurs in Arizona, USA, (b) study plots in the South Kaibab (left of green National Forest boundary line) and Flagstaff major areas (right of green line), and (c) study plots along the Mogollon Rim. These three areas are the only ones where OSS presence varied. OSS was present in all plots around Prescott and was absent in all plots in the North Kaibab, White Mountains, and Coronado.

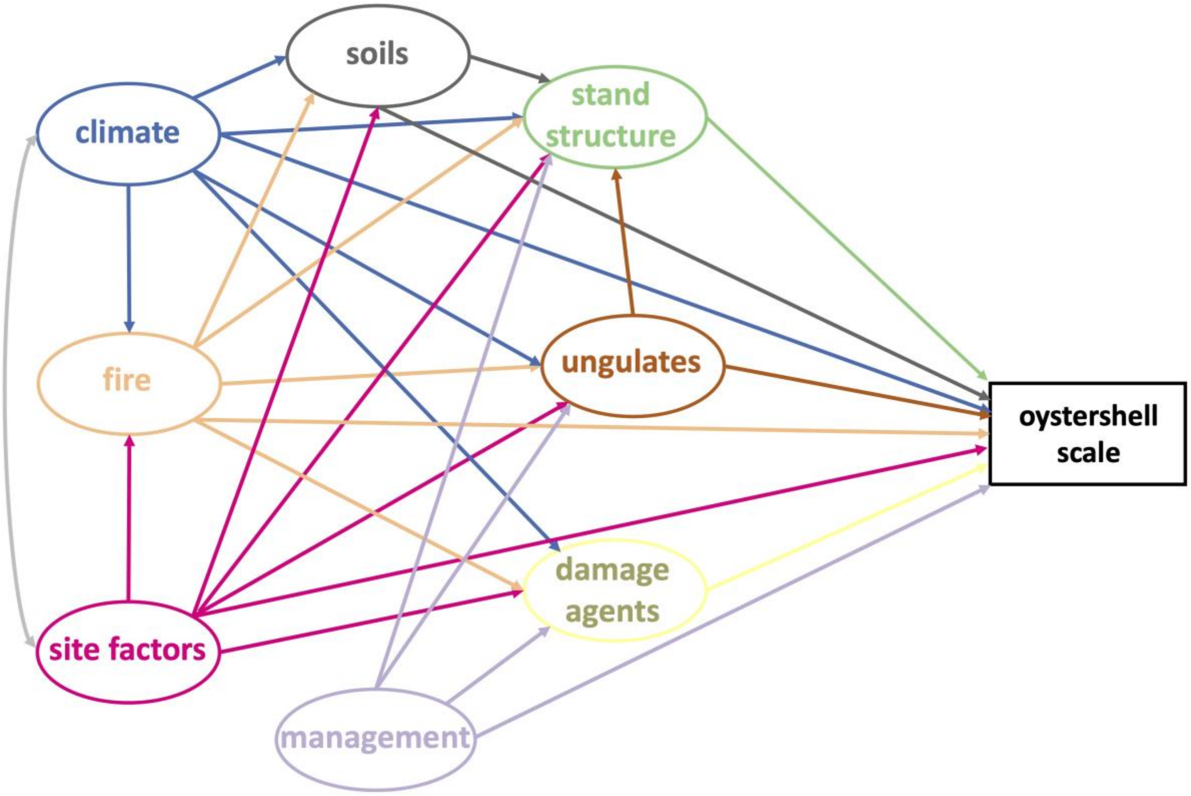

Figure 3.3. *A priori* structural equation model (SEM) illustrating hypothesized directional relationships among influencing factors and plot-level OSS abundance. Arrows indicate causal relationships, and colors correspond to each of the eight categories of influencing factors. See Table 3.1 for complete list of measured variables included in each of these eight categories.

Figure 3.4. OSS severity across four aspen stem size classes. Data shown were taken only from the 64 study plots in which OSS was observed and include only live trees. OSS severity was assessed using the rating system devised by Crouch et al. (2021), which rates OSS severity on each tree from ground level to 6 m. Each tree's stem up to 6 m is divided into thirds, and severity is rated for each 2 m section (or shorter for trees < 6 m tall) on both the north and south sides of the tree. The ratings are as follows: light (no OSS present), trace (only a handful of OSS present), light (OSS covers < 50% of section), severe (OSS covers > 50% of section).

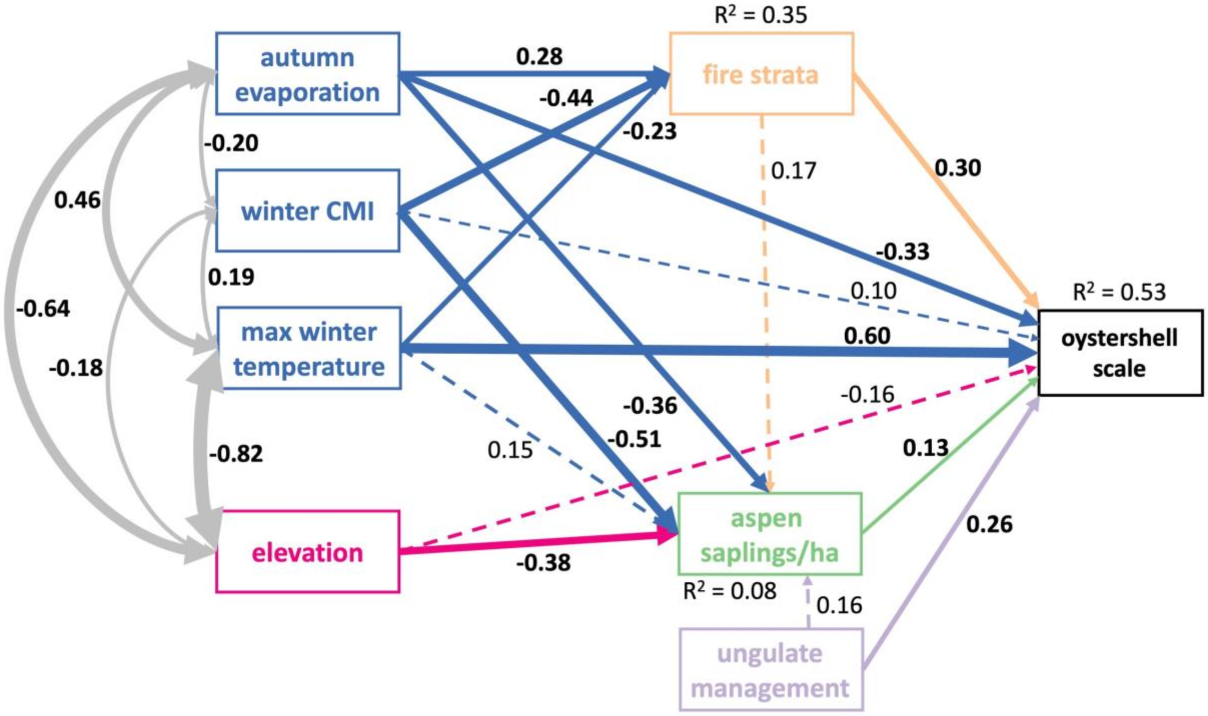

Figure 3.5. Optimal SEM for OSS abundance that minimized AIC and maximized response R^2. Significant ($p < 0.05$) path coefficients are shown in bold, and their corresponding paths are depicted as solid lines. In contrast, insignificant coefficients are not bolded, and their corresponding paths are shown as dashed lines. Path thickness indicates strength of its coefficient, with wider paths indicating stronger relationships.

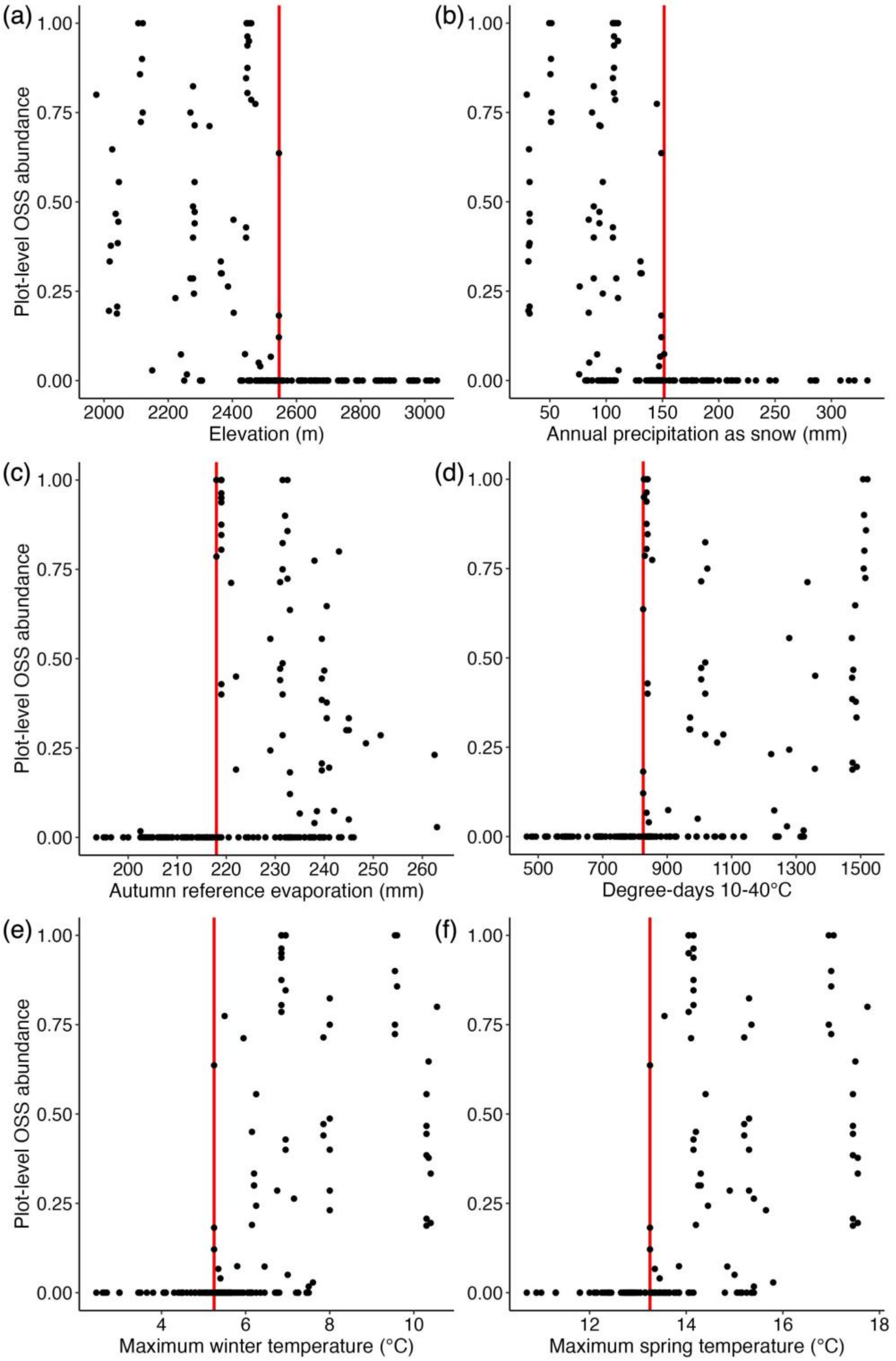

Figure 3.6. Relationships between plot-level OSS abundance and (a) elevation, (b) snowfall, (c) autumn evaporation, (d) degree-days above 10°C and below 40°C, (e) maximum winter temperature, and (f) maximum spring temperature. Red lines indicate thresholds above or below which OSS does not occur in aspen ecosystems in Arizona.

Supplementary Material

Appendix 3.1. Means and standard errors for the 92 continuous variables considered as potential influencing factors of plot-level OSS abundance, summarized across each of the seven major areas in our study.

	Mean (standard error)						
Influencing factor	**North Kaibab**	**South Kaibab**	**Flagstaff**	**Prescott**	**Mogollon Rim**	**White Mountains**	**Coronado**
Stand structure							
Aspen basal area[a]	4.2 (4.2)	6.4 (9.7)	13.0 (13.5)	8.8 (11.6)	3.0 (7.2)	11.1 (10.7)	11.4 (20.2)
All hosts basal area	4.2 (4.2)	6.4 (9.7)	13.0 (13.5)	9.0 (11.7)	3.0 (7.2)	11.1 (10.7)	11.4 (20.2)
Non-host basal area	12.0 (14.2)	7.6 (9.1)	9.8 (15.5)	4.4 (4.7)	12.5 (10.8)	13.5 (17.0)	19.7 (25.9)
Aspen overstory density[b]	28.8 (41.7)	105.2 (167.2)	213.9 (275.6)	73.1 (98.1)	126.3 (303.6)	282.5 (304.5)	63.9 (110.1)
Aspen sapling density	586.4 (890.9)	76.5 (203.5)	468.3 (1,063)	479.8 (867.3)	91.8 (276.8)	95.5 (223.3)	0.0 (0.0)
Aspen tall regeneration density	4,419 (7,335)	1,018 (1,858)	1,924 (9,285)	3,885 (4,868)	244.9 (521.0)	4,456 (11,177)	2,757 (5,284)
Aspen short regeneration density	8,471 (13,683)	6,802 (7,215)	9,164 (20,734)	3,242 (2,107)	9,427 (4,314)	8,220 (20,026)	22,310 (14,194)
All hosts overstory density	28.8 (41.7)	105.2 (167.2)	213.9 (275.6)	73.1 (98.1)	126.3 (303.6)	282.5 (304.5)	63.9 () (110.1)
All hosts sapling density	586.4 (890.9)	76.5 (203.5)	468.3 (1,063)	514.9 (892.6)	91.8 (276.8)	95.5 (223.3)	0.0 (0.0)
All hosts tall regeneration density	4,419 (7,335)	1,018 (1,858)	1,924 (9,285)	4,669 (4,822)	244.9 (521.0)	4,456 (11,177)	2,757 (5,284)
All hosts short regeneration density	8,471 (13,683)	6,802 (7,215)	9,164 (20,734)	3,909 (2,421)	9,427 (4,314)	8,220 (20,026)	22,310 (14,194)
Non-host overstory density	188.5 (238.3)	74.6 (99.7)	110.9 (170.9)	58.5 (66.3)	118.6 (145.8)	147.2 (180.7)	156.3 (207.9)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Non-host sapling density	167.5 (370.8)	76.5 (169.5)	37.0 (111.4)	46.8 (111.9)	107.1 (208.9)	87.5 (230.3)	85.3 (156.5)
Non-host tall regeneration density	293.2 (575.7)	191.3 (451.8)	40.5 (157.6)	1,029 (2,346)	168.3 (352.6)	127.3 (344.0)	596.8 (961.0)
Non-host short regeneration density	3,958 (8,123)	1,224 (2,314)	498.2 (1,454)	1,720 (2,765)	3,015 (4,526)	1,384 (5,698)	5,741 (8,153)
Ungulates							
Browse[c]	0.37 (0.28)	0.32 (0.35)	0.30 (0.34)	0.25 (0.20)	0.25 (0.26)	0.33 (0.24)	0.28 (0.30)
Ungulate barking[c]	0.00 (0.01)	0.06 (0.17)	0.03 (0.10)	0.00 (0.00)	0.06 (0.15)	0.00 (0.02)	0.00 (0.00)
Total ungulate scat[d]	8.4 (9.6)	3.0 (5.5)	1.1 (3.0)	0.4 (0.7)	3.1 (5.0)	6.0 (3.6)	3.0 (3.9)
Elk scat	0.0 (0.0)	2.8 (5.5)	0.4 (1.0)	0.0 (0.0)	3.1 (5.0)	5.0 (3.7)	0.0 (0.0)
Deer scat	8.0 (8.7)	0.2 (0.5)	0.3 (0.8)	0.4 (0.7)	0.0 (0.0)	0.6 (1.0)	3.0 (3.9)
Cattle scat	0.4 (1.4)	0.0 (0.0)	0.4 (2.3)	0.0 (0.0)	0.0 (0.0)	0.3 (0.7)	0.0 (0.0)
Damaging agents[c]							
Sucking & gall-forming insects	0.16 (0.14)	0.05 (0.08)	0.07 (0.13)	0.09 (0.09)	0.16 (0.26)	0.11 (0.20)	0.08 (0.10)
Bark beetles	0.00 (0.01)	0.00 (0.01)	0.01 (0.03)	0.00 (0.00)	0.00 (0.00)	0.02 (0.05)	0.00 (0.00)
Wood-boring insects	0.48 (0.24)	0.24 (0.21)	0.17 (0.19)	0.30 (0.17)	0.16 (0.20)	0.24 (0.19)	0.03 (0.04)
Defoliating insects	0.60 (0.19)	0.56 (0.21)	0.55 (0.31)	0.61 (0.24)	0.68 (0.15)	0.75 (0.17)	0.85 (0.15)
Cytospora canker	0.01 (0.02)	0.03 (0.07)	0.02 (0.04)	0.03 (0.04)	0.02 (0.04)	0.03 (0.07)	0.00 (0.00)
Hypoxylon canker	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.00)	0.01 (0.02)	0.00 (0.00)
Ceratocystis canker	0.04 (0.05)	0.00 (0.02)	0.01 (0.03)	0.02 (0.02)	0.01 (0.03)	0.08 (0.10)	0.00 (0.01)
Sooty bark canker	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)
All cankers	0.53 (0.14)	0.32 (0.24)	0.34 (0.26)	0.09 (0.11)	0.11 (0.16)	0.54 (0.19)	0.03 (0.05)
Foliar & shoot diseases	0.18 (0.14)	0.24 (0.19)	0.18 (0.27)	0.06 (0.08)	0.19 (0.13)	0.14 (0.13)	0.74 (0.18)
Decay diseases	0.01 (0.04)	0.02 (0.04)	0.05 (0.11)	0.05 (0.06)	0.00 (0.00)	0.03 (0.05)	0.00 (0.01)
Abiotic damage	0.00 (0.01)	0.01 (0.03)	0.02 (0.07)	0.02 (0.04)	0.01 (0.01)	0.00 (0.01)	0.00 (0.01)
Other animal damage	0.01 (0.04)	0.01 (0.02)	0.01 (0.02)	0.00 (0.00)	0.00 (0.00)	0.01 (0.02)	0.00 (0.00)
Site factors							
Elevation (m above sea level)	2697 (67)	2393 (139)	2582 (159)	2059 (46)	2305 (51)	2853 (119)	2582 (159)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Aspect[e]	0.75 (0.66)	1.21 (0.65)	0.87 (0.71)	1.71 (0.35)	0.77 (0.74)	0.78 (0.76)	1.79 (0.20)
Slope (°)	4.9 (4.5)	11.6 (10.0)	8.0 (7.2)	7.1 (4.3)	2.7 (3.0)	7.0 (2.5)	16.3 (7.4)
Heat load (MJ/cm^2/yr)	0.99 (0.02)	0.96 (0.07)	0.98 (0.08)	0.95 (0.03)	1.00 (0.03)	1.00 (0.05)	0.87 (0.10)
Radiation (MJ/cm^2/yr)	0.99 (0.04)	0.92 (0.12)	0.96 (0.08)	0.94 (0.05)	1.00 (0.01)	1.00 (0.04)	0.84 (0.09)
UTM easting	396422 (1886)	410677 (8727)	434335 (5411)	364491 (8218)	494638 (13092)	650996 (18608)	520833 (1262)
UTM northing	4039131 (8562)	3909453 (7935)	3910738 (4513)	3807999 (14347)	3805194 (7929)	3759419 (11454)	3589789 (621)
Soils							
Soil pH in H_2O (pHx10)	65.6 (4.3)	65.3 (2.6)	63.0 (1.7)	63.2 (2.1)	62.4 (1.7)	64.0 (1.1)	57.0 (1.7)
CEC (mmol(c)/kg at pH 7)	205.9 (9.7)	241.2 (12.1)	235.1 (7.5)	178.7 (2.6)	254.0 (9.4)	263.3 (6.0)	223.5 (20.7)
Nitrogen (cg/kg)	97.4 (12.2)	96.6 (16.3)	105.3 (13.8)	133.6 (36.8)	108.7 (14.3)	123.6 (16.7)	166.0 (21.2)
Soil organic carbon (dg/kg)	126.9 (6.8)	125.8 (20.6)	138.2 (21.5)	118.8 (28.5)	115.9 (15.1)	156.0 (18.8)	144.0 (12.4)
Bulk density (cg/cm^3)	149.0 (3.2)	151.7 (4.0)	148.0 (4.1)	150.0 (6.1)	151.7 (5.2)	140.3 (2.9)	132.1 (2.0)
Sand content (g/kg)	413.0 (9.2)	240.2 (28.8)	298.2 (57.8)	407.0 (66.7)	253.9 (25.6)	352.0 (68.2)	565.6 (25.7)
Clay content (g/kg)	265.1 (10.8)	336.7 (27.3)	255.7 (24.1)	302.1 (51.4)	357.1 (32.4)	226.6 (36.6)	153.8 (22.6)
Coarse fragments (cm^3/dm^3)	170.2 (38.2)	146.0 (60.9)	166.0 (63.1)	188.4 (30.9)	188.4 (36.3)	247.0 (19.5)	258.3 (20.3)
Climate							
Degree-days below 0°C	332.2 (20.4)	285.4 (41.1)	389.9 (63.3)	112.6 (1.2)	168.6 (20.4)	323.3 (53.2)	181.6 (36.8)
Degree-days above 5°C	2,039 (77.9)	1,987 (152.8)	1,670 (148.8)	2,783 (22.6)	2,478 (67.2)	1,595 (125.2)	2,255 (241.9)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Degree-days below 18°C	3,745 (91.7)	3,679 (194.5)	4,121 (225.0)	2,685 (12.5)	3,057 (98.9)	4,031 (210.2)	3,196 (271.3)
Degree-days above 18°C	185.7 (5.8)	159.6 (10.2)	88.6 (6.0)	373.8 (5.9)	288.4 (14.2)	46.9 (15.2)	171.5 (11.3)
Degree-days 10 – 40°C	1,059 (56.2)	990.1 (105.9)	773.9 (103.1)	1,493 (18.1)	1,307 (40.1)	662.4 (74.8)	1,106 (168.5)
Number of frost-free days	190.4 (5.8)	174.6 (10.2)	159.2 (6.0)	255.2 (5.9)	249.2 (14.2)	178.9 (15.2)	237.7 (11.3)
Frost-free period	133.1 (6.2)	108.4 (9.3)	93.7 (4.7)	173.9 (5.4)	173.7 (12.1)	107.7 (16.0)	158.2 (10.0)
Winter temperature (max)[f]	5.1 (0.3)	7.0 (0.9)	5.3 (1.1)	10.1 (0.4)	6.8 (0.7)	5.9 (0.5)	6.5 (0.9)
Spring temperature (max)	13.2 (0.3)	14.7 (0.8)	13.2 (0.8)	17.3 (0.3)	14.8 (0.5)	12.9 (0.7)	14.5 (1.1)
Summer temperature (max)	25.5 (0.3)	26.7 (0.8)	24.7 (1.3)	28.2 (0.1)	26.2 (0.3)	22.2 (0.7)	23.6 (1.2)
Autumn temperature (max)	16.5 (0.3)	18.0 (0.9)	16.1 (1.3)	18.9 (0.3)	17.2 (1.0)	15.6 (0.7)	17.2 (1.1)
Winter temperature (min)	-7.3 (0.3)	-7.3 (0.7)	-8.4 (0.6)	-2.2 (0.4)	-2.8 (1.1)	-7.9 (1.2)	-3.2 (0.6)
Spring temperature (min)	-0.9 (0.5)	-1.4 (0.6)	-2.4 (0.7)	3.1 (0.4)	3.0 (0.7)	-1.6 (0.9)	1.4 (0.8)
Summer temperature (min)	11.2 (0.4)	8.8 (0.6)	7.8 (0.4)	13.5 (0.3)	13.1 (0.6)	8.1 (0.7)	11.8 (0.9)
Autumn temperature (min)	1.8 (0.4)	0.4 (0.7)	-0.7 (0.3)	5.6 (0.3)	5.3 (0.9)	0.8 (1.0)	5.6 (0.7)
Winter temperature (mean)	-1.1 (0.2)	0.1 (0.7)	-1.3 (0.9)	4.0 (0.0)	2.3 (0.5)	-0.9 (0.7)	2.3 (0.7)
Spring temperature (mean)	5.9 (0.3)	6.8 (0.7)	5.6 (0.8)	10.5 (0.1)	9.1 (0.3)	5.5 (0.7)	8.5 (0.9)
Summer temperature (mean)	18.2 (0.4)	17.7 (0.7)	16.2 (0.9)	21.0 (0.1)	19.7 (0.2)	14.9 (0.5)	17.6 (1.0)
Autumn temperature (mean)	8.6 (0.3)	9.2 (0.7)	7.7 (0.8)	12.8 (0.1)	11.5 (0.4)	7.8 (0.6)	11.2 (0.9)
Precipitation as snow (annual)[g]	152.7 (24.5)	93.6 (20.3)	151.6 (73.0)	29.0 (7.6)	66.8 (3.5)	131.3 (53.3)	83.2 (29.9)
Winter precipitation[e]	208.7 (24.9)	211.2 (26.0)	226.8 (50.5)	274.0 (76.3)	357.7 (52.2)	228.6 (44.1)	397.4 (20.7)
Spring precipitation	165.1 (7.0)	122.0 (11.9)	135.4 (23.8)	123.0 (14.4)	134.7 (19.4)	97.1 (26.4)	104.1 (5.5)

Influencing factor	**North Kaibab**	**South Kaibab**	**Flagstaff**	**Prescott**	**Mogollon Rim**	**White Mountains**	**Coronado**
Summer precipitation	111.1 (4.5)	160.6 (11.0)	175.2 (13.9)	259.6 (13.9)	261.9 (32.7)	230.7 (25.4)	345.9 (27.2)
Autumn precipitation	84.6 (2.7)	113.3 (12.9)	111.2 (20.6)	188.4 (21.7)	228.3 (55.3)	153.9 (13.6)	232.9 (12.3)
Winter relative humidity[h]	53.0 (0.6)	48.2 (1.7)	48.8 (1.3)	56.9 (2.6)	64.1 (4.0)	48.5 (4.0)	62.9 (0.5)
Spring relative humidity	53.9 (1.0)	49.0 (0.9)	49.6 (1.0)	55.8 (1.9)	62.2 (2.7)	52.7 (2.5)	57.8 (0.7)
Summer relative humidity	57.1 (0.6)	48.2 (1.0)	50.2 (2.4)	57.7 (1.0)	60.7 (2.6)	57.3 (2.5)	62.4 (0.5)
Autumn relative humidity	53.7 (0.6)	46.1 (1.8)	47.5 (2.9)	58.6 (1.6)	62.4 (4.3)	53.2 (3.8)	63.4 (1.1)
Winter reference evaporation[g]	0.0 (0.0)	46.3 (26.9)	13.3 (15.6)	121.7 (3.1)	86.8 (3.4)	0.0 (0.0)	98.4 (13.9)
Spring reference evaporation	259.2 (13.3)	291.8 (10.0)	264.7 (23.7)	314.8 (5.9)	275.0 (8.6)	260.4 (20.9)	287.6 (14.2)
Summer reference evaporation	454.0 (3.4)	500.8 (14.6)	465.9 (25.4)	490.4 (5.0)	457.1 (12.8)	413.0 (15.8)	426.0 (18.2)
Autumn reference evaporation	213.9 (1.5)	240.9 (9.6)	222.3 (13.8)	237.4 (4.1)	217.0 (13.9)	217.0 (9.4)	224.3 (10.7)
Winter CMD[g]	0.0 (0.0)	11.5 (8.2)	5.9 (7.2)	21.3 (6.1)	3.5 (2.6)	0.0 (0.0)	0.0 (0.0)
Spring CMD	178.7 (3.9)	170.4 (21.7)	147.5 (14.7)	206.3 (7.5)	159.2 (14.5)	186.1 (24.8)	182.0 (12.5)
Summer CMD	355.5 (5.7)	393.1 (45.9)	353.9 (57.8)	260.6 (2.9)	281.0 (61.0)	204.8 (26.6)	209.4 (27.0)
Autumn CMD	150.3 (2.5)	169.4 (23.0)	154.5 (31.0)	100.6 (5.0)	103.8 (31.5)	79.8 (18.9)	121.7 (7.2)
Winter CMI[g]	17.4 (2.6)	15.6 (2.2)	18.7 (5.5)	17.8 (8.0)	29.0 (5.5)	18.3 (4.8)	31.9 (3.1)
Spring CMI	0.2 (1.0)	-8.2 (1.9)	-3.4 (4.3)	-13.1 (2.1)	-7.0 (2.5)	-6.4 (3.7)	-10.9 (2.7)
Summer CMI	-33.0 (0.7)	-33.2 (2.3)	-26.5 (4.0)	-21.4 (1.0)	-16.0 (4.8)	-14.1 (3.7)	-1.7 (5.0)
Autumn CMI	-14.0 (0.6)	-15.3 (1.8)	-11.4 (3.9)	-9.6 (2.8)	-1.2 (6.6)	-5.5 (2.1)	-0.1 (3.1)
Annual dryness index[i]	0.08 (0.01)	0.07 (0.01)	0.06 (0.01)	0.06 (0.01)	0.05 (0.01)	0.06 (0.01)	0.04 (0.01)
Annual heat moisture index[j]	44.3 (3.1)	35.3 (4.6)	33.1 (7.1)	24.2 (2.4)	23.6 (5.8)	25.5 (4.9)	20.8 (2.2)

Influencing factor	North Kaibab	South Kaibab	Flagstaff	Prescott	Mogollon Rim	White Mountains	Coronado
Summer heat moisture index[k]	224.3 (8.6)	143.6 (34.5)	124.6 (35.0)	61.1 (0.7)	83.8 (28.2)	56.9 (9.1)	72.0 (9.4)

[a] basal area = $m^2\ ha^{-1}$

[b] density = trees ha^{-1}

[c] proportion of aspen stems affected by damaging agent

[d] scat = pellet piles/plot

[e] 0–2 (0 = 225°, 1 = 135° or 315°, 2 = 45°)

[f] temperature = °C

[g] precipitation, evaporation, CMD, CMI = mm

[h] relative humidity = %

[i] annual dryness index = annual degree days above 5°C ÷ annual precipitation

[j] annual heat moisture index = (annual temperature + 10) ÷ (annual precipitation ÷ 1000)

[k] summer heat moisture index = warmest month temperature ÷ (summer precipitation ÷ 1000)

Seasons for climate variables are winter (December – February), spring (March – May), summer (June – August), autumn (September – November).

Chapter 4: Oystershell scale phenology, intensification, and spread on aspen in Arizona, USA

Abstract

Oystershell scale (*Lepidosaphes ulmi*; OSS) is an invasive insect that threatens sustainability of aspen (*Populus tremuloides*) in the southwestern United States. OSS invasions of aspen ecosystems have created challenges for land managers who are tasked with maintaining healthy aspen ecosystems for the ecological, economic, and aesthetic benefits they provide. OSS threatens these values by contributing to mortality of aspen, especially of intermediate-sized, recruiting stems that are the aspen forests of the future. Active management is required to suppress OSS populations and mitigate damage to aspen ecosystems, but before management strategies can be implemented, critical knowledge gaps about OSS biology and ecology must be filled, including its phenology, rates of OSS intensification and spread, and the rate of OSS-induced aspen mortality. This study sought to fill these gaps by addressing three questions: (1) What is the timing of OSS's life cycle on aspen in northern Arizona, USA and does climate influence life cycle timing? (2) What are the short-term rates of OSS intensification on trees and OSS spread among trees in wildland aspen stands? (3) What is the short-term rate of aspen mortality in OSS-infested stands? We found that immature life stages persist throughout the year and observed two waves of first-instar crawlers, one throughout the summer and the second in mid-winter. The first wave seemed to be driven by warming temperatures, but the cause of the second wave is unknown and might represent the initiation of a second generation. We also found that OSS causes high levels of aspen mortality (annual mortality rate

= 10.4%) and seems to spread rapidly within aspen stands (annual spread rate = 10–12.3%). We conclude by providing recommendations for future OSS research, including suggestions for more precisely quantifying OSS phenology, and by discussing how our results can inform management of OSS and invaded aspen ecosystems.

Keywords: invasive insect, *Lepidosaphes ulmi*, life cycle, mortality, pest management, *Populus tremuloides*

Introduction

Oystershell scale (*Lepidosaphes ulmi*; OSS) is an invasive insect that threatens sustainability of aspen (*Populus tremuloides*) populations in the southwestern United States (Crouch et al. 2021; Crouch 2023). Although the native range and introduction history of OSS are uncertain, the species was likely transported to North America by European settlers on infested plant material (Griswold 1925; Beardsley and Gonzalez 1975). OSS was first reported as a pest of apple trees (*Malus* spp.) in the 1700s and is now present throughout much of North America, especially in urban and ornamental settings (Griswold 1925; Miller and Davidson 2005b). Despite the species' polyphagous nature, its pervasiveness in North America, and its long invasion history, OSS has rarely been a major pest in wildland forest settings (but see Sterrett 1915; DeGroot 1967; Houston 2001). OSS was first reported on aspen in wildland forest settings in Arizona, USA by Fairweather (1992) and Zegler et al. (2012), but in both cases OSS abundance was low, and impacts were minimal. However, in 2016 OSS was observed causing dieback and mortality of aspen in wildland forest settings (Grady 2017), and severe outbreaks have since been observed in aspen ecosystems throughout Arizona and in other western states, including Nevada and Utah (Crouch et al. 2021; Crouch 2023).

OSS is an armored scale (Hemiptera: Diaspididae) that feeds by inserting its stylet through the bark of woody host plants to feed on the fluid of non-vascular cells (Griswold 1925; Beardsley and Gonzalez 1975). OSS is polyphagous, with around 100 host genera globally, and is most common on woody, deciduous plants with relatively thin bark (Miller and Davidson 2005b). Twelve host genera (*Acer*, *Alnus*, *Ceanothus*, *Cornus*, *Frangula*, *Fraxinus*, *Juglans*, *Lupinus*, *Populus*, *Ribes*, *Salix*, and *Symphoricarpos*) have been documented in the western US (Crouch et al. 2021). As an obligate parasite, OSS completes its entire life cycle on woody tissue of living hosts (Samarasinghe 1965). The exact timing of OSS's life cycle on aspen in Arizona is unknown (Crouch et al. 2021), but the life cycle's general pattern is as follows (Fig. 4.1). OSS overwinters as eggs beneath the tests of dead females (Beardsley and Gonzalez 1975), and eggs hatch in late spring or early summer, after which the newly emerged first instars (hereafter referred to as crawlers) begin actively dispersing along the host's stem or branches (Miller and Davidson 2005b). This dispersal stage lasts only a few days until a crawler finds a suitable feeding site, where it will remain through adulthood (Griswold 1925). As crawlers mature, they develop a waxy outer shell, or test, which protects them from predators and adverse climatic conditions (Beardsley and Gonzalez 1975). In bisexual populations, males shed their tests and fly to mate with females; however, female-only populations occur and reproduce via parthenogenesis (Beardsley and Gonzalez 1975; Miller and Davidson 2005b). Females lay 50–100 eggs beneath their tests, after which they die and shrivel, and the eggs remain protected under the test throughout the winter (Griswold 1925; Miller and Davidson 2005b). Questions remain about OSS dispersal mechanisms and distances, but long-distance dispersal is likely driven by human movement of infested plants, whereas short- and intermediate-distance dispersal are likely driven by wind, potentially with animal assistance (Griswold 1925; Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010). Crawlers do not actively move more than 1 m due to limited energy reserves and susceptibility to adverse climatic conditions (Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010).

OSS invasions of aspen ecosystems have created challenges for managers of national forest land, who are tasked with maintaining healthy aspen ecosystems (USDA Forest Service 2014, 2018). Aspen ecosystems are highly valued because of their ecological importance (Campbell and Bartos 2001; Rogers et al. 2020), positive impact on local economies (McCool 2001; Rogers 2017), and aesthetic and cultural values (Dahms and Geils 1997; McCool 2001; Assal 2020). However, OSS threatens these values by contributing to mortality of aspen, especially of intermediate-sized, recruiting stems (Crouch 2023). Mortality of aspen recruits threatens long-term sustainability of aspen ecosystems because recruits are the aspen forests of the future (Crouch 2023). OSS invasions also complicate aspen management in Arizona because OSS is especially common in fenced ungulate exclosures (Crouch 2023), which are 2 m tall fences built to exclude ungulates and are one of the most effective strategies for promoting aspen recruitment (Shepperd and Fairweather 1994; Bailey et al. 2007; Crouch et al. 2023). OSS invasions may render exclosures ineffective by disproportionately killing recruiting stems, the very size class exclosures are designed to promote (Crouch 2023). Active management is required to suppress OSS populations and mitigate damage to aspen ecosystems; however, before management strategies can be implemented, critical knowledge gaps about OSS biology and ecology must be filled (Crouch et al. 2021). OSS phenology is one such gap because knowing the timing of the crawler stage is imperative for properly timing management interventions (Beardsley and Gonzalez 1975). For example, if silvicultural tactics, such as sanitation thinning, are conducted when crawlers are active, managers may inadvertently spread OSS throughout the stand. In addition, some horticultural oils and insecticides are specifically targeted at the crawler stage, when OSS is the most vulnerable (Miller and Davidson 2005a; Quesada et al. 2018), making knowledge of OSS phenology a prerequisite for treatment implementation. Information on rates of OSS intensification and spread and how quickly OSS causes aspen mortality is also critical for informing management because such information can help managers determine how quickly a stand may be overrun with OSS and which stands should be prioritized for treatment. However, rates of intensification, spread, and OSS-induced aspen mortality remain unknown (Crouch et al. 2021).

This study sought to fill these knowledge gaps by studying OSS-invaded aspen stands in northern Arizona. We addressed three questions about OSS's biology and ecology that are critical for informing management of this high-impact invasive insect: (1) What is the timing of OSS's life cycle on aspen in northern Arizona and does climate influence life cycle timing? (2) What are the short-term rates of OSS intensification on trees and OSS spread among trees in wildland aspen stands? (3) What is the short-term rate of aspen mortality in OSS-infested stands?

Methods

Study Area

Our study was conducted at two sites in northern Arizona, which we refer to as the Nordic Village and Spring Valley study sites. The Nordic Village study site was located 32 km north of Flagstaff, Arizona (35°230 N, 111°460 W) at an elevation of 2455 m. This site consisted of nine study plots in two ungulate exclosures, which were 2.8 and 6.8 ha in size spaced 500 m apart. The Spring Valley study site was located 40 km northwest of Flagstaff (35°210 N, 111°580 W) at a slightly lower elevation of 2285 m. This site consisted of three plots in two ungulate exclosures, which were 0.7 and 3.4 ha in size spaced 80 m apart. These study sites were included in the first peer-reviewed report of OSS in wildland aspen stands (Crouch et al. 2021) and were selected for this study because they were the first sites at which we obtained measurements of OSS presence and severity, allowing for the longest possible chronology of repeated measurements. In addition, the study sites were among the first areas where OSS was observed causing dieback and mortality of aspen in 2016 (Grady 2017), making these high-priority areas for OSS monitoring and management.

OSS Phenology

To document the timing of OSS's life cycle, we collected OSS samples from the two study sites at regular intervals from April 2021 to April 2022. During the growing season from April to October 2021, we collected samples approximately every two weeks (range 10–15 days). In October 2021, we switched to sampling roughly every three weeks (range 16–24 days) until April 2022 because we expected less life cycle activity to occur outside of the growing season and because of site access challenges due to snow accumulation. We collected OSS samples from 33 trees in nine plots at the Nordic Village site (2–5 trees/plot) and from 13 aspen trees in three plots at the Spring Valley site (4–5 trees/plot) (Table 4.1). Plots were phased into the study in a piecemeal fashion in spring 2021 as they became accessible with snow melt, and plots were also phased out in a piecemeal fashion in winter 2021–22 as snow accumulated and sites again became inaccessible. Study trees were selected by locating the first three large aspen trees (> 5 cm diameter at breast height [dbh; height = 1.37 m]) and the first three small aspen trees (< 5 cm dbh) nearest plot center. We initially selected 66 trees before the growing season began, but 20 of them proved to be dead. We excluded these dead trees from our study. We selected trees with relatively severe OSS infestations to ensure that enough OSS was present for samples to be collected regularly throughout the year; however, severe infestations were not present in every plot, necessitating selection of trees with lighter infestations. On the large tree closest to plot center, we installed two climate data loggers (Onset HOBO Pro v2), one each on the north and south sides of the stem. These loggers recorded temperature and relative humidity every 15 minutes throughout the duration of the study.

To collect OSS from the study trees for life cycle analysis, we scraped approximately 1 mm of OSS into vials for each of the 46 study trees during each sampling visit (Table 4.1). Less than 1 mm was scraped into the vial for some trees, such as smaller trees with lighter infestations or trees later in the study period that had their OSS populations depleted. One sample was obtained from small trees around the entire circumference of the stem when possible, whereas two samples were taken from large trees, one each on the north and south sides of the stem. We also cleared a section of OSS on each stem to provide a reference area in which only OSS from the study year would recolonize. On small trees, this cleared section was 10 cm in height and wrapped around the circumference of the stem. On large trees, we cleared a 10 cm x 10 cm section on both the north and south sides of the stem. These sections were cleared at breast height (1.37 m) for large trees or at the center of the stem for small trees. Once these cleared sections began to be colonized by new OSS, we scraped the entire section of OSS into a vial to serve as a reference sample. These reference samples allowed us to better determine which OSS individuals we collected were established during the study period versus which individuals were present on trees before our study began. In total, 39 reference samples were collected from June to December 2021. After collection, all OSS samples were kept in cold storage for laboratory analysis.

We analyzed samples by taking photographs of the OSS in each sample and analyzing these photos to determine which life stages were present. To take photos of the samples, each sample vial was emptied onto a petri dish, and the OSS were spread into a single layer on the dish. The petri dish was labeled using four different symbols, and up to three photos were taken either directly above or below three randomly selected symbols, whichever direction had more OSS (Fig. 4.2). This allowed us to obtain a stratified random sample from each sample vial. Some vials contained insufficient OSS to take three photos, such as for smaller trees with lighter infestations or for trees later in the study period that had their OSS populations depleted. In these cases, only one or two photos were taken. Photos were taken using a Canon 6D/Macro 100 mm lens, and each photo captured an area of 4 mm x 6 mm. Once the photos were obtained, we analyzed each photo by counting the number of individuals present in each life stage, including eggs, first instars (i.e., crawlers), second instars, young third instars, and mature third instars (Miller and Davidson 2005a, 2005b) (Fig. 4.3).

We calculated the proportion of each of these life stages present in each photo and used descriptive statistics to summarize changes in the proportion of life stages present throughout our 13-month study period. We also averaged the temperature and relative humidity data obtained from each plot at a daily resolution, allowing us to compare OSS phenology and climate patterns. Because we wanted to explore the relationship between crawler emergence and climate in more depth, we calculated correlation coefficients between proportion of crawlers observed each month, local mean temperature and humidity obtained from climate data loggers installed in each plot, and additional downscaled climate data obtained at the site level from the PRISM database (Daly et al. 2008) at a monthly resolution. These downscaled climate variables included mean precipitation, minimum and maximum vapor pressure deficit (VPD), and minimum and maximum temperatures. We then used the *nlme* package (Pinheiro et al. 2022) to fit seven linear mixed-effects models with OSS crawler density as the response, each of the seven climate variables as predictors, and the sampling month as a random effect.

OSS Intensification, OSS Spread, and Aspen Mortality

In each of the 12 study plots in which OSS samples were collected for phenological analysis, we also assessed OSS presence, OSS severity, and aspen tree condition for three consecutive years. These data allowed us to quantify annual rates of OSS intensification on trees and OSS spread among trees as well as the rate of aspen mortality. These data were collected in June–August

2020, 2021, and 2022. Each of the nine monitoring plots 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 (Zegler et al. 2012). All trees with dbh ≥ 10.1 cm were measured in the 8 m overstory plot, whereas all trees < 10.1 cm in dbh were measured in the 4 m regeneration plot. In the regeneration plot, we classified stems into three size classes: short regeneration (< 1.4 m tall), tall regeneration (> 1.4 m tall and < 5.1 cm dbh), and saplings (5.1–10.1 cm dbh) (Zegler et al. 2012). For each aspen tree in the monitoring plots, we recorded tree condition (i.e., live or dead), height, dbh, and OSS presence and severity. We assessed OSS severity using the system devised by Crouch et al. (2021), which rates the severity of OSS on each tree from ground level to 6 m. Each tree's stem up to 6 m was divided into thirds, and severity was rated for each 2 m section (or shorter for trees < 6 m tall) on both the north and south sides of the tree, resulting in six ratings for each tree. Severity was rated from 0 to 3: 0 = no OSS present (light), 1 = only a handful of OSS present (trace), 2 = OSS covers < 50% of section (light), 3 = OSS covers > 50% of section (severe). For stems sampled for OSS phenology, we assumed that the scraped off areas had similar OSS severity as the surrounding areas on the stem. To convert the six ratings for each tree into a single quantitative variable representing OSS severity, we calculated the mean percentage of each rating (i.e., 1% for 1, 25% for 2, and 75% for 3) and averaged the six ratings for each tree. Thus, OSS severity ranged from 0 to 0.75, with 0 indicating a tree without OSS and 0.75 indicating a tree with the highest possible severity rating (i.e., OSS covering > 50% of all six stem sections rated).

To quantify OSS intensification, we summarized mean OSS severity on aspen stems in each of the three measurements periods. We used repeated measures analysis of variance

(ANOVA) to determine whether there were significant changes in OSS severity over time. Specifically, we used the *nlme* package (Pinheiro et al. 2022) to fit a linear mixed-effects model with OSS severity as the response, measurement year as the fixed effect, and the hierarchical nested structure of our data (i.e., trees [n = 366] within plots [n = 12] within sites [n = 2]) as a random effect. We used the “anova” function in R (R Core Team, 2022) to conduct repeated measures ANOVA and the *emmeans* (Lenth, 2022) and *multcomp* (Hothorn et al. 2008) packages to conduct Tukey-adjusted, post-hoc pairwise comparisons. We also used the same ANOVA procedure, without the repeated measures component, to determine if there were differences in OSS severity between the north and south sides of aspen stems. Thus, OSS severity was the response, tree side was the fixed effect, and the hierarchical nested structure of our data was a random effect. To explore the influence of climate on OSS intensification, we obtained precipitation, temperature, and VPD data for both of our study sites from the PRISM database (Daly et al. 2008) and calculated mean values for each of the three study years at both sites.

To quantify OSS spread and aspen mortality, we relied on descriptive statistics, specifically means and standard errors, to calculate rates of spread and mortality. 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.

Results

OSS Phenology

During our first OSS sample collections in April 2021, most individuals were eggs or mature third instars (Fig. 4.4). Throughout the summer, density of eggs decreased, while density of mature third instars increased, before density of both life stages balanced out again in the fall. A few crawlers were already present in April, and their presence increased through July when crawlers made up 1.5% (standard error [SE] = 0.2%) of samples (Fig. 4.5a). Presence of second instars and young third instars also increased during the summer (Fig. 4.5a) as temperature and relative humidity increased (Fig. 4.5b, 4.5c). The first wave of crawlers tapered out in the fall, with crawler densities approaching zero in October and November 2021. However, a second wave of crawlers emerged mid-winter, reaching a peak in January 2022 that approached the summer 2021 peak in density. Second instar and young third instar densities also decreased in fall and early winter. Second instar densities remained low throughout winter with increases in December, January, and March. Young third instars reached a clear second peak in March 2022.

Climate variables, particularly those capturing temperature, had strong relationships with proportion of crawlers observed in our study sites (Table 4.2). This included local climate data collected from plot-level climate data loggers as well as downscaled climate data obtained at the site level from PRISM (Daley et al. 2008). Mean, minimum, and maximum monthly temperatures all had significant ($p \leq 0.021$) positive relationships with crawler density, as did maximum VPD ($p = 0.021$). Mean relative humidity, precipitation, and minimum VPD had insignificant relationships ($p \geq 0.111$) with crawler density.

OSS phenology varied little between the two study sites. Both sites experienced peak crawler emergence in July, with a second crawler emergence in mid-winter, although the winter peak occurred in December for Spring Valley and in January for Nordic Village. Comparing samples taken on the north versus the south side of trees, there was generally more crawler activity observed on the north side (mean = 0.8%, SE < 0.01%) than on the south side (mean = 0.6%, SE < 0.01%). The same was true for second (north mean = 1.7% [SE = 0.01%], south mean = 0.7% [SE < 0.01%]) and young third instars (north mean = 4.6% [SE = 0.02%], south mean = 3.1% [SE = 0.02%]), whereas differences in tree side patterns for eggs and mature third instars were negligible (data not shown).

OSS Intensification

Mean OSS severity for the aspen that were alive in 2020 was 0.21 (SE = 0.01). In 2021, severity increased to 0.27 (SE = 0.01), which included trees that died between sampling in 2020 and 2021 (Fig. 4.6a). In 2022, severity decreased to 0.19 (SE = 0.01), again including trees that died between sampling in 2021 and 2022. Sample sizes decreased over time (366 trees in 2020, 349 in 2021, 313 in 2022) due to study trees dying. Repeated measures ANOVA indicated that there were significant ($p < 0.001$) differences in OSS severity across the three measurement periods. OSS severity in 2021 was significantly greater than in 2020 and 2022, and severity in 2020 was significantly greater than in 2022 (Fig. 4.6b). When comparing differences in OSS severity between tree sides, north sides had significantly ($p < 0.001$) greater severity (mean = 0.25, SE = 0.01) than south sides (mean = 0.18, SE = 0.01) based on ANOVA.

OSS Spread

During the first survey in 2020, 25 of 366 live aspen were not infested with OSS across the 12 study plots. Only two of these uninfested stems were located in the Nordic Village site, while the remaining 23 were located in the Spring Valley site (Table 4.3). Uninfested stems represented 51.1% (SE = 7.5%) of all live stems in Spring Valley and only 0.6% (SE = 0.4%) of live stems in Nordic Village in 2020. One of the two uninfested stems in Nordic Village, an overstory tree, became infested in 2021, while the other stem, which was short regeneration, died before the 2021 survey. In Spring Valley, four of the 23 uninfested stems became infested in 2021, and no new stems were infested in 2022. Thus, across both study sites, OSS spread to 20.0% (SE = 8.0%) of previously uninfested stems during our two-year study period (Table 4.3). OSS also spread to aspen suckers that regenerated after the 2020 survey. In 2021, 39 new suckers established in the study sites, and in 2022, six new suckers established. Of these 45 new stems, 12 became infested by OSS: eight in 2021 and four in 2022. When considering these newly established stems, the rate of OSS spread to uninfested stems was 24.3% (SE = 5.1%) during our two-year study period (Table 4.3).

Aspen Mortality

In 2020, there were 366 live aspen trees across the 12 study plots. Before the 2021 survey, 48 of those aspen died, and between the 2021 and 2022 surveys, an additional 28 aspen died, resulting in an annual mortality rate of 10.4% (SE = 1.6%) (Table 4.4). Of the 76 aspen that died, 24 were short regeneration, 21 were tall regeneration, 15 were saplings, and 16 were overstory trees. OSS was present on all but five of the 76 trees that died, and the five that lacked OSS were all short regeneration stems. Looking at all 76 trees that died, mean OSS severity in the year before death was 0.32 (SE = 0.05). Short regeneration stems that died had the lowest mean OSS severity (mean = 0.09, SE = 0.06), followed by saplings (mean = 0.33, SE = 0.12), tall regeneration (mean = 0.45, SE = 0.11), and overstory trees (mean = 0.50, SE = 0.12). For comparison, mean OSS severity for trees that remained alive throughout the study was 0.20 (SE = 0.01). Short regeneration that remained alive had the lowest mean OSS severity (mean = 0.03, SE = 0.02), followed by saplings (mean = 0.19, SE = 0.03), overstory trees (mean = 0.22, SE = 0.02), and tall regeneration (mean = 0.29, SE = 0.06).

Discussion

We expected OSS would progress through a clear single life cycle, with a wave of crawlers followed by a wave of second instars and so on. Previous studies of OSS in western North America have documented OSS egg hatch in May through July (Schuh and Mote 1948; Madsen and Arrand 1971; Spackman 1980; Miller and Davidson 2005b), and we did not find evidence in the literature of OSS egg hatch lasting more than two months or of multiple generations occurring in western North America. Therefore, we were surprised by the persistence of immature life stages throughout the year, albeit at low densities compared to eggs and mature individuals. In particular, we did not anticipate continued presence of crawlers during winter (Fig. 4.5a). We observed an initial wave of crawlers in June through August, which coincided with warming temperatures and tapered off in the fall as temperatures decreased (Fig. 4.5b). Indeed, increased crawler density was significantly associated with warmer mean, minimum, and maximum temperatures and with greater VPD, all of which were obtained as downscaled climate data from PRISM with the exception of mean temperature, which was obtained locally from climate data loggers installed in each plot. This pattern is consistent with the previously documented relationship between OSS egg hatch and accumulation of degree-days (Kozár 1990). In contrast, the second wave of crawlers we observed in January is unprecedented in the OSS literature and, perplexingly, did not coincide with an increase in temperature. Humidity was relatively high before this second crawler wave, with a 10-day period from December 26 to January 4 when mean humidity exceeded 80% (Fig. 4.5c). However, the summer wave of crawlers emerged during a dry period, and humidity had an insignificant relationship with crawler density, which casts doubt upon the role of humidity in promoting OSS egg hatch.

The prolonged summer crawler wave, which exceeded three months, and the second wave in winter could be explained by diapause and/or the initiation of a second generation. Diapause is a temporary state of dormancy triggered by adverse environmental conditions (Tougeron 2019) and has been observed in certain armored scale species (Beardsley and Gonzalez 1975) including OSS (Fountain et al. 2012). However, diapause in scale insects has only been documented in summer (Beardsley and Gonzalez 1975; Fountain et al. 2012), which would fail to explain the winter wave of OSS crawlers, unless OSS in Arizona experiences winter diapause. Instead, the second wave may be a second generation of OSS, a phenomenon that has been documented in Europe and eastern North America (Schmutterer 1951; Turnipseed and Smith 1953; Garrett 1972; Miller and Davidson 2005b). Further research into patterns and drivers of OSS phenology is needed to determine if the second wave of OSS crawlers occurs every winter in Arizona, if the second wave is indeed a second generation or is caused by unprecedented winter diapause, and what factors, climatic or otherwise, cause this second wave of crawlers to emerge.

OSS second instar density generally mirrored that of crawlers, albeit at higher densities, whereas patterns of young third instar density did not track neatly with crawler emergence. This could be due to challenges in identifying young third instars, long-term persistence of this life stage on aspen stems even after dying, or drawbacks with the sampling method we used. In contrast to eggs, crawlers, and second instars, distinguishing between young third and mature third instars is less precise because of the visual similarities between these life stages (Fig. 4.3). Young third instars might also persist longer on aspen stems than crawlers. This becomes a potential issue when considering our sampling approach, in which we collected a portion of all OSS individuals on a given tree, not just the individuals that emerged during the study period. Using this method, we collected individuals, including dead ones, that were established on study trees prior to the measurement period in addition to those that were newly established during the study period. This could explain the relatively high density of young third instars throughout the year, even when crawlers and second instars were almost completely absent. Three approaches to OSS collection might result in a more precise assessment of the species' phenology. First, sticky traps could be used more precisely detect crawler emergence (Fountain et al. 2012). Second, scraping off small reference areas of OSS (< 10 cm x 10 cm) and tracking these cleared reference areas with high-resolution photos, rather than collecting the re-colonizing OSS as we did, might be more effective for tracking OSS development throughout the year. Finally, live samples of aspen branches or stems infested with OSS might be tracked for development of OSS life stages, although killing aspen branches or stems might affect OSS development.

We were also surprised by the significant decrease in OSS severity in the third and final year of our study (Fig. 4.6b). Although we would expect OSS severity to continue increasing over time, as it did between 2020 and 2021, we have four hypotheses regarding why severity declined in 2022. First, OSS severity may have decreased because the most severely infested trees may be the most likely to die (Crouch 2023), resulting in a perceived reduction in stand-level OSS severity on the remaining live trees. However, we explored the effect of removing trees that eventually died from our dataset, and although the size of the OSS severity dip decreased without trees that eventually died, the overarching pattern of a dip in OSS severity in 2022 remained. Second, the decline in OSS could be due to a density-dependent population collapse. Our study plots had relatively high rates of OSS infestation and severity compared to other OSS-invaded aspen ecosystems (Crouch 2023), perhaps because these plots were among the first to experience OSS outbreaks (Crouch et al. 2021). Thus, the observed decline in OSS severity could be due to a lack of suitable feeding sites for new OSS to colonize. If this were the case, though, plots with the highest OSS severity in 2020–2021 should have had the greatest decrease in severity in 2022, which was not a consistent pattern among study plots (Fig. 4.6a).

Given the lack of support for these first two hypotheses, we suspect that climate or the winter wave of crawler emergence caused OSS severity to decrease in 2022. Climate is the most important driver of OSS abundance at the stand level, with warmer and drier conditions resulting in more OSS (Crouch 2023). On average, 2022 was wetter at both sites, with higher precipitation and lower minimum and maximum VPD than 2020 and 2021 (Table 4.5), lending support to our hypothesis that a less favorable climate drove the decline in OSS severity in 2022. Alternatively, the wave of crawlers that emerged in winter 2021–2022 may have experienced high mortality due to cold temperatures. If this was the case, then losing a substantial portion of the next OSS generation might also explain why severity significantly decreased the following summer. To better understand the rate of OSS intensification, more research must be conducted in stands with lower levels of infestation. The same is true for understanding rates of OSS spread because our findings related to spread were limited due to high levels of infestation at the start of the study.

We observed higher OSS severity and increased life cycle activity on the north side of aspen trees compared to the south side, confirming initial observations that OSS tends to be more abundant on the north side of trees (Crouch et al. 2021). These initial observations explain why the OSS severity rating system assesses the north and south sides of stems separately (Crouch et al. 2021), and our study suggests that this approach is merited due to differences in OSS severity and development between tree sides. We expected that these differences may have been driven by different microclimates on the north versus south sides of trees, which is why we installed climate data loggers on the north and south sides of stems. However, climate differed less than anticipated between tree sides. On average, north sides were only 0.2°C cooler (SE = 0.02) and 0.3% more humid (SE = 0.05) than south sides. Therefore, we suspect that less direct sunlight, rather than a cooler or more humid microclimate, drove increased OSS development and severity on the north versus south sides of trees. Other armored scale insect species have shown a preference for feeding sites exposed to less sunlight (Gentile and Summers 1958; Mayfield and Jetton 2020). If this is true for OSS, thinning infested aspen stands may increase aspen resistance to OSS because a more open canopy resulting in increased sunlight exposure to stems might make trees less suitable for OSS infestation. However, sudden, direct exposure of aspen stems to sunlight after thinning may cause sunscald (Krasnow et al. 2012), creating potential infection courts for pathogens and leading to mortality. Aspen is also sensitive to mechanical damage from logging equipment and susceptible to subsequent infection by canker-causing fungi and decay diseases (Walters et al. 1982; Jones and Shepperd 1985), so thinning must be implemented with care.

We observed an annual aspen mortality rate of 10.4%, which is substantial compared to previously documented rates of aspen mortality in Arizona and to rates of tree mortality from other invasive insects and diseases. For example, Fairweather et al. (2008) documented an annual aspen mortality rate of 7.9% from 2000 to 2007 during an acute aspen mortality event caused by interactions among drought, a severe frost event, defoliation by western tent caterpillar (*Malacosoma californicum*), and other factors. Similarly, Kane (2012) documented an annual aspen mortality rate of 5.2% from 1996 to 2008 in mixed-conifer forests. Our observed mortality rate was higher than both these studies, although our observation period was shorter, and our study area was smaller. For further comparison, the documented annual rate of mortality of eastern hemlock (*Tsuga canadensis*) from hemlock woolly adelgid (*Adelges tsugae*) is ~2–12% (Eschtruth et al. 2006; Ford et al. 2012), of coast live oak (*Quercus agrifolia*) and California black oak (*Quercus kelloggii*) from *Phytophthora ramorum* is ~3–5% (Cobb et al. 2020), and of American elm (*Ulmus americana*) from Dutch elm disease (*Ophiostoma novi-ulmi*) is ~10–20% (Hauer et al. 2020). Again, many of these studies were conducted at larger spatial and longer temporal scales than our study, and our observed 10.4% annual aspen mortality rate is likely on the high end of OSS-induced mortality because OSS presence and severity were relatively high in our study sites (Crouch 2023). Despite these caveats, our study is the first to estimate annual mortality rates of aspen caused by OSS, and our findings can give forest managers a high-end approximation for how quickly aspen stands may deteriorate after OSS invades.

The findings of our study can be used to inform management of OSS and aspen ecosystems invaded by OSS. The prolonged crawler emergence that we observed complicates management strategies, such as sanitation thinning, that seek to avoid the crawler stage. Our findings suggest that there may be no time of year when crawlers can be completely avoided, but crawler density is lowest in October through November and February through March. On the other hand, strategies geared toward targeting the crawler stage, such as application of horticultural oils or insecticides, should be applied in June through August when crawler density is highest. We also found that OSS caused high levels of mortality and seemed to spread rapidly within aspen stands, emphasizing the need for early intervention when invasions are detected in aspen ecosystems. There is a dire need to assess the efficacy of management interventions, such as silvicultural treatments, prescribed fire, and systemic insecticides (Crouch et al. 2021), and important questions remain regarding the long-term trajectory of aspen stands infested by OSS. We also do not know whether adequate regeneration and recruitment will occur to replace dying trees, representing an important research need and providing motivation for continued monitoring of aspen ecosystems invaded by OSS.

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Tables

Table 4.1. Summary of sample sizes by study site for OSS phenology data collection. Table shows number of study plots, number of large (> 5 cm dbh) and small (< 5 cm dbh) aspen stems from which OSS samples were collected, number of collection dates and vials containing OSS collected, and number of photos taken of OSS samples.

Study site	Sample size					
	Study plots	Large stems	Small stems	Collection dates	Vials collected	Photos
Nordic Village	9	26	7	25	915	2608
Spring Valley	3	9	4	19	416	1172
Total	**12**	**35**	**11**	**28**	**1331**	**3780**

Table 4.2. Univariate relationships between proportion of first-instar crawlers observed in our study samples and seven climate variables, all of which were summarized at a monthly resolution. These relationships are based on correlation coefficients and linear mixed models.

Predictor	**Correlation coefficient**	**Model coefficient**	**Standard error**	***p* value**	**Marginal R^2**
Mean temperature (°C)[a]	0.45	0.0004	0.0002	0.021	0.12
Relative humidity (%)[a]	0.07	< 0.0001	0.0001	0.879	< 0.01
Precipitation (mm)[b]	0.35	< 0.0001	< 0.0001	0.111	0.09
Minimum temperature (°C)[b]	0.51	0.0006	0.0002	0.002	0.19
Maximum temperature (°C)[b]	0.47	0.0005	0.0002	0.011	0.15
Minimum VPD (hPa)[b]	0.31	0.0014	0.0011	0.204	0.06
Maximum VPD (hPa)[b]	0.43	0.0005	0.0002	0.021	0.13

[a] Local climate data obtained at the plot level from data loggers installed on the north and south sides of one aspen tree in each study plot.

[b] Downscaled climate data obtained at the site level from PRISM (Daly et al. 2008) at a monthly resolution.

Marginal R^2 is based solely on the model's fixed effects, which was the climate variable.

Table 4.3. Summary of OSS spread. Table shows the number of uninfested and newly infested (in parentheses) aspen trees during each sampling year, along with the cumulative infestation rate. Table includes counts for trees that were established at the beginning of our study in 2020 (^{orig}) and for all trees including new aspen that established after 2020 (^{new}).

	# trees uninfested by OSS (# trees newly infested by OSS)			**Cumulative infestation rate (%)**
Study Site	**2020**	**2021**	**2022**	
Nordic Village^{orig}	2	0 (1)	0 (0)	50.0
Spring Valley^{orig}	23	12 (4)	12 (0)	17.4
Total^{orig}	**25**	**12 (5)**	**12 (0)**	**20.0**
Nordic Village^{new}	2	12 (9)	12 (4)	42.9
Spring Valley^{new}	23	31 (4)	31 (0)	11.9
Total^{new}	**25**	**43 (13)**	**43 (4)**	**24.6**

Table 4.4. Summary of aspen mortality. Table shows the number of living aspen stems and stems that died (in parentheses) in each sampling year, along with the annual mortality rate, across four stem size classes.

	# trees alive (# trees that died) in each sampling year			**Annual mortality rate (%)**
Size class	**2020**	**2021**	**2022**	
Overstory trees	201	196 (5)	185 (11)	4.0
Saplings	72	62 (10)	57 (5)	10.4
Tall regeneration	40	23 (14)	20 (7)	26.3
Short regeneration	53	34 (19)	24 (5)	22.6
Total	**366**	**315 (48)**	**286 (28)**	**10.4**

Aspen stem size classes: short regeneration (< 1.37 m tall), tall regeneration (> 1.37 m tall and < 5.1 cm dbh), saplings (5.1–10.1 cm dbh), overstory trees (> 10.1 cm dbh)

Table 4.5. Downscaled climate data obtained from the PRISM database (Daly et al. 2008) for both our study sites during each measurement year.

Study site and sampling year	**Precip (mean)**	**Temp (min)**	**Temp (mean)**	**Temp (max)**	**VPD (min)**	**VPD (max)**
NV 2020	39.5	0.3	8.1	16.0	2.6	16.4
NV 2021	35.0	0.5	8.3	15.9	2.5	15.8
NV 2022	49.1	0.9	8.1	15.3	1.9	13.7
SV 2020	41.2	0.8	8.7	16.5	2.7	17.3
SV 2021	37.6	1.0	8.9	16.9	2.7	17.3
SV 2022	48.0	1.6	9.0	16.4	2.1	15.3

Study site abbreviations: NV (Nordic Village), SV (Spring Valley). Climate abbreviations: precip (precipitation), temp (temperature), VPD (vapor pressure deficit). Climate units: precip (mm), temp (°C), VPD (hPa). Climate data for each study year represent means from the previous September (e.g., 2019 for sampling year 2020) to August of the present sampling year (e.g., 2020) because August was the latest that we assessed severity in our study plots in any year.

Figures

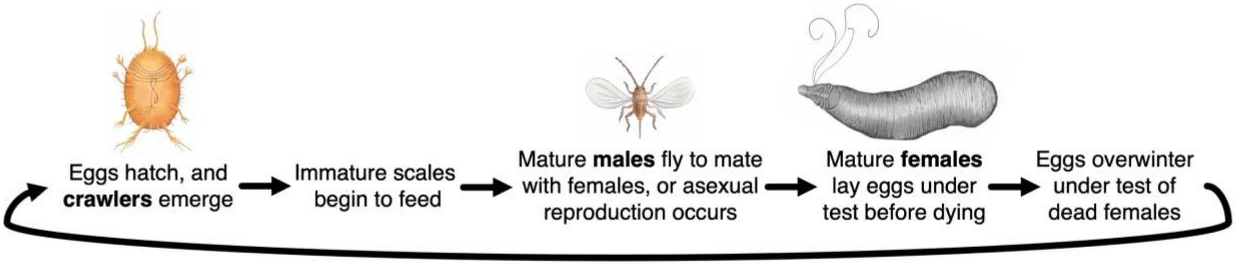

Figure 4.1. The general pattern of OSS's life cycle. The exact timing of these stages on aspen in Arizona remains unknown, which is a need our study sought to address. Words in bold indicate the life stage shown in the accompanying drawing. OSS illustrations by D.E. DePinte.

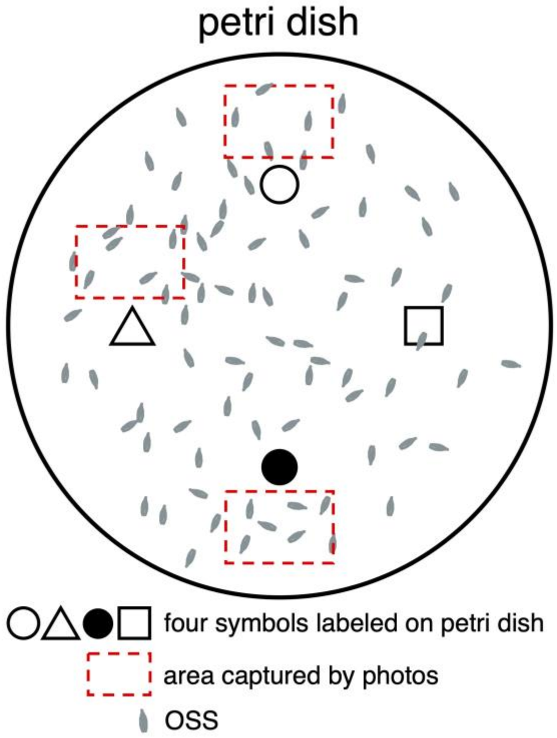

Figure 4.2. Diagram of petri dish and sampling method used to take photos of OSS samples for phenological analysis. Vials of OSS were emptied onto the petri dish, and the OSS were spread into a single layer. The petri dish was labeled using four different symbols, and up to three photos were taken either directly above or below three of the randomly selected symbols, whichever direction had more OSS. This allowed us to obtain a stratified random sample of OSS from each vial.

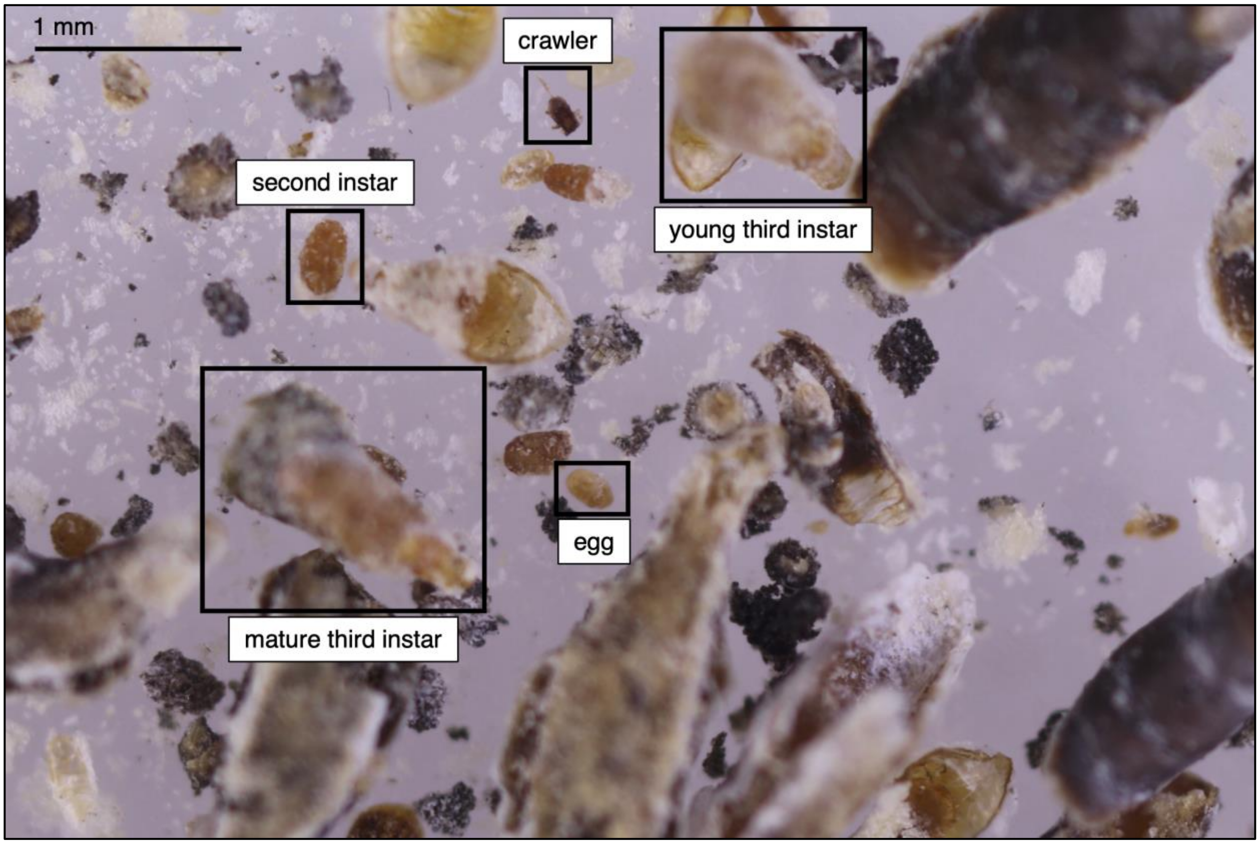

Figure 4.3. Photo from January 20, 2022 showing each of OSS's five life stages. The white material in the background is woolly flocculants created by OSS (Crouch et al. 2021).

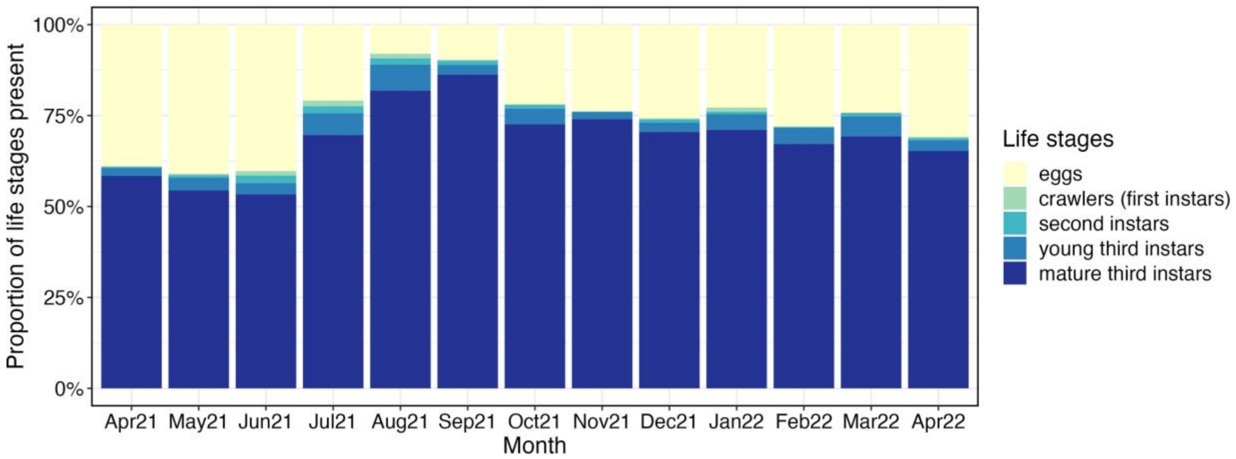

Figure 4.4. Proportion of OSS life stages present in samples collected from aspen trees in northern Arizona, summarized by month from April 2021 to April 2022.

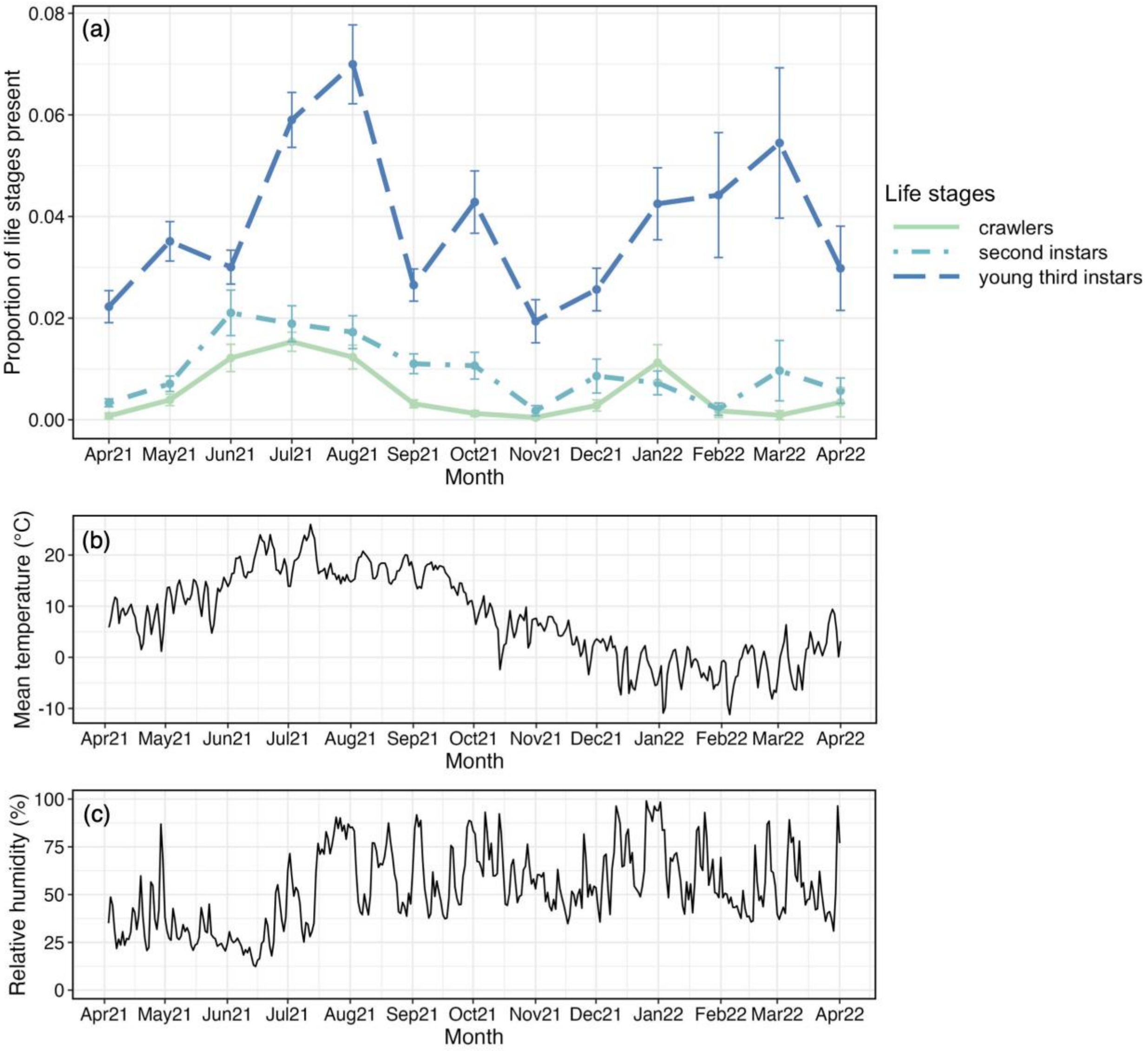

Figure 4.5. (a) Proportion of OSS crawlers, second instars, and young third instars in samples collected from aspen trees from April 2021 to April 2022 alongside mean daily (b) temperature and (c) relative humidity during the study period. These climate data were obtained from local data loggers placed in each of the 12 study plots.

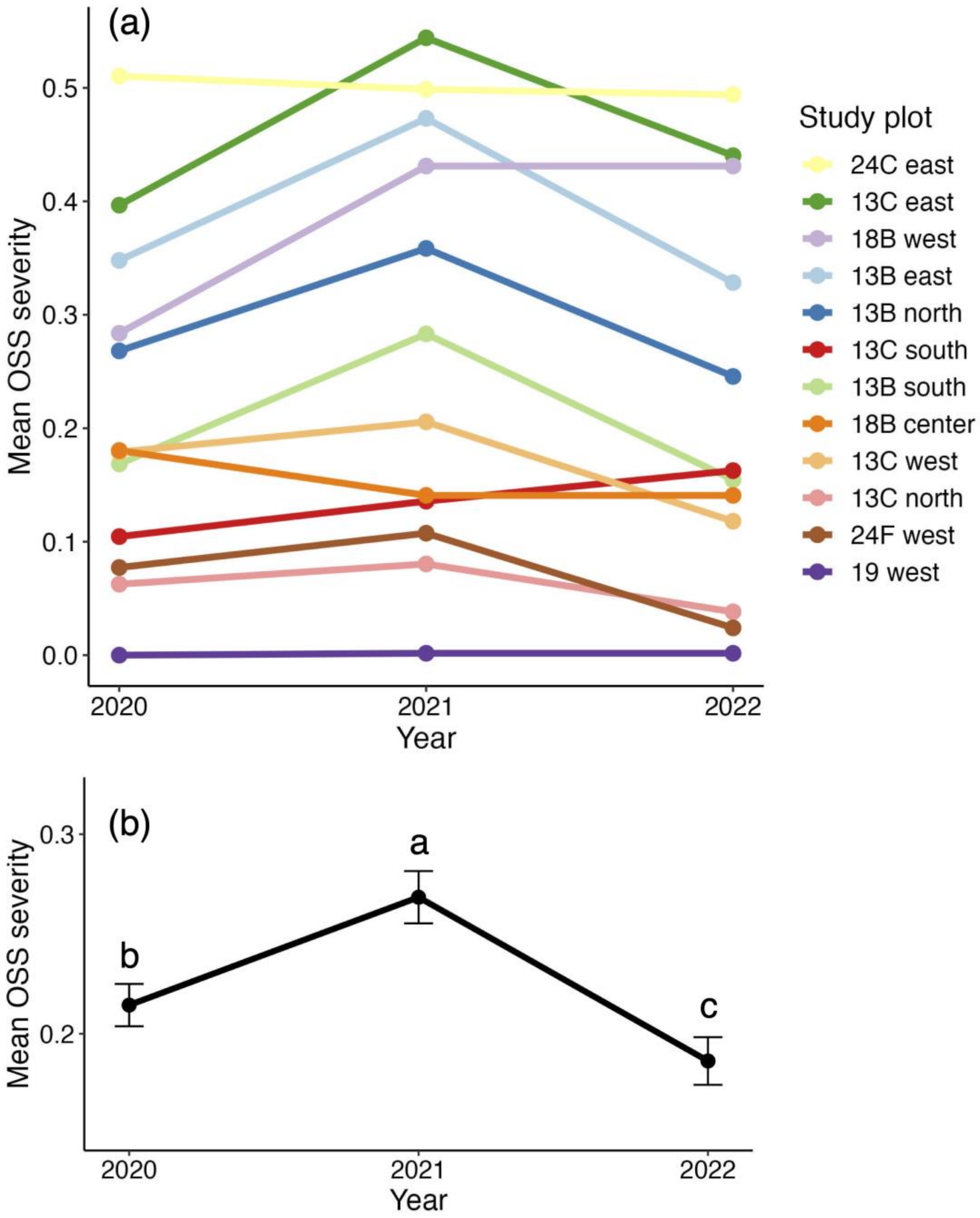

Figure 4.6. Mean OSS severity on aspen trees through time (a) in each of the 12 study plots and (b) averaged across all study plots, with different letters indicating significant differences ($p < 0.05$) among years based on repeated measures ANOVA. Across all 12 plots, OSS severity in 2021 was significantly greater than in 2020 and 2022, and severity in 2020 was significantly greater than in 2022. OSS severity was assessed using the system devised by Crouch et al. (2021) (see Methods for details on the rating system and subsequent severity calculations). OSS severity ranged from 0 to 0.75, with 0 indicating a tree without OSS and 0.75 indicating a tree with the highest possible severity rating (i.e., OSS covering > 50% of all six stem sections rated).

Chapter 5: Research brief: updating the status of our knowledge on aspen and oystershell scale management in Arizona

Forests have experienced extensive mortality in recent decades due to climate change, insect and disease outbreaks, novel disturbance regimes, and interactions among these factors [1–3]. These interactions between climate change and threats to forest health are driving novel changes in forest ecosystems, requiring managers to develop new strategies for maintaining ecologically important foundation tree species on the landscape. Aspen is one such foundation species that is under threat, and this research brief provides new guidelines for managing aspen ecosystems in Arizona, including specific recommendations for managing the invasive insect oystershell scale (OSS). The brief explains why aspen ecosystems are important, summarizes recommendations for aspen and OSS management, and outlines monitoring and management needs that managers can help to address.

Importance of Aspen Ecosystems

Aspen is an important foundation species in the western US because it is one of the only hardwood species that forms dominant, single-species stands [4]. The conservation value of aspen is especially pronounced along the southwestern edge of its range, which includes Arizona, because aspen occupies less than 2% of forested land in the region [5–8]. Aspen ecosystems provide critical habitat for many plants, animals, invertebrates, and fungi and make a disproportionately large contribution to biodiversity compared to neighboring conifer-dominated stands [4,9–11]. Aspen ecosystems also have a positive impact on local economies and provide important aesthetic and cultural values [12,13]. Aspen's importance may increase further in the future because it is one of the few species that can regenerate following the loss of overstory seed sources [14]. Therefore, aspen has the potential to increase overall forest resilience after high-severity fire.

Aspen Management

Aspen ecosystems in Arizona face a singular collection of threats, from a warming climate and increased fire activity to chronic ungulate browse and outbreaks of OSS. Managing for aspen ecosystem resilience and adaptive capacity is critical for confronting this array of threats and preparing for an increasingly uncertain future [8]. Given projected aspen migration into higher elevations under climate change [15] and OSS outbreaks in lower elevation aspen stands [16], the contemporary management paradigm of conserving existing aspen populations at all costs must shift to promoting aspen population flexibility across the landscape [8]. To accomplish this goal and increase aspen resilience and adaptive capacity, we propose that aspen management in Arizona should seek to (1) promote diversity in age structure across the landscape, particularly by enhancing regeneration and recruitment, (2) mitigate negative impacts of ungulate browse on recruitment, and (3) enhance structural, adaptive, and functional complexity (Fig. 1.3) [8,17].

To sustain aspen in the future, management must 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. Fire is a highly effective strategy for promoting aspen regeneration across the landscape. Aspen's regeneration potential was limited throughout the 20th century due to fire suppression and exclusion [5,18–20]. As a result, many seral aspen stands are in advanced stages of succession to conifers [5,7,21]. However, opportunities for aspen regeneration have increased in recent decades as climate change has facilitated more frequent, larger, and more severe wildfires [22], a pattern that is likely to continue with continued climatic warming [23]. An important advantage of fire over other regeneration tactics, such as clearfelling, is that fire facilitates both asexual and sexual reproduction of aspen [24]. Post-fire sexual reproduction has the dual benefits of allowing aspen to establish in new areas via seedlings while also increasing genetic diversity and, potentially, adaptation to a warming climate [24–26]. Although more fires in a warmer climate are likely to benefit aspen, we found that warmer, drier conditions are unfavorable for aspen regeneration in Arizona. Therefore, managers should target areas with lower drought stress, more precipitation, and lower heat load when considering areas for aspen regeneration treatments, ungulate management, and assisted colonization or gene flow [27,28].

Aspen regeneration success is contingent upon ensuing recruitment, which is far more difficult to promote as indicated by low levels of sustainable recruitment in Arizona. Successful management of aspen recruitment requires consideration of two important limiting factors: ungulate browse, especially by non-native elk, and OSS. Ungulate exclosures are extremely successful at reducing browse and promoting recruitment, but exclosures have major drawbacks. They are costly to install and maintain [21,29], limit aspen to confined areas thereby reducing adaptive capacity [8], and are strongly associated with OSS outbreaks [16]. Because OSS 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: (1) directly reducing ungulate population sizes to facilitate landscape-level recruitment, (2) managing for aspen at higher elevations, which should be more suitable for aspen in a changing climate and less susceptible to OSS, and (3) mitigating damage from OSS via suppression strategies.

Oystershell Scale (OSS) Monitoring and Management

OSS is already widespread in Arizona, so management tactics intended to eradicate this pest are unlikely to succeed. Eradication is further complicated by OSS's ability to infest an array of different host species and by the fact that small populations are exceedingly difficult to detect due to OSS's small size and cryptic coloring, which blends in well with aspen bark [16]. Instead of eradication, management should focus on suppressing OSS population sizes and mitigating damage to native ecosystems. OSS causes high levels of mortality and seems to spread rapidly within aspen stands, emphasizing the need for early intervention when invasions are detected. Three strategies, in particular, might help to suppress OSS populations: (1) increased application of fire at the landscape scale, (2) reduced reliance on ungulate exclosures, and (3) decreased aspen stand density.

Fire has a negative influence on OSS, and although frequency and size of wildfires will likely increase as climate warming continues [22,23], managers may consider implementing prescribed fire to suppress OSS infestations in individual aspen stands. Frequent, low-severity fire may be detrimental to aspen stands, especially in the presence of chronic ungulate browse [8], so fire should be implemented with caution and infrequency when managing for OSS. Advantages of fire as an OSS management strategy include low cost of implementation, the ability to kill OSS on multiple host species including understory plants, and the fact that fire is a natural component of aspen ecosystems [16]. Another strategy managers may consider is reducing use of ungulate exclosures. Reducing reliance on exclosures should help reduce OSS population sizes, although this will require finding other ways to overcome chronic ungulate browse that threatens aspen ecosystem resilience, adaptive capacity, and sustainability [8]. One reason ungulate exclosures might promote OSS abundance is by creating unnaturally dense stands because no browsing has occurred to reduce stand density. These dense stands with abundant recruiting stems are the structure that seems most favorable for OSS population growth. A third strategy managers may consider for managing OSS is reducing aspen stand density via thinning. Thinning might also promote aspen resistance to drought, as reduced growth rates which occur in dense stands are associated with increased mortality during drought [8,30–32]. However, thinning must be implemented with care because aspen is sensitive to mechanical damage from logging equipment and susceptible to subsequent infection by canker-causing fungi and decay diseases [33]. Before we can wholeheartedly recommend use of prescribed fire or silvicultural strategies like thinning to manage OSS, experimental research is needed to assess the efficacy of these strategies for suppressing OSS.

In terms of suggested timing of treatment implementation, we observed prolonged OSS crawler emergence in northern Arizona, which complicates management strategies that seek to avoid the crawler stage, such as sanitation thinning. There may be no time of year when crawlers can be completely avoided, but crawler density is lowest in October through November and February through March. There is limited evidence to suggest that the risk of spreading OSS from infested slash to residual uninfested aspen is low. In a small pilot study tracking OSS development on aspen logs that were cut in May, we did not observe re-colonization of aspen on those cut logs throughout the summer. More research with larger sample sizes and with aspen cut at different times of year is needed, but these promising preliminary results suggest that OSS may not survive for long, if at all, on cut or dead hosts. Strategies that seek to target the crawler stage, such as application of horticultural oils or insecticides, should be applied in June through August when crawler density is highest.

Monitoring and Management Needs

Critical to managing any invasive species is robust monitoring to identify where the species occurs and what impacts it has. Continued monitoring of OSS is necessary both in areas of Arizona where the species has not yet been found (e.g., southern Arizona, North Kaibab, and White Mountains) and in areas where OSS already occurs, which would allow us to document potential changes to the species' range (i.e., will OSS migrate to higher elevations in the future?). We also recommend monitoring OSS in urban areas that contain aspen and in surrounding wildland aspen ecosystems, both of which may harbor sleeper populations of OSS [34]. Our research findings can help managers prioritize which aspen ecosystems to monitor. For example, OSS is most likely to occur on warmer, drier sites, in areas that have not recently experienced fire, and in stands that have dense recruitment, such as those inside fenced ungulate exclosures. Specifically, the climatic and elevation thresholds we identified (Fig. 3.6) can guide monitoring efforts. Although elevation is the easiest metric for managers to use when searching for OSS, the 2545 m threshold we observed in Arizona is liable to change across aspen's expansive range and as the climate continues to warm. Instead, the climate thresholds we observed are likely to be more consistent, and these climate data can be easily obtained for specific locations via ClimateNA (https://climatena.ca/).

There is dire need to assess the efficacy of OSS management interventions, such as silvicultural treatments, prescribed fire, and systemic insecticides [16]. In particular, we lack data on pre- and post-treatment application of prescribed fire in OSS-infested aspen stands. Prescribed fire could be one of the most efficient treatment options for suppressing OSS populations but remains an understudied tactic. Silvicultural trials assessing clearfelling and sanitation thinning are underway on the Flagstaff Ranger District of the Coconino National Forest and the Williams Ranger District of the Kaibab National Forest, and a small insecticide trial is planned for the Mogollon Rim Ranger District of the Coconino National Forest. Ongoing monitoring of these trials will be critical for informing future OSS suppression efforts.

Continued monitoring of aspen in existing and new monitoring plots is critical to address several questions that are relevant to the species' management. Although ample research on aspen responses to management was conducted in the 20th century, it is unclear whether and how those results hold up in an increasingly arid climate and in the face of novel disturbance regimes [8]. There are ample opportunities for contemporary experimental research on aspen management in Arizona. The following is a list of management-oriented research questions identified by Crouch et al. [8].

- Is there a certain fire size or area of aspen treated that will saturate ungulate browse and allow aspen to recruit without exclosures or reduced ungulate population sizes?
- What silvicultural systems are appropriate for promoting aspen resilience and adaptability?
- What are the appropriate prescribed fire parameters (e.g., return interval, intensity) for promoting aspen resilience and adaptability?
- What are the impacts of harvesting equipment on soil compaction and subsequent aspen regeneration?
- When is the optimal time to remove fenced exclosures?
- At what point has a declining aspen stand's root system died back enough that overstory removal or fire will no longer result in successful regeneration?
- Most studies on aspen regeneration only monitor short-term responses to management or disturbance. What is the long-term trajectory of aspen following fire, fencing, and silvicultural management, especially in mixed stands and after partial cutting?

Do you have questions or want to become involved in aspen/OSS research?

If you have questions about research on aspen or OSS monitoring/management, please contact Connor Crouch (connor.crouch@nau.edu) from Northern Arizona University. If you manage aspen ecosystems in Arizona and would like to become involved in experimental OSS or aspen management, please contact Dr. Kristen Waring (kristen.waring@nau.edu) from Northern Arizona University. If you have observed oystershell scale in a new area (e.g., North Kaibab, White Mountains, or southern Arizona), please contact Amanda Grady (amanda.grady@usda.gov) from USDA Forest Health Protection.

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