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Oystershell scale: an emerging invasive threat to aspen in the southwestern US

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Abstract Oystershell scale (OSS; *Lepidosaphes ulmi*) is an emerging invasive insect that poses a serious threat to conservation of quaking aspen (*Populus tremuloides*) in the southwestern US. Although OSS has been an urban pest in the US since the 1700s, it has recently spread into natural aspen stands in northern Arizona, where outbreaks are causing dieback and mortality. We quantified the ongoing outbreak of OSS at two scales: (1) local severity at two sites and (2) regional distribution across northern Arizona. Our regional survey indicated that OSS is widespread in lower elevation aspen stands and is particularly pervasive in ungulate exclosures. Advanced regeneration had the highest levels of infestation and mortality, which is concerning because this size class is an underrepresented component of aspen stands in northern Arizona. If OSS continues to spread and outbreaks result in dieback and mortality like we observed, then aspen in the southwestern US, and perhaps beyond, will be threatened. Three interacting factors contribute to OSS's potential as a high-impact invasive insect that could spread rapidly: (1) its hypothesized role as a sleeper species, (2) potential interactions between OSS and climate change, and (3) the species' polyphagous nature. Invasive pests like OSS pose an imminent threat to native tree species and, therefore, represent an immediate research and monitoring priority. We conclude with recommendations for future research and monitoring in order to understand OSS's biology in natural aspen stands, quantify impacts, limit future spread, and mitigate mortality and loss of aspen and other host species.

Keywords Forest health · Invasive species · *Lepidosaphes ulmi* · *Populus tremuloides* · Sleeper species

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Introduction

Invasive species are among the leading global threats to forest sustainability and biodiversity (Chornesky et al. 2005). Species are considered invasive when they are non-native to an ecosystem and their introduction causes, or is likely to cause, harm to the environment, the economy, or human health (Executive Office of the President 2016). Invasive forest pests have caused the decline of numerous tree species

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worldwide. Examples from the US include the near extinction of American chestnut (*Castanea dentata*) caused by *Cryphonectria parasitica* (Anagnostakis 1987), ongoing mortality of ash species (*Fraxinus* spp.) due to emerald ash borer (*Agrilus planipennis*) (Herms and McCullough 2014), and dieback and decline of multiple five-needle pines due to infection by *Cronartium ribicola*, the causal agent of white pine blister rust (Kinloch 2003). Some of these tree species, such as American chestnut, provide essential ecological services and are considered keystone species (Ellison et al. 2005), whereas others, like southwestern white pine (*Pinus strobiformis*), provide critical wildlife habitat and biodiversity but are not considered keystone species (Looney and Waring 2013).

Quaking aspen (*Populus tremuloides*) is the most widely distributed tree species in North America (Little 1971) and is considered a keystone species in the conifer-dominated western US (Campbell and Bartos 2001). Aspen provides critical habitat for a wide range of species (DeByle 1985; Rogers 2017) and makes a disproportionately large contribution to biodiversity (Chong et al. 2001; Kuhn et al. 2011). Aspen stands also provide a variety of ecosystem services, including significant contributions to carbon sequestration (Woldeselassie et al. 2012), nitrogen mineralization (Stump and Binkley 1993), water yield potential (LaMalfa and Ryle 2008), and revenue from hunting, tourism, and recreation (McCool 2001; Rogers 2017). Aspen also has cultural and aesthetic value as an iconic tree species of the American West (Assal 2020), perhaps best demonstrated by the phenomenon of “leaf peeping,” whereby recreationists travel to the high country in autumn to enjoy aspen’s beautiful golden leaves (Johnson et al. 1985).

The southwestern edge of aspen’s range runs through Arizona, USA, where the species is limited by the annual balance of temperature and precipitation and generally is not found below 2200 m in elevation (Alexander 1974; Rehfeldt et al. 2009). Aspen tends to occur in small stands within the ponderosa pine (*Pinus ponderosa*) forest type at these lower elevations (Shepperd and Fairweather 1994). As elevation increases, aspen stands generally become larger and more abundant, growing in the mixed-conifer and spruce-fir forest types (Alexander 1974; Reynolds et al. 2013). Acute aspen mortality events and chronic aspen decline have been documented across the western US during the past two decades (Gitlin et al. 2006; Fairweather et al. 2008; Worrall et al. 2010; Zegler et al. 2012; Singer et al. 2019). A combination of abiotic events, biotic agents, and chronic ungulate herbivory have contributed to high levels of aspen mortality in northern Arizona, ranging from 50 to 95% at some low elevation (< 2300 m) sites (Fairweather et al. 2008; Zegler et al. 2012). Chronic ungulate herbivory has also reduced aspen regeneration and recruitment in Arizona and across the Colorado Plateau (Fairweather et al. 2008; Zegler et al. 2012; Rogers 2017). Arizona is on the hot, dry southwestern edge of aspen’s range, and as a result, aspen in this region is experiencing increasing environmental stress from a warming climate (Zegler et al. 2012; Kane et al. 2014). We are focused here on an emerging invasive insect causing aspen dieback and mortality, not on general aspen ecology and health. Readers are referred to recent reviews on aspen ecology and health, including Frey et al. (2004), Morelli and Carr (2011), Rogers (2017), Landhäusser et al. (2019), and Singer et al. (2019) for more detailed information.

The emergence of an invasive insect, oystershell scale (OSS; *Lepidosaphes ulmi* L.), poses a serious threat to conservation of aspen in the southwestern US (Fig. 1). Although the species’ origin is uncertain, OSS is believed to have arrived in North America with European settlers, similar to many other introduced forest pests (Aukema et al. 2010), and was reported as a pest of apple trees (*Malus* spp.) as early as the 1700s (Howard 1894; Miller et al. 2005). OSS is now present throughout the US and much of Canada (Tothill 1919; Ciesla 2011) and is a common pest of many deciduous tree species, including aspen, in urban settings (Ciesla 2011; Cranshaw 2013). Although OSS is polyphagous and pervasive in North America, it has only been a serious pest of a few species in natural forest settings (Johnson and Lyon 1988; Ciesla 2011). OSS has killed entire stands of ash (*Fraxinus* spp.) in Ohio, USA (Sterrett 1915) and caused dieback and mortality of American beech (*Fagus grandifolia*) in New York and Maine, USA (DeGroot 1967; Houston 2001). Concerningly, OSS has recently spread into natural aspen stands in northern Arizona, where outbreaks are causing aspen dieback and mortality (Grady 2017). This acute mortality is occurring within the context of broader, chronic aspen decline (Fairweather et al. 2008; Zegler et al. 2012). As aspen stands in northern Arizona experience both the impacts of an increasingly warm climate and the unprecedented outbreaks

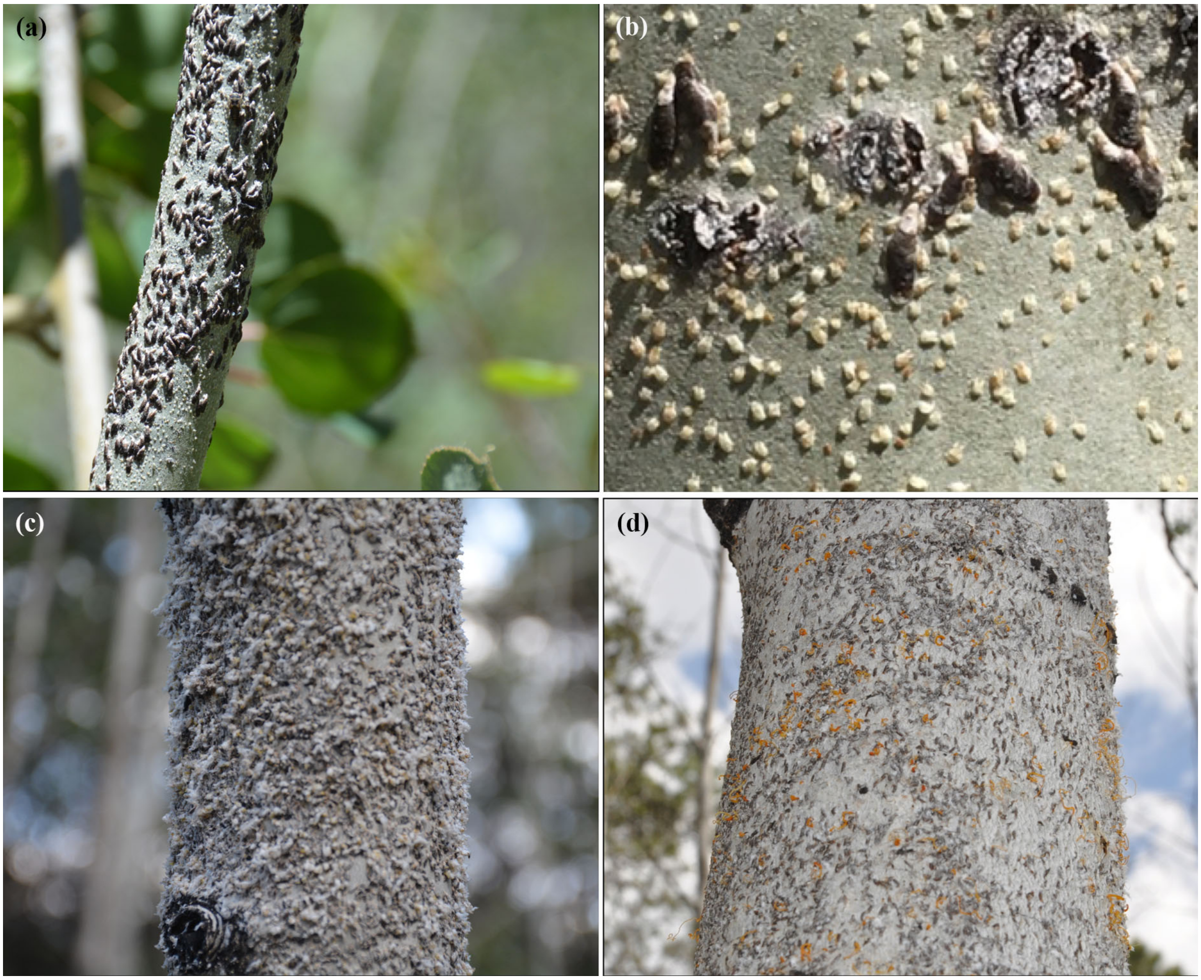

Fig. 1 OSS is an invasive insect that has recently spread into natural aspen stands in northern Arizona. OSS outbreaks are causing dieback and mortality of aspen due to the feeding activity of OSS, which causes cell death below the bark. Photographs show **a** OSS feeding on an aspen stem, **b** OSS crawler emergence from the overwintering egg site beneath dead females, **c** woolly flocculants created by OSS, and **d** OSS in association with *Cytospora* fungi

of OSS, they may be a harbinger of change for aspen throughout the rest of its range.

The generally accepted pattern of species invasions follows three stages: arrival, establishment, and spread (Liebhold et al. 1995). During the arrival phase, a species immigrates into new areas beyond its native range. Immigrations may occur via a multitude of vectors and along a variety of pathways, but to move into the next phase, the species must arrive alive in the new location. The second phase, establishment, occurs after the species arrives and requires a population to be persistent, or naturalized, in the new location (Liebhold et al. 1995). Following establishment, a population may be constrained by environmental variables that restrict population growth. Often, established populations are small but increasing, and only when the population growth rate increases do humans notice the species or the damage it causes. This is particularly true for sap-sucking insects, including armored scales, that do not cause noticeable damage until populations are large (Beardsley and Gonzalez 1975; Miller and Davidson 2005; Ciesla 2011). At this point, the species shifts into the spread phase, a period of rapid population growth and widespread geographic expansion (Liebhold et al. 1995). We hypothesize that OSS is a sleeper species that has awoken in northern Arizona and recently entered the spread phase of invasions (Liebhold et al. 1995; Frank and Just 2020).

Sleeper species were originally defined by Groves (1999) to describe invasive plants that had established in an area but had yet to increase their population size exponentially. The NRC (2002) went on to define such species more broadly, including all species whose populations remain at slow growth rates for long periods of time prior to widespread expansion.

Existing information on OSS is generally found in older publications and focuses on host species other than aspen, often in urban settings. We seek to address the lack of information about OSS outbreaks in natural aspen stands by outlining the biology of OSS, assessing its current distribution and impacts in northern Arizona, and highlighting potential management strategies and challenges. We then discuss our concerns about OSS's hypothesized role as a sleeper species, potential interactions between OSS and climate change, and OSS's polyphagous nature, all of which contribute to its potential as a high-impact invasive insect that could spread rapidly. We conclude with recommendations for future research and monitoring.

Biology of OSS

Oystershell scale, sometimes called mussel scale, is an insect in the order Hemiptera, family Diaspididae. OSS is a sap-sucking armored scale that inserts its stylet through the thin bark of woody host tissue to feed on fluids of non-vascular cells (Fig. 1a) (Griswold 1925; Beardsley and Gonzalez 1975). The life cycle is completed entirely on the woody host tissue (i.e., the surface of the bark on stems and branches), but some individuals attach to and feed on fruit such as apple (Wearing and Colhoun 2011; Fountain et al. 2012). There are two forms of OSS in the US—the lilac (banded) and apple (brown) forms—both of which infest species in the *Populus* genus as primary hosts (Griswold 1925; Johnson and Lyon 1988). The OSS life cycle and number of generations vary by form, host, and location across its range in the US and around the world (Griswold 1925; Johnson and Lyon 1988; Ciesla 2011). Reproduction of most armored scales is bisexual; however, bisexual and parthenogenetic races of OSS occur (Beardsley and Gonzalez 1975; Miller and Davidson 2005). One to two generations have been documented in the US, and regions with cooler climates and higher elevations commonly have only one generation per year (Johnson and Lyon 1988). In Colorado, USA, OSS has been reported as univoltine with asexual reproduction (Cranshaw 2013), and early research described only parthenogenetic races in North America (Ferris 1937).

OSS overwinters as eggs beneath the protective waxy shells, or tests, of dead females (Johnson and Lyon 1988), and eggs hatch in late spring or early summer depending upon the location. Emergence is variable across the western US, ranging from May in Oregon (Schuh and Mote 1948) to late June or early July in Wyoming (Spackman 1991). In northern Arizona most eggs hatch in early June (Fig. 2); however, we observed prolonged egg hatch and crawler emergence through July and August 2020. It is unclear if egg hatch is prolonged or if multiple forms occur in Arizona. Following eclosion, first instar nymphs, also known as crawlers, disperse along the host's stem or branch to establish a feeding site (Fig. 1b). This dispersal stage lasts only a few days until the crawler finds a suitable site and begins to feed (Quesada et al. 2018). Crawlers mature over the summer (Fig. 2), developing a waxy outer shell, or test, for protection (Fig. 1a) (Beardsley and Gonzalez 1975). Individuals remain at their feeding site through adulthood. In areas with bisexual populations, males

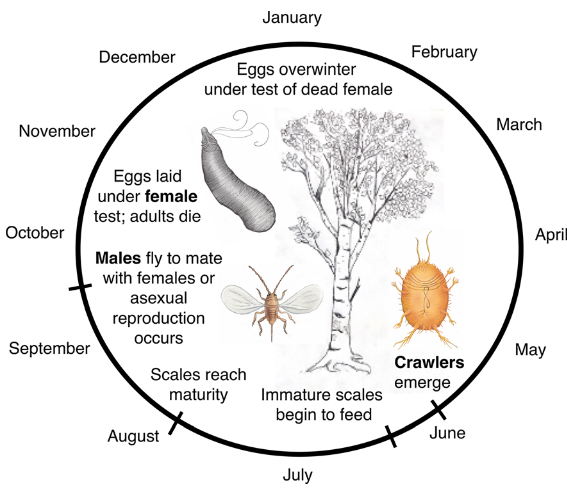

Fig. 2 Diagram of OSS's life cycle on aspen in northern Arizona. Understanding timing of the crawler stage is particularly important for management of OSS because the insect disperses and is most vulnerable during this stage. It is unclear whether the population in northern Arizona is bisexual or parthenogenic, so both strategies are shown here. Aspen illustration by Evan Hofstetter; OSS illustrations by D.E. DePinte

shed their tests and fly to locate females during the fall (Fig. 2). It is unclear whether the population in northern Arizona is bisexual or parthenogenetic, so we include both strategies in the biology and life cycle timeline (Fig. 2). Females can lay 50–100 eggs under their test, after which the female dies and shrivels (Griswold 1925; Copland 1984). The dead female's test protects the eggs over the winter until the eggs hatch and crawlers emerge the following spring or summer (Fig. 2) (Ciesla 2011).

OSS dispersal is limited due to the sessile nature of most life stages and environmental restrictions on crawlers (Griswold 1925; Beardsley and Gonzalez 1975; Miller and Davidson 2005). This dispersal stage is limited to a few days and a short distance, generally less than 1 m, because of the nymphs' low energy reserves (Beardsley and Gonzalez 1975; Koteja 1985; Magsig-Castillo et al. 2010). Temperature, humidity, dustiness, host species, and population density influence dispersal speed and behavior (Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010). OSS prefers shady environments (Furniss and Carolin 1977), and avoidance of direct sunlight has been recorded for several species of Diaspididae (Gentile and Summers 1958; Mayfield and Jetton 2020). In addition to active crawling, OSS may be passively dispersed via wind or animal assistance (Griswold 1925; Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010; Wearing and Colhoun 2011). Blank et al. (1997) suggest that dispersal distance depends on the strength and uniformity of prevailing winds. In northern Arizona, strong spring winds coincide with emergence of OSS crawlers, but exact dispersal distances within and among trees in natural forest settings are unknown. In New Zealand, Wearing and Colhoun (2011) reported the proportion of fruit contaminated from OSS infested shelterbelts decreased from $> 90\%$ to $< 1\%$ at 64 m away from the shelterbelt. However, windblown crawlers are known to travel up to several kilometers (Greathead 1990). Non-host screening may also influence dispersal. Like other insects, OSS can also disperse great distances via passive transport on infested material (Beardsley and Gonzalez 1975; Aukema et al. 2010).

When viewed under a hand lens, the origin of OSS's name becomes clear: the insect's test closely resembles an oyster shell. The test is grey or brown in color (Fig. 1a), although we have observed that the test of immature individuals tends to appear yellow-orange to pink. The adult body underneath the test is pale yellow, but the actual body is generally not visible beneath the grey-brown test. The adult female test is subcircular, moderately convex, with the exuviae subcentral and about 1.3 mm in length. For immature males, the test is smaller and elongate. The adult male, which resembles a tiny gnat, sheds its test and is capable of flight. However, adult males lack mouthparts for feeding. Another invasive scale insect, willow or poplar scale (*Diaspidiotus gigas*), is known to infest aspen, but it is easily distinguished from OSS because willow scale is round in shape (Progar et al. 2014).

OSS infestations initially affect only a few branches or small areas of the stem, but because they are persistent and have significant reproductive capacity, they can encrust entire stems and branches, leading to branch dieback and eventually death of the host plant (Griswold 1925; Johnson and Lyon 1988). On many plants, OSS blends in well with the underlying bark, so extensive colonies and injury symptoms may develop before OSS is observed (Ciesla 2011). Large colonies can form a crust of females that appear as dark, sooty patches on the white bark of aspen. Other signs of OSS include waxy or woolly flocculants (Fig. 1c), which we have observed during the past few summers. Necrosis of the host's tissue may occur at the feeding site, and bark splitting often occurs on areas of the stem heavily infested with OSS (Griswold 1925; Beardsley and Gonzalez 1975). OSS damage may also increase host susceptibility to secondary pathogens by weakening host defenses or creating infection courts. For example, *Cytospora* fungi are commonly associated with mortality in stressed aspen and have been observed in association with OSS damage (Fig. 1d).

OSS is polyphagous on many deciduous tree species and is common in urban settings (Johnson and Lyon 1988; Townsend 2005; Ciesla 2011). Urban settings in the context of this paper are inclusive of trees in any unnatural, developed setting including urban trees (sensu stricto), orchards, nurseries, and ornamental trees. There are over 100 known hosts of OSS, including apple, poplar (*Populus* spp.), willow (*Salix* spp.), lilac (*Syringa* spp.), maple (*Acer* spp.), plum and cherry (*Prunus* spp.), birch (*Betula*), beech (*Fagus* spp.), ash, pear (*Pyrus* spp.), and *Cotoneaster* spp. (Richards 1962). Hosts reported from Idaho and Utah, USA include Bebb willow (*Salix bebbiana*), narrowleaf willow (*Salix exigua*), Scouler's willow

(*Salix scouleriana*), narrowleaf cottonwood (*Populus angustifolia*), black cottonwood (*Populus balsamifera*), Fremont cottonwood (*Populus fremontii*), and dogwood (*Cornus* spp.) (FHP 2018, 2019). In northern Arizona we have observed OSS on boxelder (*Acer negundo*), Arizona alder (*Alnus oblongifolia*), California buckthorn (*Frangula californica*), Arizona ash (*Fraxinus velutina*), Arizona walnut (*Juglans major*), narrowleaf cottonwood, and Bebb willow. We have also observed OSS on understory plants, namely snowberry (*Symphoricarpos* spp.), ceanothus (*Ceanothus* spp.), and lupine (*Lupinus* spp.).

Local severity and regional distribution

We quantified the ongoing outbreak of OSS in Arizona at two scales: (1) local severity at two sites with known OSS infestations and (2) regional distribution across aspen stands in north-, east-, and west-central Arizona (Table 1). All of these subregions fall within the area that we have been referring to as northern Arizona, but we have classified the larger northern Arizona landscape into these three subregions to paint a finer geographic picture of our observation landscape. Although formal documentation of OSS in natural forest settings is rare, we also gathered observations of OSS outside of Arizona to determine if and where it has spread.

Local severity.

We evaluated the local impact of OSS outbreaks by quantifying OSS severity and aspen mortality at two sites in northern Arizona with known infestations. Both sites were located in aspen stands within the ponderosa pine forest type. The Nordic Village (NV) study site was located about 30 miles north of Flagstaff, Arizona (35°23′N, 111°46′W) at an elevation of 2455 m. This site consisted of two ungulate exclosures approximately 2.8 and 6.8 ha in size and spaced 500 m apart. The Spring Valley (SV) study site was located near Parks, Arizona (35°21′N, 111°58′W) at a slightly lower elevation of approximately 2285 m. The SV site consisted of five smaller ungulate exclosures ranging in size from 0.6 to 1.6 ha and spaced 30–60 m apart. Exclosures are tall fences erected around aspen stands to exclude ungulates, including elk, deer, and cattle, from browsing aspen regeneration. Exclosures are important to monitor because they are the most effective strategy for promoting aspen regeneration and recruitment at many sites in northern Arizona (Shepperd and Fairweather 1994; Bailey and Whitham 2002; Fairweather et al. 2008). The genetic diversity of the aspen exclosures discussed in this paper is unknown. While host genetics may play a role in the spread and

Table 1 OSS presence, absence, and observed elevation range across the observation landscape in northern Arizona. Observation locations include permanent aspen monitoring plots, ungulate exclosures, and incidental observations. Information on geographic location and climate is also shown. Mean annual temperature and precipitation values were obtained from locations at median elevations where aspen occurs in each of the four national forests. These values represent 30-year averages and were obtained from the PRISM database (Daly et al. 2008)

Geographic location in Arizona	National Forest	Observation type	OSS observed	OSS not observed	Observed elevation range of OSS (m)	Elevation range of sampling locations (m)	Mean annual temperature (°C)	Mean annual precipitation (cm)
North-central	Coconino	Exclosures	50	53	2107–2533	1990–2566	7.4	70.8
North-central	Coconino	Monitoring plots	16	108	2169–2449	2169–2868	7.4	70.8
North-central	Kaibab	Exclosures	44	0	2154–2523	2154–2523	7.1	59.3
West-central	Prescott	Incidental	4	n/a	2020–2148	2020–2148	10.6	66.0
East-central	Apache-Sitgreaves	Incidental	12	n/a	2166–2373	2166–2373	9.6	88.0

intensification of OSS, no research has focused on this question.

We assessed OSS presence and severity and aspen mortality in fall 2018 for the NV exclosures and in summer 2019 for the SV exclosures. We divided the two large NV exclosures into smaller units: the 2.8 ha exclosure was divided into three units, and the 6.8 ha exclosure was divided into six units. Within each of these nine units and within the five smaller SV exclosures, we established a network of monitoring plots. Four plots were located 20 m from the approximate center of each unit or exclosure. In the SV exclosures, a fifth monitoring plot was also established at the center because aspen stem density was lower in these exclosures, requiring us to sample more area to capture a sufficient number of aspen stems. Each monitoring plot consisted of a circular regeneration plot with a 4 m radius nested within an 8 m radius overstory plot. In the 8 m overstory plot, all trees with diameter at breast height (dbh) > 10.1 cm were measured. In the 4 m regeneration plot, we classified stems into three size classes: saplings (5.1–10.1 cm dbh), tall regeneration (< 5.1 cm dbh; > 1.4 m tall), and short regeneration (< 1.4 m tall). We assessed OSS severity using five categories: none (OSS not present), trace (only a few OSS present), light (dispersed infestation, small pockets of OSS present), moderate (dense infestation of OSS in larger pockets), and severe (very dense infestation, cannot see stem beneath OSS). However, we have since developed a quantitative rating system (Box 1) that we will use for future monitoring and research.

Across all seven exclosures, OSS was present on 79.6% (standard error [SE] = 0.98%) of aspen stems (Fig. 3a). Using the OSS severity rating, 21.3% (SE = 0.99%) of aspen stems were categorized as trace infestations, 16.4% (SE = 0.90%) were light, 7.8% (SE = 0.65%) were moderate, and 34.0% (SE = 1.15%) were severe. The two NV exclosures had a lower proportion of stems infested (59.2%, SE = 1.29%) than the five SV exclosures (89.6%, SE = 1.90%). Similarly, OSS infestation was more severe in the SV exclosures, with 57.6% (SE = 3.07%) of aspen stems severely infested compared to 16.3% (SE = 0.97%) in the NV exclosures. The difference in infestation between the two study sites could be explained by differences in climate or time since establishment. The SV exclosures occur at a lower elevation than the NV exclosures, so a slightly warmer climate may have directly improved conditions for OSS population growth. On the other hand, aspen in the SV exclosures may be under increased stress from warmer temperatures (Zegler et al. 2012; Kane et al. 2014) and, as a result, may be more susceptible to OSS. Differences in infestation might also be the result of earlier OSS establishment in the SV exclosures. OSS was documented on aspen near the SV site as early as 2009 (Zegler et al. 2012), whereas the first report of OSS on aspen near the NV site did not occur until nearly a decade later (Grady 2017).

OSS was present on aspen stems of all sizes (Fig. 3b). Among the four aspen stem size classes we explored, tall regeneration had the greatest OSS presence and severity, with 89.7% (SE = 1.37%) of stems infested and 51.2% (SE = 2.25%) of stems rated as severe. Mean infestation on the other three size classes was lower, with OSS present on 53.1–62.1% (SE = 1.53–2.87%) of aspen stems and with

Box 1 Quantitative OSS rating system

OSS severity is rated on each tree from ground level to 6 m. Each tree's stem (up to 6 m) is divided into thirds for rating, and severity is rated on the north and south side of each tree. Each stem section and side are then rated using the following numeric system (see Online Resource 1 for illustrations of each severity rating)

Rating	Description
0	No OSS present
1	Trace—only a handful of OSS present
2	Light—OSS covers < 50% of the section
3	Severe—OSS covers > 50% of the section

For regenerating stems, this rating will encompass the entire tree including the crown, whereas for overstory trees, the rating may only encompass the bole. In addition, it should be indicated whether OSS is present or absent in the tree's crown. Binoculars should be used for trees taller than 6 m, and a hands lens is recommended for field identification of OSS

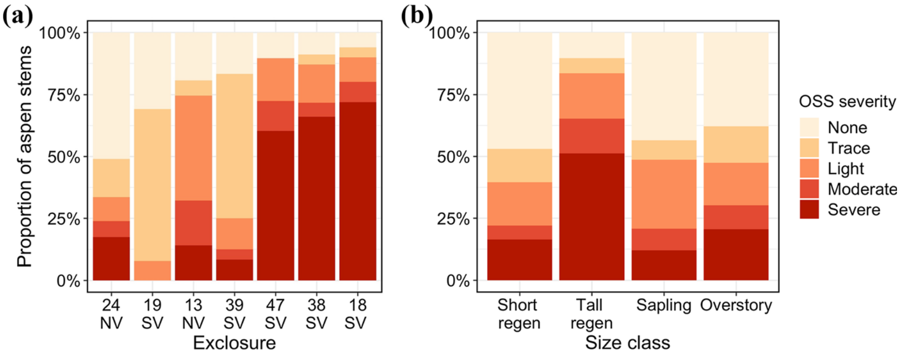

Fig. 3 Proportion of aspen stems infested by OSS **a** in seven ungulate exclosures in the Nordic Village (NV) and Spring Valley (SV) study sites and **b** across four stem size classes. Exclosures are the most successful strategy for promoting aspen regeneration at lower elevation sites in northern Arizona, but OSS threatens the long-term success of these exclosures. The high degree of infestation on tall regeneration is concerning because this size class is an important and underrepresented component of aspen stands in northern Arizona

12.0–20.6% (SE = 1.28–1.55%) of stems rated as severe. Tall regeneration also had the highest degree of mortality among the four size classes. Half of tall regeneration stems were dead (SE = 2.25%), whereas 5.1% (SE = 0.70%) of overstory trees, 27.5% (SE = 2.13%) of saplings, and 36.3% (SE = 2.76%) of short regeneration stems were dead. We cannot say with certainty that OSS killed these trees, but given the intense severity, OSS was likely an inciting factor of the mortality we observed (Manion 1991; Worrall et al. 2010). The increased infestation on and mortality of tall regeneration is concerning because this size class is an important and underrepresented component of aspen stands in northern Arizona (Zegler et al. 2012; Clement et al. 2019). Aspen regeneration is especially valuable in exclosures because the primary goal of exclosures is to promote regeneration and recruitment of aspen by preventing ungulate herbivory (Fairweather et al. 2008; Zegler et al. 2012). Concerningly, our observations indicate that OSS outbreaks threaten the long-term success of these exclosures.

Regional distribution.

We quantified the distribution of OSS in northern Arizona by mapping observations of the species across north-, east-, and west-central Arizona (Table 1, Fig. 4). These observations, which were obtained with assistance from local foresters, include a combination of aspen monitoring plots, ungulate exclosures, and incidental observations. Observations were made in 2017–2020. We created one map of all observed OSS locations (Fig. 4a) and two finer-scale maps (Fig. 4b, 4c) which include locations where OSS was not observed. All three maps show the potential range of aspen estimated by Little (1971) and digitized by Thompson et al. (1999). The finer-scale maps also show the observed range of aspen, which is sparse and patchy compared to Little's (1971) estimated range (Fig. 4b, 4c). This observed aspen range map was obtained by aerially detecting aspen from a fixed wing aircraft and then augmenting flight data with remotely sensed imagery, resulting in fine-scale aspen mapping over our study area (DePinte 2018). Although updated range maps based on FIA data and predictive modeling are available in Ellenwood et al. (2015), the maps used here (DePinte 2018) are based on observed aspen in the study area and are the most accurate estimation of where aspen occurs.

Our monitoring efforts indicated that OSS is widespread in natural aspen stands across the observation landscape and is contributing to aspen dieback and mortality (Fig. 4a). Observations of OSS were restricted to aspen at the lower extent of its elevational range, generally occurring below 2500 m (Table 1). The highest observed OSS infestation was 2533 m in elevation, and the lowest observed infestation was 2020 m in elevation. The upper limit of OSS observations likely represents an elevational or climatic constraint for OSS because aspen exists above 2500 m in the region. This elevational limit was particularly evident on the San Francisco Peaks north of Flagstaff, where many aspen stands at higher elevations exist but OSS was generally not observed (Fig. 4b). In contrast, the lower limit of OSS observations in our survey

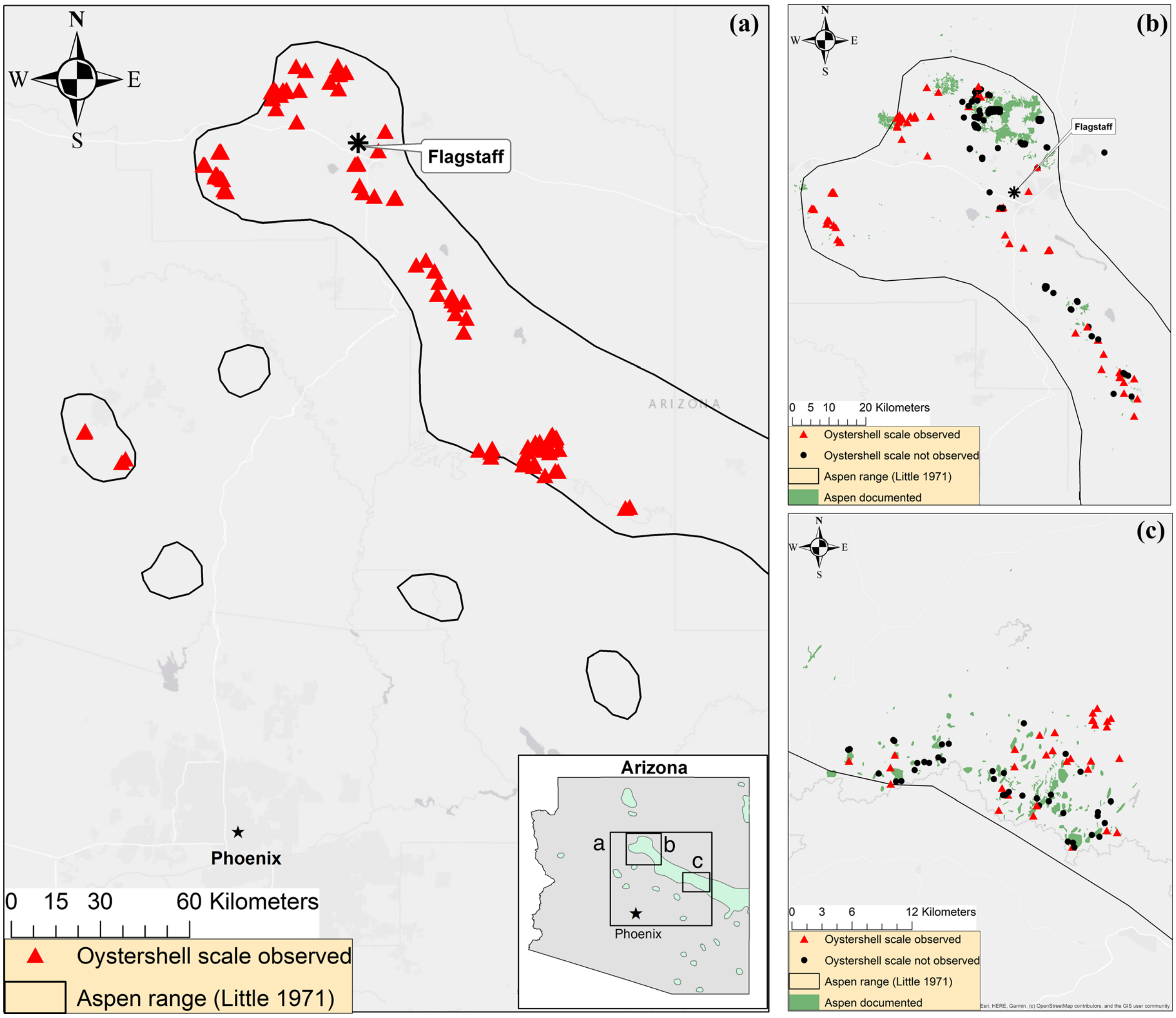

Fig. 4 Maps showing **a** the extent of OSS across northern Arizona and **b, c** locations where OSS has and has not been observed. These observation locations include aspen monitoring plots, ungulate exclosures, and incidental observations. See text for details regarding the different aspen range maps. The white lines in the base map represent interstates, and the darker gray areas represent administrative boundaries, urban areas, and surface water

corresponds with the lower limit of aspen's elevational range in Arizona, not a climatic limitation of OSS. We know that OSS occurs at lower elevations in urban settings but not whether OSS is present at lower elevations in natural forest settings, representing a need for increased monitoring and reporting.

OSS is particularly pervasive in ungulate exclosures, which are generally constructed at lower elevations where aspen stands are small and heavily affected by ungulate herbivory. We assessed OSS presence in 147 of the 303 exclosures in the north-central subregion (Fig. 4a) and found that OSS was present in 63.9% (SE = 3.96%) of the exclosures sampled (Table 1). These findings further emphasize the threat that OSS poses to the long-term success of exclosures as a management strategy for promoting aspen regeneration. In contrast to exclosures, OSS was less pervasive in monitoring plots. The species was present in 12.9% (SE = 3.01%) of the 124 permanent monitoring plots established by USDA Forest Service Forest Health Protection in the north-central subregion. Incidental observations have also been made in the east- and west-central subregions. These subregions include areas where OSS is widespread, although only a few of these observations have been formally documented and geolocated (Ellen Mering, Forester, Apache-Sitgreaves NF, personal communication). The presence of OSS in these subregions has prompted the development of more extensive monitoring programs.

Beyond northern Arizona, FHP (2018, 2019) has documented OSS in natural forest settings in Idaho (Custer County) and Utah (Beaver, Wayne, and Utah Counties) on hosts listed in the Host range section. OSS has been observed in natural aspen stands in the Black Hills Mountain Range in South Dakota, USA, in the Niobrara National Scenic River Way in Nebraska, USA (Kurt Allen, Entomologist, Forest Health Protection, personal communication), and throughout New Mexico, USA (Bernalillo, Cibola, Mora, and Santa Fe Counties) (Greg Reynolds, Plant Pathologist, Forest Health Protection and John Formby, Forest Health Specialist, New Mexico Forestry, personal communication). We have also observed OSS on aspen in a natural forest setting in the Schell Creek Mountain Range in Nevada, USA and on narrowleaf willow (*Salix exigua*) near Escalante National Monument in Utah. OSS has been documented on aspen in urban settings in Colorado, including Fort Collins (Bradley Lalande, Forest Pathologist, Forest Health Protection, personal communication) and Durango (Andrew Clements, FIA Forester, Colorado State Forest Service, personal communication), and we have observed OSS on urban aspen in Flagstaff, Arizona and Rock Springs, Wyoming. See Online Resource 2 for a supplemental map of all these locations. Across North America, OSS occurrence in natural forest settings is poorly documented, but the species may be widespread in the interior western US, representing a need for increased monitoring and reporting.

Potential management strategies

The first line of defense against invasive species like OSS is to prevent new invasions (Lodge et al. 2006; Simberloff et al. 2013). When prevention fails, early detection and rapid response following the invader's arrival and establishment have a greater success rate and lower economic cost than mitigation of invaders after widespread ecological and economic harm has occurred (Simberloff et al. 2013). The severity and extent of OSS infestations in northern Arizona and the potential for rapid spread of OSS throughout the western US make research and development of rapid response management strategies an immediate priority.

Natural controls.

Several natural enemies of OSS exist, and they have been studied extensively in apple and stone fruit orchards (Ewing and Webster 1912; Tothill 1919; Lord and MacPhee 1953; Karsemeijer 1973; Miller and Davidson 2005). These enemies include mites (Hemisarcoptidae), parasitoid wasps (Aphelinidae), and lady bird beetles (Coccinellidae) (Tothill 1919; Lord and MacPhee 1953). Two important natural enemies of OSS in North America are *Meisarcoptes malus*, a predatory mite that feeds on OSS eggs and other life stages, and *Aphtis mytelaspidis*, a chalcid that parasitizes OSS (Ewing and Webster 1912; Progar et al., 2014). In northern Arizona we have observed predation of OSS by the twice-stabbed lady beetle (*Chilocorus stigma*) and an unidentified red-colored mite. We have also observed parasitism by an unknown species, which leaves a single round exit hole on the OSS test.

Given the absence of significant predation, temperature might be the most effective limiting factor for OSS populations. Although further study is warranted, OSS outbreaks in northern Arizona generally occur below 2500 m in elevation (Table 1), which is considered low to moderate elevation for aspen in this region (Alexander 1974). Research is needed to understand the correlation between elevation and OSS infestation, but temperature is a likely explanation. Fitness and abundance of other scale insect pests has been linked to climate (Frank 2020; Just et al. 2020), and low temperatures are known to reduce survival of overwintering OSS eggs (Tothill 1919). Therefore, colder temperatures at higher elevations might directly limit OSS. Alternatively, the environmental stress caused by warmer, drier conditions at lower elevations might predispose aspen to infestation by OSS.

Management in urban settings

Management strategies for OSS infestations on high-value trees are consistent with strategies used for other armored scales (Miller and Davidson 2005). Effective management practices in urban settings include pruning, scrubbing, horticultural oils, and insecticides.

OSS is an obligate parasite, so pruning infested branches is an effective management practice (Townsend 2005; Cranshaw 2013; Karren et al. 2019). However, OSS commonly attacks aspen stems, which renders pruning ineffective. An effective management tactic for infested stems is gentle scrubbing with a soft dish pad (Cranshaw 2013; Karren et al. 2019), but scrubbing is impractical when the branches of taller trees are infested because OSS is either out of sight or inaccessible. Therefore, pruning and scrubbing can be complementary, yet expensive and labor intensive, management techniques.

OSS infestations in urban settings can also be managed through application of horticultural oils at two different times during the species' life cycle (Miller and Davidson 2005; Ciesla 2011; Quesada et al. 2018). Dormant season oils can be applied during the host's dormant season to smother overwintering OSS eggs (Miller and Davidson 2005; Cranshaw 2013; Karren et al. 2019). However, the eggs' waxy test keeps them well protected and often prevents all eggs from being killed by dormant oil application (Townsend 2005; Cranshaw 2013; Karren et al. 2019). A more effective approach is to apply growing season oils in late spring or early summer to target the species' crawler stage (Townsend 2005; Cranshaw 2013). OSS is most vulnerable during the crawler stage of its life cycle (Fig. 2) when it lacks a protective waxy test (Griswold 1925; Johnson and Lyon 1988; Miller and Davidson 2005; Quesada et al. 2018). The drawback to summer oils is that they require precise timing and repeated applications to be effective (Quesada and Sadof 2017) and should be avoided when plants are stressed by heat, drought, or wind (Miller and Davidson 2005). An advantage of horticultural oils, though, is that they are only active when wet, which minimizes potential negative impacts on non-target species (Miller and Davidson 2005).

The final option for management of OSS infestations in high-value, urban trees is through application of contact insecticide sprays or systemic insecticides. Like summer horticultural oils, insecticide sprays are targeted at the species' crawler stage, so proper timing of application is critical (Miller and Davidson 2005; Quesada et al. 2018). In addition, full coverage of a severely infested tree is a challenge for both insecticide sprays and horticultural oils (Karren et al. 2019), but systemic insecticides overcome the issues of timing and coverage by moving systemically within the plant. Several insecticides are registered for use on armored scales, including common broad-spectrum neonicotinoids and pyrethroids, which act on the insect's nervous system (Quesada and Sadof 2017; Quesada et al. 2018). Dinotefuran is a neonicotinoid that is effective against armored scales and can be applied as a soil drench, foliar spray, or bark spray (Simon-Delso et al. 2015). A drawback of soil drench applications is that they require an adequate supply of water to be taken up by the host, whereas bark sprays do not need to be applied with a significant amount of water (Quesada and Sadof 2017). Systemic bark sprays are also preferred over soil drench products on sites with rocky soil conditions that increase the potential for run-off into nearby waterways. Although systemic insecticide treatments are expensive, they are perhaps the most effective tool for managing OSS infestations in urban settings (Karren et al. 2019). However, repeated use of insecticides may lead to resistance and may also have negative impacts on non-target species (Lord and MacPhee 1953; Miller and Davidson 2005).

Management in natural aspen stands

Treatments for managing OSS on high-value trees are often expensive or time-consuming and are impractical for use at the landscape scale. The current OSS outbreak in northern Arizona is the first reported outbreak on aspen outside of an urban setting. Therefore, there are no scientifically proven strategies for managing OSS in natural aspen stands, which makes research and development of such strategies an immediate priority. Here, we outline potential strategies for managing OSS in natural aspen stands, highlight experimental treatments that are underway on national forest land in northern Arizona, and discuss challenges of managing OSS at the landscape scale.

Silviculture is one potential tool for managing OSS in natural aspen stands. Silvicultural strategies play a critical role in management of other forest insects and diseases, including non-native species (Waring and O'Hara 2005; Muzika 2017). Silvicultural practices are a component of integrated management of beech bark disease (*Cryptococcus fagisuga* and *Neonectria* spp. complex), emerald ash borer, and gypsy moth (*Lymantria dispar*) (Ostrofsky and McCormack 1986; Muzika 2017). Silvicultural strategies were part of an integrated pest management program to slow the spread of the invasive scale insect, *Matsucoccus feytaudi*, on maritime pine (*Pinus pinaster*) in Italy (Sciarretta et al. 2016). Silviculture could be an effective tool for managing OSS directly by removing infested hosts or indirectly by improving host vigor (Waring and O'Hara 2005); however, the relationship between OSS and host vigor is currently unknown. Clearfell treatments, which remove all mature trees from a stand, could hypothetically eradicate OSS from the stand because it is an obligate parasite and requires living host tissue to complete its life cycle. This might be practical in northern Arizona where aspen stands are relatively small, but presence of OSS on understory plants or aspen regeneration would make clearfelling alone insufficient for eradication. On the other hand, sanitation thinning, which removes heavily infested trees, might improve vigor of residual trees, allowing them to better defend against OSS. This would not eradicate OSS from the stand, so additional practices may be needed for successful management of the species. At present, the efficacy of silvicultural strategies is unknown because they have not been implemented and monitored over an extended period of time and because little is known about OSS's dispersal distance, rate of spread on and between hosts, and preference for vigorous versus stressed hosts.

Land managers in the north-central subregion of Arizona are testing the effectiveness of silvicultural strategies in managing OSS because the need to reduce mortality of aspen from OSS is urgent (Fig. 5). This subregion is at the epicenter of OSS's spread into natural aspen stands, and it was in these stands where OSS outbreaks were first observed (Zegler et al. 2012; Grady 2017). Land managers will be implementing a clearfell treatment, in which the harvested stems will be placed into slash piles and burned. A sanitation thinning treatment is also being tested in which aspen stands will be thinned to roughly 3 m $\times$ 3 m spacing and the least infested stems will be prioritized as leave trees. These experimental treatments will be applied in the same exclosures highlighted in Fig. 3a, and we will continue to monitor these stands to assess treatment efficacy.

Fire is an effective management strategy in aspen ecosystems (Brown and DeByle 1989; Shepperd 2001) and is a promising potential tool for OSS management. The thin bark of aspen makes it sensitive to fire, so relatively low intensity fire can induce high levels of aspen mortality. However, after undergoing a disturbance that causes overstory mortality, aspen generally responds by producing abundant suckers, which should eventually grow to replace the dead overstory (Schier 1973; Long and Mock 2012). Prescribed fire is an effective management strategy for other forest insects and diseases (Parker et al. 2006), and in the case of OSS, fire could directly destroy the insect or indirectly kill it by killing host plants. Prescribed fire has a few advantages over other potential strategies for OSS management. First, fire can kill multiple host species on site including small shrubs which may harbor OSS. Second, fire can be applied relatively inexpensively over large areas compared to silvicultural operations or application of insecticide. Finally, fire is a natural component of aspen stands and poses less risk and controversy than application of insecticides or large-scale silvicultural operations. There are many considerations and complexities in the application of prescribed fire including current fuel load, timing and intensity of the fire, and proximity to homes or other permanent structures. However, the natural relationship between aspen and fire paired with the obligate nature of OSS make fire a promising strategy for management of OSS.

Other potential strategies for managing OSS in natural aspen stands include application of systemic insecticides or biological control using a fungal entomopathogen. Of the strategies proven effective for OSS management in urban settings, systemic insecticides have the most promise for adaptation to the landscape scale. Unlike the other urban-oriented approaches, systemic insecticides can be applied efficiently on the landscape through soil drenching or bark sprays. Although application of systemic insecticides has not been attempted in natural aspen stands, these insecticides may be effective because they can target OSS on any woody tissue of all infested hosts. The full coverage provided by systemic insecticides would be difficult, if not impossible, to achieve through pruning, scrubbing, horticultural oils, or spray insecticides. However, potential non-target impacts of insecticides are a major drawback for their use in natural forest settings. Another unproven, but potentially promising, approach to OSS management at the landscape scale is application of fungal entomopathogens, such as *Beauveria bassiana*. This fungus occurs naturally in temperate mixed conifer

Fig. 5 Photograph of overstory aspen mortality caused by OSS on the Coconino NF. The foreground shows a pile of aspen stems that have been cut, and will later be burned, as part of an experimental clearfell treatment to manage OSS

forests (Ormond et al. 2010) and is an important biological control agent for an array of agricultural and forest pest species (USEPA 2000). OSS is a known host of *B. bassiana* (Leatherdale 1970; Evans and Prior 1997), and further study is warranted to determine whether *B. bassiana* or other fungal entomopathogens would be effective biological controls of OSS in natural aspen stands.

There are a number of challenges that complicate management of OSS in natural aspen stands. The insect's small size makes early detection difficult. Unless extremely close attention is paid during surveys, OSS will likely go undetected until outbreaks become severe enough that large patches of the insect are visible or hosts begin to exhibit symptoms of infestation, such as crown dieback or mortality. OSS's small size also makes methods of eradication that depend on detection (e.g., scrubbing, pruning, or targeted spraying of oils and insecticides) difficult because a single individual can easily go unnoticed, particularly if it is present in the tree's crown. Similarly, small insects like OSS are more easily transported to new areas inadvertently because individuals are so difficult to detect (Ciesla 2011). Another significant challenge for OSS management is the wide array of host species it can attack as a polyphagous pest. When a pest is present on more than one host species in a given area, management inherently becomes more challenging because certain strategies will become ineffective if used alone. For example, in exclosures at the SV site, we observed OSS on understory plants (*Ceanothus* spp. and *Lupinus* spp.) in addition to aspen. As a result, silvicultural strategies designed to remove infested aspen, such as clearfelling, will not eradicate OSS from the stand, necessitating the use of an additional strategy, such as prescribed fire, to remove OSS from the understory. Therefore, management of OSS in natural aspen stands must account for presence of OSS on other host species.

Implications of potential future spread

More than 85% of the over 450 non-native insects introduced to the US have not caused notable damage to trees in urban or natural forest settings (Aukema et al. 2010). However, among the minority that do, a few threaten conservation of their host species. Invasive sap-sucking insects, including scale insects, that fall into this category include hemlock woolly adelgid (*Adelges tsugae*), balsam woolly adelgid (*Adelges piceae*), and beech scale, which vectors beech bark disease (Bentz et al. 2020). If OSS continues to spread and outbreaks result in dieback and mortality like we have observed in northern Arizona, then conservation of aspen in the southwestern US, and perhaps beyond, will be threatened. Three interacting factors contribute to OSS's potential as a high-impact invasive insect that could spread rapidly: (1) its hypothesized role as a sleeper species, (2) potential interactions between OSS and climate change, and (3) the species' polyphagous nature.

We hypothesize that OSS is a sleeper species because it has been in the US for three centuries (Howard 1894; Miller et al. 2005), but until recently, it was not a concern in natural forest settings (Ciesla 2011). The earliest report that we have found of OSS in natural aspen stands was in 1991 in the Prescott NF (Fairweather 1992). In this report, OSS infestations were severe on large aspen in one portion of the stand, but not all trees were infested (Fairweather 1992). The first peer-reviewed report of OSS's presence in natural aspen stands was from data collected in 2009 and 2010 on the Kaibab NF (Zegler et al. 2012). At that time, OSS populations were relatively small and were not causing significant aspen dieback or mortality (Zegler et al. 2012). However, Grady (2017) later documented outbreaks of OSS causing dieback and mortality in aspen exclosures on the Kaibab NF, and we also observed severe outbreaks of OSS in the same exclosures in 2019 (see Local severity section). This pattern of early establishment with slow population growth rates and minimal impacts followed by a rapid growth in population and widespread expansion is characteristic of a sleeper species (NRC 2002). OSS's awakening closely resembles the predicted future population growth and spread of gloomy scale (*Melanaspis tenebricosa*), which is hypothesized to be a sleeper species that may spread from urban areas into natural forests settings with continued warming and urbanization (Just et al. 2020). It is unclear which factor(s) led to the awakening of OSS, but an increasingly warm climate and stressed hosts are likely explanations (Frank and Just 2020).

Northern Arizona has experienced warmer and drier conditions resulting from climate change (Salzer and Kipfmueller 2005; Woodhouse et al. 2010), and these climatic changes may have led, indirectly or directly, to OSS outbreaks in natural aspen stands. Aspen in this region is under increasing environmental stress from a warming climate (Zegler et al. 2012), and stress, particularly from drought, increases the susceptibility of aspen to insects and diseases (Marchetti et al. 2011). This stress may, therefore, increase susceptibility of aspen to OSS, enabling further spread and intensification (Frank 2020). On the other hand, a warmer climate may have directly improved conditions for OSS population growth by increasing the species' fitness and abundance (Frank 2020; Frank and Just 2020). Because OSS appears to be limited to aspen stands below 2500 m (Table 1), cold temperatures may be a limiting factor for its spread, which is consistent with other scale insect pests (Frank 2020; Just et al. 2020) and OSS in other locations (Furniss and Carolin 1977). Temperature changes that have already occurred may have enabled OSS's spread outside urban areas (Frank and Just 2020; Just et al. 2020), and in the future, warmer temperatures at higher elevations and latitudes may promote further spread of OSS (Frank 2020). The former would threaten the largest, healthiest aspen stands in northern Arizona, which occur at higher elevations, and the latter would threaten the rest of aspen's range in the western US because Arizona is situated on the southwestern edge of the tree's range.

The polyphagous nature of OSS may also contribute to future spread. Trees in urban settings can provide landscape connectivity for invasive pests into forest habitats (Rossi et al. 2016). As a polyphagous pest that has been in the US for centuries, OSS is particularly well suited to take advantage of urban connectivity to natural aspen stands. This connectivity was the likely pathway of OSS spread from urban settings to natural aspen stands and could be an important mechanism by which the species spreads and new outbreaks occur (Frank and Just 2020; Just et al. 2020). In the conifer-dominated western US, rivers and creeks might promote connectivity within forested areas and from urban areas to natural forests because riparian vegetation is generally deciduous, and therefore, potentially susceptible to OSS. Similarly, many urban parks in the western US contain aspen and other susceptible hosts, such as *Ceanothus* spp., providing another direct connection from urban areas to natural forests. The challenge presented by OSS's role as a generalist is common for a forest health concern. For example, sudden oak death is more prevalent near forest edges because understory hosts of the disease's pathogen, *Phytophthora ramorum*, are more abundant in the edge environment (Kelly and Meentemeyer 2002). Similarly, current and future OSS outbreaks might be more common near urban areas or in the presence of other host species.

Research and monitoring needs

Invasive pests like OSS pose an imminent threat to native tree species and, therefore, represent an immediate research and monitoring priority to better understand the pest's biology, quantify the extent of the problem and its ecological effects, and develop proactive solutions. Here, we provide recommendations for future research and monitoring in order to understand OSS's biology in natural aspen stands, quantify impacts, limit future spread, and mitigate mortality and loss of aspen and other host species.

1. *Increased monitoring* Extensive surveys to determine the extent of OSS in western North America would help us better understand the species' current distribution. Landscape-scale monitoring would be most effective if integrated into existing permanent monitoring networks, such as the Forest Health Monitoring or Forest Inventory and Analysis networks (Smith 2002). Priority could be given to detection in plots where aspen occurs, but because OSS is polyphagous, monitoring should ideally occur in any plot where known host species are present. Given OSS's hypothesized role as a sleeper species, increased monitoring in natural forest settings may reveal sleeper populations that have the potential to rapidly intensify in the future. Monitoring should also occur in urban settings, which could indicate areas where future expansion into natural forests is a risk and may shed light on OSS connectivity between urban and natural landscapes. Moreover, OSS connectivity through urban pathways presents a unique opportunity for future public engagement and citizen science projects, which can be highly effective in documenting extent and impacts from invasive pests and pathogens (Meentemeyer et al. 2015).

We have included the OSS rating system that we will use for future monitoring and research (Box 1), and we invite other scientists and managers to use this system for their monitoring. Similar to Hawksworth's (1977) Dwarf Mistletoe Rating (DMR) system, the OSS rating system divides the tree into three sections, each of which receive separate severity ratings (see Online Resource 1 for illustrations of severity ratings). The north and south sides of the tree are also rated separately because we have observed that OSS is often more abundant on the north side of trees. We are collecting data on this for our ongoing research, but we hypothesize that increased solar radiation on the south side of trees provides a less favorable microclimate for OSS.

2. *Biological unknowns* Although OSS is a well-known urban pest that has been in the US for centuries, we know little about its behavior in natural forest settings. Understanding the species' biology is a critical step for developing informed management strategies. For example, quantifying dispersal of the invasive beech scale has facilitated understanding of how beech bark disease develops and how the insect and disease can be managed (Wainhouse 1980; Giencke et al. 2014). To better understand the impacts of OSS in aspen stands, continued observation of infested stands over time will allow us to quantify its rate of intensification and spread, as well as the patterns and timing of mortality. Other components of OSS biology that are unknown include dispersal distances in natural forest settings, its ability to survive on dead or cut hosts, temperature and humidity requirements for different OSS life stages, the relationship between OSS and host tree vigor, and the role of native insects as natural control agents.

3. *Limiting factors* There is a need to assess which biotic and abiotic factors significantly affect OSS presence and severity in natural aspen stands. Fitness and abundance of other scale insect pests has been linked to climate (Frank 2020; Just et al. 2020), so understanding OSS's elevational and climatic limitations would be particularly valuable information. For example, population density of California red scale (*Aonidiella aurantii*) is lower at higher elevations (Hutchinson 1947), and cold temperatures restrict the range of gloomy scale (Frank and Just 2020). Understanding which factors limit OSS populations is a critical step in development of a risk and hazard rating system, which is an integral component of integrated pest management (Hicks et al. 1987). A risk and hazard rating system for OSS would allow managers to identify which aspen stands have the greatest potential for infestation in the future or which stands

should be prioritized for proactive management of OSS.

4. *Fungal interactions* Interactions between OSS and fungal pathogens of trees are a compelling area of future study. Insects can directly vector fungal pathogens and create wounds which serve as infection courts for pathogens (Hinds 1985; Webber and Gibbs 1989). A relevant example of such an interaction is beech bark disease, which is caused by the invasive beech scale damaging the host's bark and forming infection courts for fungal pathogens (Ehrlich 1934; Houston 1994). Although a connection between OSS and fungal pathogens has not been firmly established, aspects of OSS infestation are conducive to infection by fungal pathogens. OSS feeding damages the delicate bark of aspen and creates infection courts, while additional stress imposed by OSS inhibits tree defenses and increases aspen's susceptibility to pathogens. *Cytospora* fungi are commonly associated with mortality in stressed aspen and have been observed in association with OSS damage (Cranshaw 2013), but little is known about the extent or impacts of this association. Further work is needed to understand potential interactions between OSS and fungal pathogens.

5. *Management strategies* In addition to a risk and hazard rating system, management strategies that are affordable, efficient, and effective at the landscape scale must be researched and developed. Research on silvicultural strategies to manage OSS is already underway in northern Arizona, but research on potential systemic insecticides and biological control agents, such as *B. bassiana*, should also be prioritized. Another potential management strategy that should be studied is prescribed fire, which could be useful for removal of OSS on understory hosts. The most effective strategy will be an integrated pest management program with a suite of tools that can be used depending on the needs and limitations of different infestations, affected hosts, and land ownership.

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Authors' contributions CDC and KMW developed the conceptual basis for the manuscript. CDC, KMW, RWH, AMG, and NPW wrote the initial draft. CDC, AMG, and NPW conducted the formal analysis. CDC, RWH, AMG, NPW, and DED created figures, illustrations, or maps for the manuscript. All authors contributed to development of the OSS rating protocol, reviewed and provided critical feedback on the initial draft, revised the manuscript, and approved the final draft.

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Code availability R code for analysis of local OSS severity is available as supplemental material (Online Resource 3).

Declaration

Conflicts of interest All authors declare no conflicts of interest.

Data availability Data analyzed in this paper will be made available upon request. Forest Service materials including the Pest Event Reports (FHP 2018, 2019) and the Prescott NF stand certification (Fairweather 1992) will also be made available upon request.

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