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

Connor Crouch, Amanda Grady, Nicholas Wilhelmi, Richard Hofstetter, Margaret Moore, Kristen Waring

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3

4 **Authors:** Connor D. Crouch^{1,2}, Amanda M. Grady³, Nicholas P. Wilhelmⁱ³, Richard W.

5 Hofstetter¹, Margaret M. Moore¹, and Kristen M. Waring¹

6

7 ¹School of Forestry, Northern Arizona University, 200 E Pine Knoll Dr, Flagstaff, AZ 86011, USA

8 ²USDA Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources

9 Building, University of Missouri, Columbia, MO 65211, USA

10 ³USDA Forest Service, Forest Health Protection, Arizona Zone, 2500 S Pine Knoll Dr, Flagstaff, AZ

11 86001, USA

12

13 Corresponding author: Connor D. Crouch (connor.crouch@usda.gov)

14 **Abstract**

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

34 **Keywords:** armored scale insect, climate change, invasion ecology, *Lepidosaphes ulmi*, *Populus*
35 *tremuloides*, sleeper species

36 **Introduction**

37 Invasive species pose a major threat to sustainability of forest ecosystems (Chornesky et al.
38 2005). Of particularly high concern are invasive species that kill foundation tree species,
39 resulting in reductions to biodiversity and other ecosystem services (Ellison et al. 2005; Ellison
40 2019). Unlike keystone species, which are low in abundance but have an outsized influence on
41 ecosystem dynamics, foundation species are common at the landscape scale and often
42 abundant at smaller spatial scales (Ellison et al. 2005; Ellison 2019). An important foundation
43 tree species in the interior western United States is quaking aspen (*Populus tremuloides*;
44 hereafter aspen), which has the widest distribution of any tree species in North America (Little
45 1971; Perala 1990). Despite its continental abundance, aspen has high conservation value in the
46 Interior West because it is one of the only hardwood species that forms pure, single-species
47 stands (Rogers et al. 2020). As such, aspen ecosystems make disproportionately large
48 contributions to biodiversity and other ecosystem services compared to neighboring conifer-
49 dominated stands (DeByle 1985; Kay 1997; Chong et al. 2001; LaMalfa and Ryle 2008; Kuhn et
50 al. 2011; Rogers et al. 2020). The conservation value of aspen is especially pronounced along
51 the southwestern edge of its range, which includes Arizona, because aspen occupies less than
52 2% of forested land (Johnson 1994; Rolf 2001; Gitlin et al. 2006; Halbritter and Bender 2011;
53 Zegler et al. 2012; Crouch et al. 2023). Concerningly, aspen in the Interior West is threatened by
54 recent outbreaks of an invasive insect, oystershell scale (*Lepidosaphes ulmi*; hereafter OSS)
55 (Crouch et al. 2021) (Fig. 1).



56

57 **Figure 1**58 **Title:** Photos of stand-level aspen mortality from oystershell scale (OSS) and close-ups of OSS on
59 aspen.60 **Legend:** Photo of young aspen stand inside of an exclosure (2 m tall fence built to exclude
61 ungulates from browsing aspen) experiencing high levels of dieback and mortality from
62 oystershell scale (OSS). Photos on the right show close-ups of OSS on aspen.
63

64 OSS is an armored scale (Hemiptera: Diaspididae) that inserts its stylet through the bark
65 of woody host plants to feed on the fluid of non-vascular cells (Griswold 1925; Beardsley and
66 Gonzalez 1975). This feeding damages host cells, resulting in cell death and cracking of the
67 host's bark under heavy infestations (Beardsley and Gonzalez 1975). Mortality of heavily
68 infested branches, stems, and stands may occur (Griswold 1925; Beardsley and Gonzalez 1975).
69 OSS is polyphagous, with around 100 host genera globally (Miller and Davidson 2005). Twelve

70 host genera (*Acer*, *Alnus*, *Ceanothus*, *Cornus*, *Frangula*, *Fraxinus*, *Juglans*, *Lupinus*, *Populus*,
71 *Ribes*, *Salix*, and *Symporicarpos*) have been documented in the Interior West (Crouch et al.
72 2021). OSS is most common on woody, deciduous plants, especially those with relatively thin
73 bark (Miller and Davidson 2005). As an obligate parasite, OSS completes its entire life cycle on
74 woody tissue of living hosts (Samarasinghe 1965; Crouch et al. 2024). All OSS life stages are
75 sessile, except for first instars (i.e., crawlers), which actively disperse along the host's stem or
76 branches in search of a suitable feeding site (Miller and Davidson 2005). Once a feeding site is
77 found, OSS will remain there through adulthood (Griswold 1925). In bisexual populations, males
78 shed their tests and fly to mate with females; however, female-only populations occur and
79 reproduce via parthenogenesis (Beardsley and Gonzalez 1975; Miller and Davidson 2005).
80 Questions remain about OSS dispersal mechanisms and distances, but long-distance crawler
81 dispersal is likely driven by human movement of infested plants, whereas short- and
82 intermediate-distance dispersal are likely driven by wind, potentially with animal assistance
83 (Griswold 1925; Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010). Crawlers do not
84 actively move more than 1 m due to limited energy reserves and susceptibility to adverse
85 climatic conditions (Beardsley and Gonzalez 1975; Magsig-Castillo et al. 2010).

86 Although the native range and introduction history of OSS are uncertain, the species
87 was likely transported to North America by European settlers on infested plant material
88 (Griswold 1925; Beardsley and Gonzalez 1975). OSS was first reported as a pest of apple trees
89 (*Malus* spp.) in the 1700s and is now present throughout much of North America, especially in
90 urban and ornamental settings (Griswold 1925; Miller and Davidson 2005). Despite the species'
91 polyphagous nature, its pervasiveness in North America, and its long invasion history, OSS has

92 rarely been a major pest in wildland forest settings (but see Sterrett 1915; DeGroot 1967;
93 Houston 2001). OSS was first reported on aspen in wildland forest settings in Arizona, USA by
94 Fairweather (1992) and Zegler et al. (2012). In both cases OSS abundance was low, and impacts
95 were minimal. However, in 2016 OSS was observed causing dieback and mortality of aspen in
96 wildland forest settings (Grady 2017), and severe outbreaks have since been observed in both
97 areas where Fairweather (1992) and Zegler et al. (2012) first observed OSS. Based on this
98 invasion history, Crouch et al. (2021) suggested that OSS may be a sleeper species, which is
99 defined as a non-native species that establishes successfully but experiences slow population
100 growth before suddenly awakening when conditions become favorable and experiencing rapid
101 population growth (Groves 1999; Bradley et al. 2018; Frank and Just 2020). It is unclear what
102 led to the awakening of OSS, but recent climatic changes, namely warmer and drier conditions
103 (Williams et al. 2022), are a likely explanation (Crouch et al. 2021). A warming climate may have
104 improved conditions for OSS by increasing the species' fitness and abundance and/or by
105 increasing susceptibility of aspen to infestation and mortality (Frank 2020; Crouch et al. 2021).
106 OSS's role as a sleeper species and its potential interactions with climate change are concerning
107 because continued climate warming may trigger OSS invasions in other areas of aspen's range
108 (Crouch et al. 2021).

109 Critical to managing any invasive species is baseline information on its occurrence and
110 impacts. The first peer-reviewed report of OSS outbreaks in aspen ecosystems indicated that
111 OSS is already widespread in northern Arizona (Crouch et al. 2021). Crouch et al. (2021) also
112 observed that OSS only occurred in the lower half of aspen's elevation range (< 2500 m) and
113 that OSS seemed to be particularly pervasive on, and damaging to, smaller recruiting stems. In a

114 survey of aspen populations across Arizona, Crouch et al. (In revision) corroborated those early
115 results by finding that there was significantly less OSS at higher elevations and that OSS
116 contributed to mortality of aspen recruits (stems > 1.37 m tall and < 12.7 cm diameter at breast
117 height [dbh; height = 1.37 m]). Both studies also found that OSS was more common in fenced
118 ungulate exclosures (2 m tall fences built to exclude ungulates from browsing on aspen) than
119 outside of them. Because recruitment is critical for self-replacement, these early findings
120 highlight the threat that OSS poses to aspen resilience and sustainability (DeRose and Long
121 2014; Crouch et al. 2023), warranting a comprehensive survey of OSS and its impacts on aspen
122 across Arizona. We do not know which factors influence OSS's presence across the landscape
123 and what specific impacts OSS has on aspen ecosystems. Obtaining this information is critical
124 for informing management of OSS and mitigating damage caused by this high-impact invasive
125 species. To fill these knowledge gaps, we sampled aspen populations across Arizona and
126 addressed three questions: (1) What is the geographic extent of OSS in Arizona ? (2) What
127 impacts does OSS have on aspen? (3) Which biotic and abiotic factors influence OSS abundance
128 in aspen ecosystems?

129

130 **Methods**

131 *Study area*

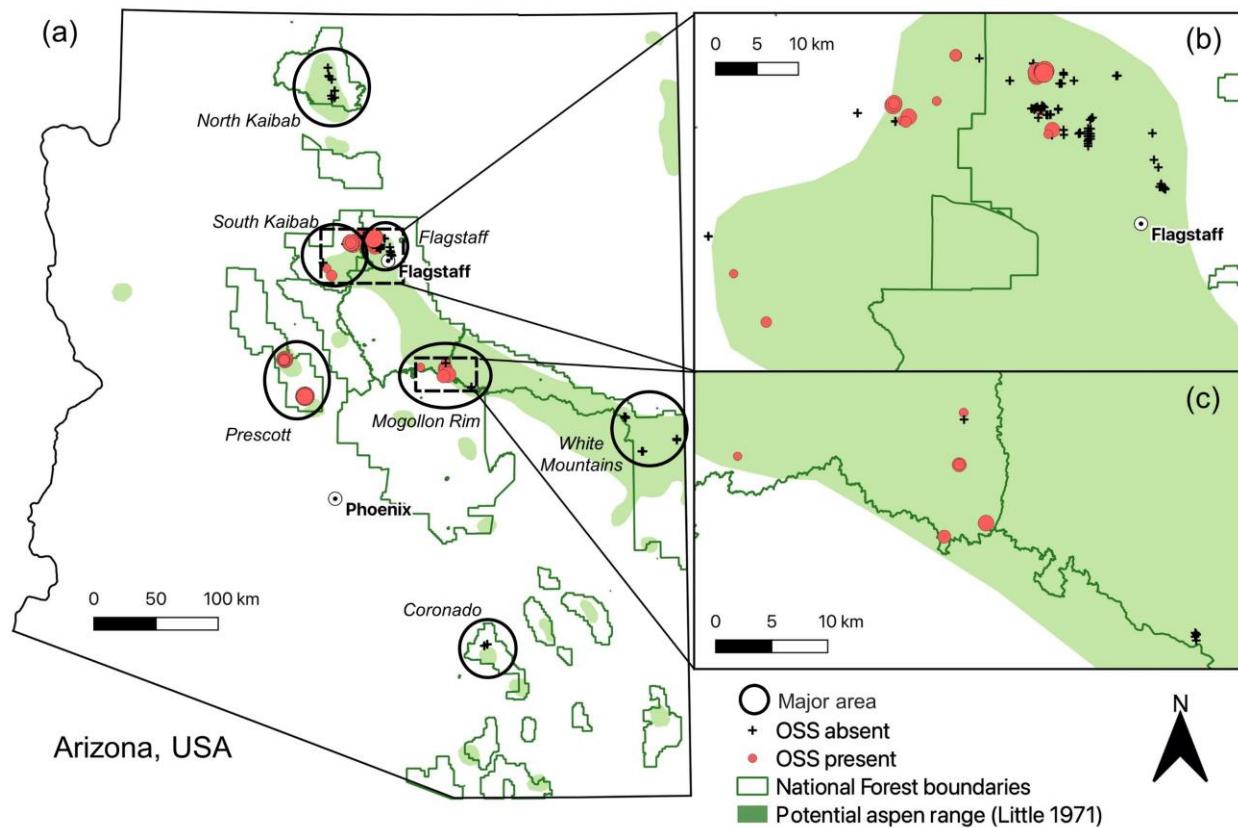
132 Our study area encompassed aspen ecosystems across Arizona, USA. Although OSS has been
133 observed on numerous hosts in Arizona (Crouch et al. 2021), our study focused on aspen
134 because the first OSS outbreaks were observed in aspen ecosystems and because of aspen's
135 importance as a foundation species. Aspen ecosystems in Arizona tend to be small (0.1–25 ha in

136 size), especially compared to more northerly latitudes of aspen's range (Zegler et al. 2012).
137 Aspen is limited to relatively high elevations (2000–3000 m), where lower temperatures and
138 higher precipitation allow the drought-intolerant species to survive (Perala 1990; Rehfeldt et al.
139 2009). At lower elevations, small stands of aspen occur on north-facing slopes or in drainages
140 with increased water availability, and as elevation increases, the aspen component tends to be
141 more abundant and less aspect-limited (Rasmussen 1941; Covington et al. 1983; Merkle 1962;
142 Fairweather et al. 2008; Zegler et al. 2012). In addition to occurring alone in small single-species
143 stands, aspen commonly co-occurs with conifers, including ponderosa pine (*Pinus ponderosa*
144 var. *scopulorum*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) at lower elevations, white
145 pine (*Pinus strobiformis* or *Pinus flexilis* var. *reflexa*) and white fir (*Abies concolor*) at mid
146 elevations, and corkbark fir (*Abies lasiocarpa* var. *arizonica*) and Engelmann spruce (*Picea*
147 *engelmannii*) at the highest elevations.

148

149 *Site selection*

150 We sampled 220 aspen plots that represent the range of conditions under which aspen exists in
151 Arizona (Fig. 2a). These plots were located across seven major areas: North Kaibab (n = 19),
152 South Kaibab (n = 26), Flagstaff (n = 113), Mogollon Rim (n = 13), White Mountains (n = 25),
153 Prescott (n = 17), and Coronado (n = 7) (Fig. 2a). All data were collected during the 2020, 2021,
154 and 2022 growing seasons (June – October), when aspen trees had leaves.



155

156 **Figure 2**157 **Title:** Maps showing absence, presence, and abundance of OSS in study plots located in
158 Arizona, USA.159 **Legend:** Maps showing absence, presence, and abundance of OSS in (a) 220 study plots across
160 seven major areas (*in italics*) where aspen occurs in Arizona, USA, (b) study plots in the South
161 Kaibab (left of green National Forest boundary line) and Flagstaff major areas (right of green
162 line), and (c) study plots along the Mogollon Rim. These three areas are the only ones where
163 OSS presence varied. OSS was present in all plots around Prescott and was absent in all plots in
164 the North Kaibab, White Mountains, and Coronado.
165

166 To ensure that we obtained a representative sample of aspen sites and conditions, we
167 stratified sites across four variables – elevation (≤ 2400 m, > 2400 m); aspect (north/east,
168 south/west); ungulate management (none, fenced enclosure or jackstraw treatment [large piles
169 of woody debris protecting aspen regeneration from ungulate browse]); and fire history (0–2
170 years post-fire, 2–20 years post-fire, $>$ 20 years post-fire) – resulting in 24 strata. We first

171 sought to obtain one plot for each stratum, which we accomplished for 21 of the 24 strata,
172 before building out a sample that was proportional to how much aspen occurs in each stratum.
173 We assessed aspen's actual occurrence in each stratum using an observed GIS layer of aspen's
174 range on three national forest ranger districts surrounding Flagstaff (Flagstaff and Mogollon
175 Rim Ranger Districts of the Coconino National Forest; Williams Ranger District of the Kaibab
176 National Forest) (DePinte 2018). Although this layer covers only three of the nine ranger
177 districts we sampled, it is the most accurate estimation of where aspen occurs in Arizona
178 because it is a fine-scale layer of aspen's recent presence based on direct observations from an
179 aircraft (DePinte 2018). We compared the proportion of aspen observed on the landscape,
180 based on area from the GIS layer, to the proportion of aspen plots we sampled, based on the
181 number of plots that fell into each stratum. We succeeded in obtaining a representative sample
182 across elevation, aspect, and fire history, with proportions of aspen observed in each stratum
183 versus aspen sampled differing by less than 7% for each stratum (Crouch et al. In revision).

184 When possible, we prioritized remeasurement of existing aspen monitoring plots to
185 reduce the number of redundant plots on the landscape and to facilitate research permission
186 on national forest land. Specifically, we revisited plots previously established by the Coconino
187 National Forest ($n = 44$), the Apache-Sitgreaves National Forest ($n = 5$), Zegler et al. (2012) on
188 the Kaibab National Forest ($n = 20$), and Northern Arizona University's Ecological Restoration
189 Institute on the San Francisco Peaks ($n = 12$). All four of these networks established plots using
190 stratified or completely random sampling, ensuring the locations of these plots lacked bias. We
191 established the remaining 139 plots by identifying aspen stands that filled target strata,
192 standing on the edge of selected stands, laying out a linear transect longways through those

193 stands, and establishing plots every 30 m along the transects. The Coconino National Forest,
194 Apache-Sitgreaves National Forest, and Ecological Restoration Institute plots were also
195 established along transects with plot spacings ranging from 100 m to 300 m. Zegler et al. (2012)
196 established sites at randomly located points within known aspen stands and sampled plots in all
197 four cardinal directions 20 m from those points.

198

199 *Field data collection*

200 Each study plot consisted of two fixed-area, circular plots: an overstory plot (8 m radius) and a
201 nested regeneration plot (4 m radius) sharing the same plot center (Zegler et al. 2012). We
202 collected GPS coordinates at the center of each study plot, recorded whether the plot fell in an
203 area of ungulate management (i.e., fenced enclosure or jackstraw treatment), and noted
204 whether there was evidence of recent conifer removal, as indicated by cut conifer stumps
205 present in or directly adjacent to the plot. For a plot to be included in our study, it had to
206 contain at least five live aspen stems between the 8 m overstory and 4 m regeneration plots
207 combined. In the 8 m overstory plot, all trees with dbh > 12.7 cm were measured. In the 4 m
208 regeneration plot, all trees > 0.02 cm in height and < 12.7 cm dbh were measured. In the
209 regeneration plot, we classified stems into three size classes adapted from Zegler et al. (2012):
210 short regeneration (< 1.37 m tall), tall regeneration (> 1.37 m tall and < 5.1 cm dbh), and
211 saplings (5.1–12.7 cm dbh). We considered both tall regeneration and saplings to be recruiting
212 stems (Crouch et al. In revision) and chose a recruitment threshold height of 1.37 m to be
213 consistent with previous studies of aspen juveniles in Arizona (Binkley et al. 2006; Zegler et al.
214 2012). For all live aspen, we measured height, dbh (except for regeneration and recruits that

215 were < 1 cm dbh), crown dieback ([percentage of dead branches above the bottom of the tree's
216 live crown] 0%, 1–33%, 34–67%, > 67%), crown ratio (percentage of total height occupied by
217 the tree's live crown), and OSS presence and severity. We assessed OSS severity using the
218 system devised by Crouch et al. (2021), which rates OSS severity on each tree from ground level
219 to 6 m. Each tree's stem up to 6 m is divided equally into thirds, and severity is rated for each 2
220 m section (or shorter for trees < 6 m tall) on both the north and south sides of the tree. Severity
221 is rated 0–3: 0 = no OSS present, 1 = only a handful of OSS present (trace), 2 = OSS covers < 50%
222 of section (light), 3 = OSS covers > 50% of section (severe). For every dead aspen and live tree
223 species other than aspen, we recorded size class and dbh.

224 For all live aspen in our study plots, we documented the top three damaging agents
225 present on each tree (Zegler et al. 2012). When more than three damaging agents were
226 present, preference was given to agents with the greatest severity of impact (i.e., most likely to
227 cause dieback and mortality) (Zegler et al. 2012). These damaging agents included insects,
228 diseases, ungulate browse, other animal damage, and abiotic damages. For insects and
229 diseases, we grouped individual species into functional groups to facilitate analysis and because
230 some biotic damages (e.g., defoliating insects) were impossible to identify based solely on
231 damage signs and symptoms. These functional groups included sucking and gall-forming
232 insects, bark beetles, wood-boring insects, defoliating insects, canker-causing diseases, foliar
233 and shoot diseases, and decay diseases (USDA Forest Service 2013; Steed and Burton 2015). As
234 explained in the previous paragraph, OSS was identified and measured separately from other
235 sucking and gall-forming insects, so that functional group excluded OSS. We assessed certain
236 cankers individually because of their potential to have outsized impacts on aspen tree health

237 compared to less pathogenic diseases (Hinds 1985; Zegler et al. 2012; Crouch et al. 2023). The
238 cankers we assessed individually were Cytospora canker (caused by *Cytospora* spp.), Hypoxylon
239 canker (caused by *Entoleuca mammatum*), Ceratocystis canker (caused by *Ceratocystis* spp.),
240 and sooty bark canker (caused by *Encoelia pruinosa*). We lumped all abiotic damages together,
241 which included fire scarring of stems, foliar drought scorch, and foliar chlorosis. We assessed
242 animal damage to aspen stems, including browse, ungulate barking (i.e., elk chewing aspen
243 bark), and other animal damage. We also indirectly quantified ungulate impacts by counting
244 ungulate scat piles within the 8 m overstory plot. We identified scat piles by species (i.e., elk
245 [*Cervus canadensis*], deer [*Odocoileus hemionus* or *O. virginianus couesi*], or cattle [*Bos taurus*])
246 and treated piles from the same species as distinct when piles were clearly separated,
247 contained more than three pellets, and differed in color or size (Bunnefeld et al. 2006; Rhodes
248 and St. Clair 2018).

249

250 *OSS extent*

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

258 4.2.1 (R Core Team 2022), using the *dplyr* package (Wickham et al. 2022) for data manipulation
259 and the *ggplot2* package (Wickham 2016) for figure creation.

260

261 *OSS impacts*

262 We assessed OSS impacts on aspen at both the tree and stand levels. At the tree level, we built
263 univariate regressions to quantify the influence of OSS presence and severity on aspen dieback
264 and crown ratio, which are metrics that capture individual stem health (Schomaker et al. 2007).
265 Tree-level OSS severity was calculated by taking the mean percentage of each category in the
266 rating system (i.e., 1% for 1, 25% for 2, and 75% for 3) and calculating the mean for the six
267 ratings recorded for each tree. We used the *nlme* package (Pinheiro et al. 2022) to fit four linear
268 mixed-effects models with crown dieback and crown ratio as responses, OSS presence and
269 severity as fixed effects, and the hierarchical, nested structure of plots (i.e., plots [n=220] within
270 study sites [n=87] within minor areas [n=19] within major areas [n=7]) as random effects. Study
271 site refers to a transect or group of plots that are clustered near each other, whereas minor
272 area refers to a group of transects or plots in a larger but still confined area (e.g., an individual
273 mountain or fire footprint). To assess OSS impacts at the stand level, we built univariate
274 regressions between plot-level OSS abundance (i.e., proportion of stems infested by OSS) and
275 aspen mortality. We used the *nlme* package (Pinheiro et al. 2022) to fit six linear mixed-effects
276 models with dead aspen basal area, dead aspen density, and density of dead aspen in each of
277 the four size classes individually as the six response variables. For these stand-level regressions,
278 we fit OSS abundance as the fixed effect and the hierarchical, nested structure of plots (i.e.,
279 plots [n=64] within study sites [n=23] within minor areas [n=9] within major areas [n=4]) as a

280 random effect. Sample sizes differ for these stand-level models compared to the tree-level
 281 models because we used only the 64 plots in which OSS occurred for these stand-level models.

282 **Table 1**

283 **Title:** List of 99 variables considered as potential influencing factors of plot-level oystershell scale (OSS) abundance.

Legend: 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 (<i>Cervus canadensis</i>) scat	1.3	0–23
Deer (<i>Odocoileus hemionus</i> & <i>O. virginianus couesi</i>) scat	1.1	0–29
Cattle (<i>Bos taurus</i>) 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 <i>Cytospora</i> spp.)	0.02	0–0.34
Hypoxylon canker (caused by <i>Entoleuca mammatum</i>)	0.002	0–0.10
Ceratocystis canker (caused by <i>Ceratocystis</i> spp.)	0.02	0–0.42
Sooty bark canker (caused by <i>Encoelia pruinosa</i>)	0.001	0–0.05
All cankers	0.33	0–1
Foliar & 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 (3.6%), 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 ₂ O (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
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

Influencing factor	Mean	Range
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 = m² 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 temperature = °Cⁿ 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).

284

285 *Factors influencing OSS abundance*

286 To assess drivers of OSS invasions in aspen ecosystems, we collected data representing an array

287 of biotic and abiotic factors that may influence plot-level OSS abundance (Table 1). In total, we

288 considered 99 variables across eight categories of potential influencing factors: stand structure,

289 ungulates, other damaging agents, fire, management, site factors, soils, and climate. Although

290 some of these factors (e.g., ungulates) are unlikely drivers of OSS invasions, we included as

291 many potential influencing factors as possible because we had no prior data on which factors
292 drive OSS invasions. Using tree diameter data, we calculated basal area of stems > 5.1 cm dbh
293 for live aspen, all OSS host species, and non-host species (Table 1). We calculated stem
294 densities (trees ha⁻¹) for live aspen, all host species, and non-host species across each of four
295 stem size classes (i.e., short regeneration, tall regeneration, saplings, and overstory trees).
296 Using the presence/absence data for all damaging agents on each live aspen stem, we
297 calculated the proportion of stems affected by each agent in each plot (Table 1).

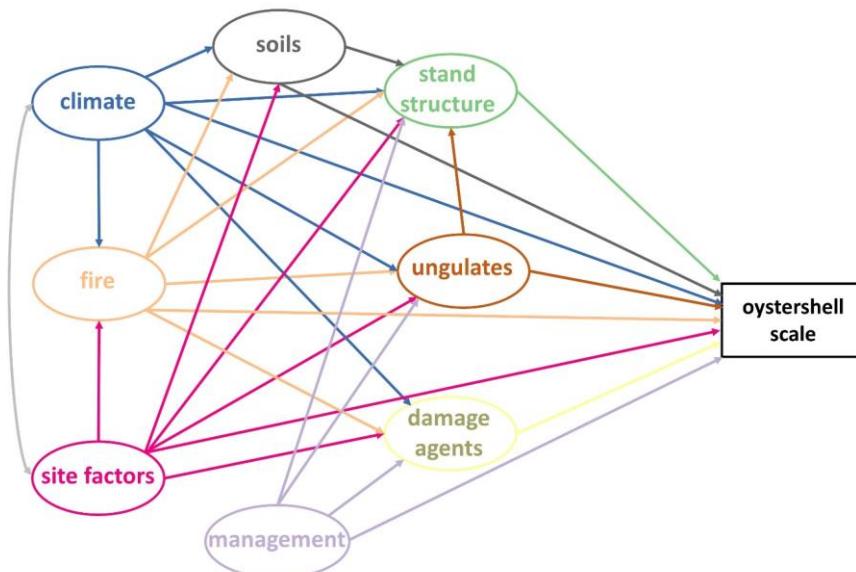
298 Using the GPS coordinates we collected at each plot's center, we calculated elevation,
299 aspect, and slope using a 30 m² digital elevation model (Table 1). We transformed raw aspect
300 into a continuous variable ranging from 0–2 with 0 representing southwest (225°) and 2
301 representing northeast (45°) (Beers et al. 1966). We also calculated heat load and potential
302 annual direct radiation, two indices that assess site-level temperature based on slope, aspect,
303 and latitude (McCune and Keon 2002). We assessed fire occurrence in each plot for the past 20
304 years using wildland fire perimeters obtained from the USDA Forest Service Region 3 GIS
305 database (<https://www.fs.usda.gov/detail/r3/landmanagement/gis>) and prescribed fire
306 perimeters from national forest staff. We assessed fire severity using data obtained from the
307 Monitoring Trends in Burn Severity program (<https://www.mtbs.gov/>), which provides fire
308 severity data at 30 m resolution. We created categorical variables to represent both fire
309 occurrence and severity in addition to a binary variable for plots that burned twice in the past
310 20 years (Table 1). Finally, we used GPS coordinates and maps obtained from national forest
311 staff to verify whether plots fell inside areas of ungulate management and conifer removal

312 treatments, and we created binary variables for both ungulate management and conifer
313 removal (Table 1).

314 We obtained soils data from SoilGrids (<https://www.isric.org/explore/soilgrids>), which
315 provides global soil mapping data at 250 m resolution (Poggio et al. 2021). We used 9 of 12
316 available soil metrics to capture variables that represent soil moisture (e.g., sand content and
317 bulk density), fertility (e.g., cation exchange capacity, nitrogen, and soil organic content),
318 rooting environment (e.g., bulk density, clay content, and coarse fragments), and chemical
319 environment (e.g., soil pH) (Table 1). We aggregated mean values for each variable to a depth
320 of 1 m because most lateral aspen roots occur within the first 1 m of the soil (Jones and DeByle
321 1985). We obtained climate data from ClimateNA (<https://climatena.ca/>), which downscales
322 PRISM data (Daly et al. 2008) at 800 m resolution (Wang et al. 2016). Because we expected
323 climate to be an important driver of OSS abundance but had no prior data on which aspects of
324 climate are the most important, we included as many climate variables as possible. Specifically,
325 we obtained variables representing annual and, when available, seasonal degree-days,
326 temperature, precipitation, humidity, Hargreaves reference evaporation (hereafter
327 evaporation), and drought for the two years preceding the date each plot was sampled (Table
328 1). We chose two years because, based on repeated observations of OSS in the same field sites
329 across multiple years indicated that most OSS we observed on trees had accumulated in the
330 preceding two years (Crouch et al. 2024). Although dead OSS are likely capable of lasting even
331 longer on host trees, more recent climate data captures the most recent trends in live OSS
332 population abundance.

333 We used random forests, structural equation modeling (SEM), and stand- and tree-level
334 regressions to determine which biotic and abiotic factors drive OSS invasions. First, we used
335 random forests to determine which of the 99 predictor variables had the strongest influence on
336 plot-level OSS abundance. Random forests are a useful tool for assessing variable importance in
337 regression and classification settings among an array of potential predictors (Breiman 2001).
338 Specifically, we used the *VSURF* package (Genuer et al. 2015), which used 50 random forest
339 runs, each of which was built using 2000 trees, to rank variable importance for each of our
340 three response variables. *VSURF* is robust in noisy, high dimensional settings and in the
341 presence of highly correlated predictors (Genuer et al. 2010). *VSURF* outputs a ranked list of
342 variables based on importance, which is calculated using out-of-box mean square error for each
343 tree. We used this ranked list of variables when building SEMs and assessing univariate
344 relationships between influencing factors and OSS abundance. We also used the climate
345 variables in this list to search for climatic thresholds beyond which OSS does not occur in
346 Arizona.

347 Once we obtained a list of the most important variables influencing OSS abundance, we
348 used SEM to assess how those variables and their interactions affect OSS abundance. SEM is an
349 insightful tool for ecological research because it allows the user to build models based on
350 theoretical understanding of an ecological system, resulting in a network of causal, multivariate
351 relationships with a complete accounting of direct and indirect relationships and the relative
352 strengths of those relationships (Grace 2006; Lefcheck 2016). Our first step in building an SEM
353 was to construct an *a priori* model based on our theoretical understanding of how biotic and
354 abiotic factors might influence OSS. This *a priori* model (Fig. 3) accounted for all 99 variables



355 **Figure 3**

356 **Title:** *A priori* structural equation model (SEM) illustrating hypothesized relationships among
357 influencing factors and OSS abundance.

358 **Legend:** *A priori* structural equation model (SEM) illustrating hypothesized directional
359 relationships among influencing factors and plot-level OSS abundance. Arrows indicate causal
360 relationships, and colors correspond to each of the eight categories of influencing factors. See
361 Table 1 for complete list of measured variables included in each of these eight categories.
362

363 that potentially influence OSS abundance using the eight categories of influencing factors (i.e.,
364 stand structure, ungulates, other damaging agents, fire, management, site factors, soils, and
365 climate). We then built a “full” SEM, which included the highest ranked variable based on
366 random forests from each of the eight categories of influencing factors (Table 1). We used a
367 combination of backward and forward selection to optimize model fit (using AIC and Fisher’s C
368 statistic) and maximize explanatory power (using R^2 of the response variable). This optimization
369 process included removing variables with low significance in the model and adding in more
370 than one variable per category (e.g., adding a second climate variable) when two variables from
371 one category had high importance values based on random forests. We also tested how
372 swapping in one variable to replace another variable of the same category (i.e., replacing fire

373 severity with fire strata) affected the model. We used the *piecewiseSEM* package to build SEMs
374 because this package accommodates use of mixed-effects models (Lefcheck 2016). For the
375 individual regressions that underlie *piecewiseSEM*, we used the *lme4* package (Bates et al.
376 2015) to fit linear mixed-effects models with the hierarchical, nested structure of plots modeled
377 as random effects.

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

395 compare height-to-diameter ratios inside versus outside areas of ungulate management to
 396 assess how these treatments influence aspen growth and, in turn, potentially influence OSS
 397 abundance.

398

399 **Table 2**

400 **Title:** Summary data for aspen stand structure, crown condition, and OSS presence.

Legend: Means and standard errors of variables representing live and dead aspen basal area, live and dead aspen density in different stem size classes, live aspen crown ratio and dieback, and OSS presence at the plot and tree levels. For categorical variables, percentage of plots or trees in each level are shown.

Variable	Mean	Std error
Live aspen basal area ($m^2 ha^{-1}$)	10.3	0.8
Dead aspen basal area ($m^2 ha^{-1}$)	4.3	0.4
Total live aspen density (trees ha^{-1})	11,618.5	1,304.2
Total dead aspen density (trees ha^{-1})	4,450.5	704.2
Live aspen short regeneration density (trees ha^{-1})	8,693.8	1,169.4
Dead aspen short regeneration density (trees ha^{-1})	3,420.9	674.6
Live aspen tall regeneration density (trees ha^{-1})	2,399.1	550.8
Dead aspen tall regeneration density (trees ha^{-1})	796.7	126.6
Live aspen sapling density (trees ha^{-1})	353.6	58.4
Dead aspen sapling density (trees ha^{-1})	165.5	42.6
Live aspen overstory density (trees ha^{-1})	172.0	17.1
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
Plot-level OSS presence (categorical)		
OSS absent	70.9	3.1
OSS present	29.1	3.1
Tree-level OSS presence (categorical)		
OSS absent	89.3	0.3
OSS present	10.7	0.3

401

402 **Results**403 *Aspen condition*

404 Mean total aspen basal area, including living and standing dead trees, in our 220 study plots
405 was $14.6 \text{ m}^2 \text{ ha}^{-1}$, of which dead trees made up 29.5% (Table 2). Mean total aspen density was
406 16,069 trees ha^{-1} , 27.7% of which were dead. Looking at individual stem size classes, study plots
407 contained an average of 239 overstory aspen ha^{-1} (28.2% of which were dead), 519 saplings ha^{-1}
408 (31.9% dead), 3,196 tall regeneration stems ha^{-1} (24.9% dead), and 12,115 short regeneration
409 stems ha^{-1} (28.2% dead) (Table 2). Of the 9965 live aspen stems we sampled, 34.2% of stems
410 had no crown dieback, 44.5% of stems had 1–33% dieback, 13.9% of stems had 34–67%
411 dieback, and 7.5% of stems had 67–99% dieback (Table 2). Mean crown ratio of live aspen was
412 52.0%.

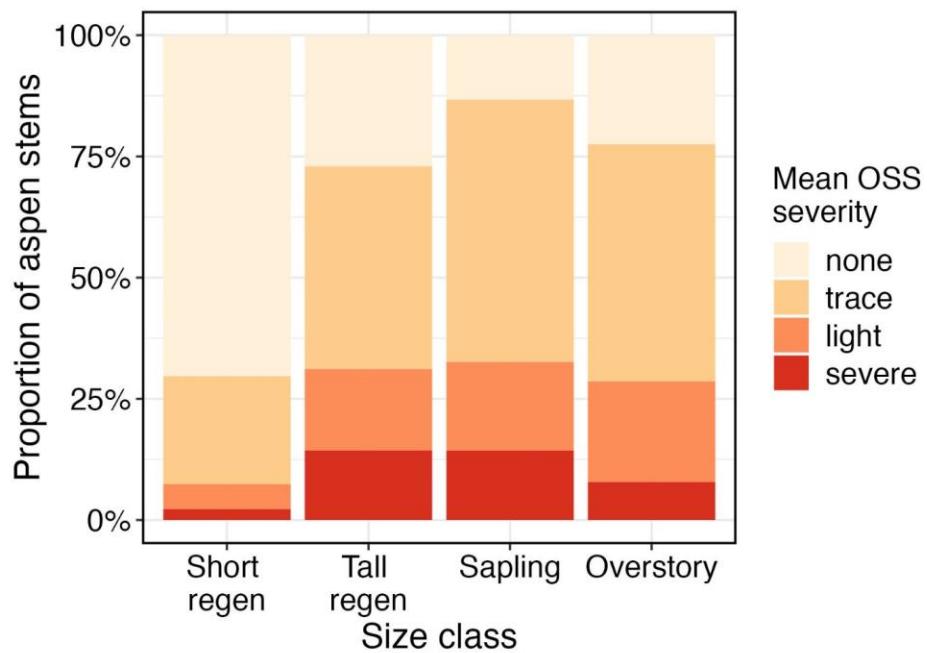
413

414 *OSS extent*

415 OSS was present in 29% of study plots and occurred in four of seven major areas where aspen
416 occurs in Arizona: South Kaibab, Flagstaff, Prescott, and Mogollon Rim (Fig. 2a). OSS was not
417 found in study plots we sampled in the North Kaibab, White Mountains, or Coronado major
418 areas. The area around Prescott had the highest plot-level rate of infestation, with OSS present
419 in all 17 plots. The South Kaibab had 65.4% of plots infested (Fig. 2b), the Mogollon Rim had
420 53.4% of plots infested (Fig. 2c), and Flagstaff had 20.4% of plots infested (Fig. 2b). Of the 9965
421 live aspen stems we sampled, 10.7% were infested with OSS (Table 2). Tree-level rates of
422 infestation across major areas were consistent with plot-level rates of infestation. When
423 looking at all plots, not just those in which OSS occurred, Prescott had the highest proportion of

424 trees infested (60.3%), followed by South Kaibab (20.8%), Mogollon Rim (16.2%), and Flagstaff
425 (7.6%).

426 OSS infested aspen stems of all sizes, although there was a higher likelihood of
427 infestation on trees taller than 1.37 m (i.e., tall regeneration stems and larger) (Fig. 4). Using
428 the OSS severity rating, 6.9% of all live aspen stems we sampled had a mean rating of trace,
429 2.3% were light, and 1.4% were severely infested. In the 64 plots where OSS was present, mean
430 severity ratings were 34.5% trace, 11.6% light, and 7.2% severe. Patterns of OSS severity across
431 stem size classes generally followed those of OSS presence, with more severe infestations
432 occurring as rate of presence increased (Fig. 4).



433 **Figure 4**
434 **Title:** OSS severity across four aspen stem size classes.
435 **Legend:** OSS severity across four aspen stem size classes. Data shown were taken only from the
436 64 study plots in which OSS was observed and include only live trees. OSS severity was assessed
437 using the rating system devised by Crouch et al. (2021), which rates OSS severity on each tree
438 from ground level to 6 m. Each tree's stem up to 6 m is divided into thirds, and severity is rated
439 for each 2 m section (or shorter for trees < 6 m tall) on both the north and south sides of the
440 tree. The ratings are as follows: light (no OSS present), trace (only a handful of OSS present),
441 light (OSS covers < 50% of section), severe (OSS covers > 50% of section).

442 **Table 3**

443 **Title:** Relationships between two measures of aspen stem health and OSS presence and
 444 severity.

Legend: 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 R² 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)

445

446 *OSS impacts*

447 OSS presence at the tree level was significantly ($p < 0.001$) associated with reduced aspen
 448 crown ratio and increased crown dieback based on univariate regression (Table 3). Trees
 449 infested with OSS were associated with a 9.8% reduction in crown ratio and a 0.5 unit increase
 450 in dieback compared to trees without OSS. Because dieback was assessed on a categorical scale
 451 from 0 to 3 (0 = 0% dieback, 1 = 1–33% dieback, 2 = 34–67% dieback, 3 = 67–99% dieback), a 0.5
 452 unit increase on the categorical scale equates to a roughly a 16% increase in dieback. Tree-level
 453 OSS severity was also significantly ($p < 0.001$) associated with reduced crown ratio and
 454 increased dieback (Table 3). Tree-level OSS severity ranged from 0 to 0.75, with 0 indicating a
 455 tree without OSS and 0.75 indicating a tree with the highest possible severity rating (OSS
 456 covering > 50% of all six stem sections rated). Thus, an increase in OSS severity of 0.1 equates
 457 to a 10% increase in OSS infestation of the tree's stem up to 6 m in height. A 0.1 unit increase in
 458 OSS severity was associated with a 3.9% reduction in crown ratio and a 0.2 unit increase in
 459 dieback, which equates to roughly 6.6% dieback. Despite the high degree of significance for all

460 four of these univariate relationships, OSS presence and severity explained a low proportion of
 461 the variance observed in aspen crown ratio and dieback ($R^2 \leq 0.03$), indicating that OSS is one of
 462 many factors influencing aspen stem health.

463 **Table 4**

464 **Title:** Relationships between six measures of dead aspen density and plot-level OSS abundance.

Legend: 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 R² is based solely on the model's fixed effect, which was plot-level OSS abundance.

^a m² ha⁻¹

^b trees ha⁻¹

465

466 For the 64 study plots in which OSS was present, plot-level OSS abundance was
 467 significantly ($p = 0.019$) associated with increased dead aspen basal area (Table 4). An increase
 468 in OSS abundance of 1, which represents the difference between no stems infested by OSS and
 469 all stems infested by OSS, was associated with an increase in dead aspen basal area of 5.7 m²
 470 ha⁻¹. For context, mean basal area of living aspen in these 64 plots was 11.4 m² ha⁻¹ and in all
 471 220 study plots was 10.3 m² ha⁻¹. We also assessed the influence of OSS abundance on five
 472 measures of dead aspen density: total dead aspen and density of the each of the four size
 473 classes. None of these univariate relationships were significant, although the tall regeneration
 474 ($p = 0.054$) and sapling ($p = 0.061$) models approached significance (Table 4). An increase in OSS
 475 abundance of 1 was associated with 1,654 more dead tall regeneration stems ha⁻¹ and 532

476 more dead saplings ha^{-1} . For context, there were 1,579 living tall regeneration stems ha^{-1} and
477 867 living saplings ha^{-1} on average in the 64 plots where OSS occurred and 2,399 tall
478 regeneration stems ha^{-1} and 354 living saplings ha^{-1} across all study plots. The models for total
479 dead aspen density, density of dead short regeneration, and density of dead overstory trees
480 were insignificant ($p \geq 0.350$).

481

482 *Factors influencing OSS abundance*

483 We considered 99 potential factors influencing plot-level OSS abundance, and random forests
484 indicated the five most important influences were autumn evaporation, elevation, degree-days
485 between 10°C and 40°C, winter climate moisture index (CMI), and autumn precipitation (Table
486 5). Based on univariate relationships between the top 25 most important influencing factors
487 and OSS abundance, the five strongest influencing factors were maximum winter temperature
488 ($R^2 = 0.43$; $p < 0.001$), winter evaporation ($R^2 = 0.41$; $p < 0.001$), maximum spring temperature
489 ($R^2 = 0.30$; $p < 0.001$), elevation ($R^2 = 0.26$; $p < 0.001$), and minimum spring temperature ($R^2 =$
490 0.21 ; $p = 0.004$).

491 The optimal SEM for plot-level OSS abundance ($AIC = 861.6$; Fisher's $C = 1.018$ with $p =$
492 0.907 [high p value indicates better fit]; response marginal $R^2 = 0.53$, conditional $R^2 = 0.88$
493 [marginal includes only fixed effects, conditional includes both fixed and random effects])
494 included seven influencing factors: autumn evaporation, winter CMI, maximum winter
495 temperature, elevation, fire strata, live aspen sapling density, and presence of ungulate
496 management (Fig. 5). Based on this SEM, all influencing factors except for winter CMI and
497 elevation had a significant ($p < 0.05$) direct effect on OSS abundance. Autumn evaporation had

498 **Table 5**

499 **Title:** Relationships between OSS abundance and the most important influencing variables
 500 based on random forests.

Legend: 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 1 for list of all influencing factors considered.

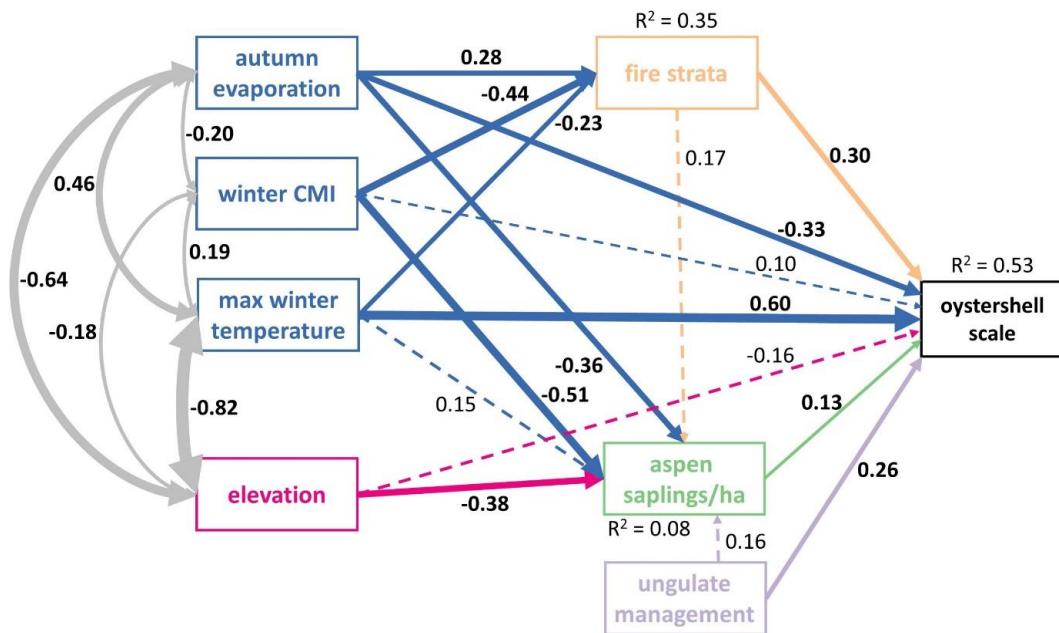
Random forests		Univariate regressions		
Rank	Influencing factor	Coefficient	Marginal R ²	p value
1	autumn evaporation	-0.003	0.014	0.195
2	elevation	< -0.001	0.263	< 0.001
3	degree-days 10–40°C	< 0.001	0.197	0.003
4	winter CMI	0.005	0.015	0.302
5	autumn precipitation	0.002	0.168	0.002
6	winter evaporation	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 R² is based solely on the model's fixed effect, which was the influencing factor shown in each row.

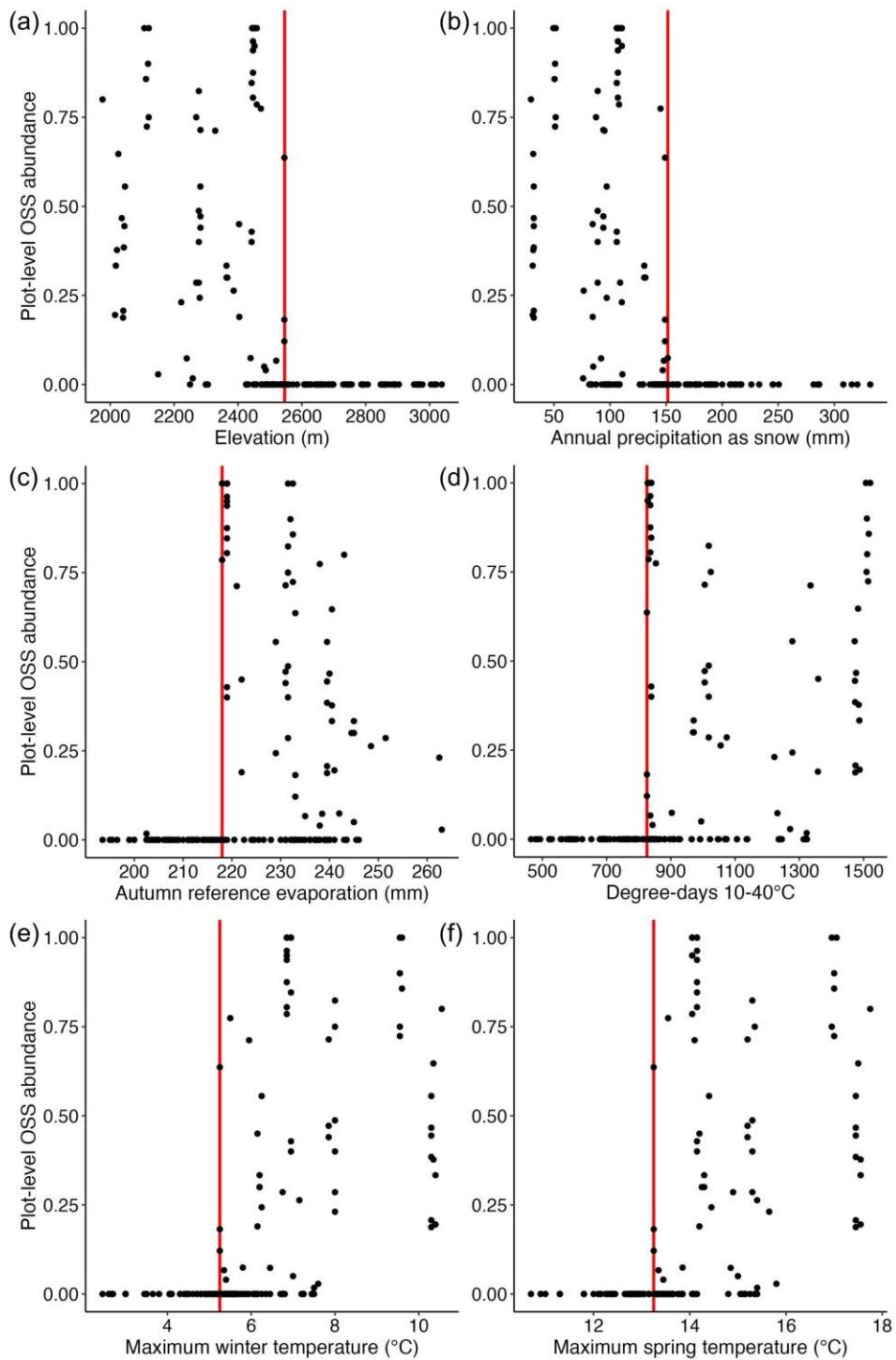
501

502 a negative direct effect (effect size = -0.33; p = 0.011) on OSS abundance, whereas maximum
 503 winter temperature (0.60; p = 0.011), fire strata (0.30; p < 0.001), live aspen sapling density
 504 (0.13; p = 0.001), and presence of ungulate management (0.26; p < 0.001) had positive direct

505 effects. Fire strata and ungulate management were categorical variables (Table 1), and SEM
 506 indicated that less recent fire and presence of ungulate management resulted in greater OSS
 507 abundance. All three climate variables had significant ($p \leq 0.003$) influences on fire strata, with
 508 recent fire being driven by less autumn precipitation, higher winter CMI, and higher maximum
 509 temperatures in winter. Thus, more autumn evaporation indirectly led to more OSS, while
 510 higher winter CMI and maximum winter temperatures indirectly led to less OSS. More autumn
 511 evaporation and higher winter CMI also resulted in significantly ($p \leq 0.003$) fewer aspen
 512 saplings, resulting in both climate variables having an additional negative indirect effect on OSS
 513 abundance. Finally, aspen sapling density was significantly ($p < 0.001$) lower at higher elevation,
 514 resulting in a negative indirect effect of elevation on OSS abundance.



515 **Figure 5**
 516 **Title:** Optimal SEM for plot-level OSS abundance.
 517 **Legend:** Optimal SEM for OSS abundance that minimized AIC and maximized response R^2 .
 518 Significant ($p < 0.05$) path coefficients are shown in bold, and their corresponding paths are
 519 depicted as solid lines. In contrast, insignificant coefficients are not bolded, and their
 520 corresponding paths are shown as dashed lines. Path thickness indicates strength of its
 521 coefficient, with wider paths indicating stronger relationships.



522 **Figure 6**
523 **Title:** Elevation and climate thresholds beyond which OSS does not occur in aspen ecosystems
524 in Arizona.
525 **Legend:** Relationships between plot-level OSS abundance and (a) elevation, (b) snowfall, (c)
526 autumn evaporation, (d) degree-days above 10°C and below 40°C, (e) maximum winter
527 temperature, and (f) maximum spring temperature. Red lines indicate thresholds above or
528 below which OSS does not occur in aspen ecosystems in Arizona.

529 To further assess the relationship between climate and OSS, we searched for thresholds
530 using the climate variables that random forests, univariate regressions, and SEM indicated were
531 the most important drivers of plot-level OSS abundance. We identified clear elevational and
532 climatic thresholds beyond which OSS does not occur in Arizona (Fig. 6). According to these
533 thresholds, OSS was not observed in plots that exceeded 2545 m in elevation, received greater
534 than 152 mm of snow annually, experienced maximum winter temperatures below 5.25°C,
535 experienced maximum spring temperatures below 13.25°C, and had fewer than 825 degree-
536 days between 10°C and 40°C (calculated as accumulated temperature difference from the
537 degree-day threshold, rather than a true accumulation of degree-days [Wang et al. 2006]). In
538 addition, OSS was not observed in plots with less than 218 mm of autumn evaporation, except
539 for one plot which had 202.5 mm of evaporation and a single aspen stem infested with OSS.

540 We also assessed univariate relationships between tree-level OSS presence and severity
541 and four measures of aspen stem size: size class, height, dbh, and height-to-diameter ratio.
542 One-way ANOVA indicated that there were significant differences ($p < 0.001$) in OSS presence
543 and severity among the four stem size classes (Table 6). OSS presence was significantly greater
544 on overstory trees and saplings compared to tall and short regeneration, and OSS presence was
545 significantly greater on tall regeneration than short regeneration. Saplings and tall regeneration
546 had significantly greater OSS severity than overstory trees and short regeneration, while
547 overstory trees had significantly greater OSS severity than short regeneration. OSS presence
548 and severity significantly ($p < 0.001$) increased with increasing height and decreasing dbh (Table
549 6). In addition, OSS presence and severity significantly ($p \leq 0.042$) increased with increasing
550 aspen height-to-diameter ratio, and one-way ANOVA indicated that height-to-diameter ratios

551 were significantly ($p < 0.001$) greater inside areas of ungulate management than outside these
 552 areas. Similar to the tree-level crown ratio and dieback results, aspen stem size explained a low
 553 proportion of the variance observed in OSS presence and severity (marginal $R^2 \leq 0.02$) (Table 6).

554 **Table 6**

555 **Title:** Relationships between tree-level OSS presence and severity and four measures of aspen
 556 stem size.

Legend: 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 SR	-12.246 c	1.936	< 0.001	0.014
	class 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 SR	0.010 c	0.008	0.239	0.021
	class 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)

557

558 **Discussion**

559 *OSS extent*

560 OSS is widely distributed throughout aspen ecosystems in central Arizona (Fig. 2a), confirming
 561 the initial report of OSS outbreaks in the region (Crouch et al. 2021). This study added plots in
 562 three areas not surveyed by Crouch et al. (2021) – North Kaibab, White Mountains, and

563 Coronado – none of which had OSS. We also added plots in the South Kaibab, Flagstaff,
564 Prescott, and Mogollon Rim major areas, identifying more sites where OSS occurs in these areas
565 than were initially reported (Grady 2017; Crouch et al. 2021). Aspen ecosystems we sampled in
566 the North Kaibab and White Mountains may be free of OSS because wetter, colder climates in
567 those areas (Supplementary table 1) may be unsuitable for OSS, as we discuss later. For
568 example, all North Kaibab and White Mountains plots occurred above 2545 m in elevation,
569 which was the threshold above which we did not observe OSS anywhere in Arizona (Fig. 6a).
570 Alternatively, these areas may have evaded OSS invasions for a different, unknown reason. For
571 example, OSS spread at the landscape scale is likely facilitated by its ability to infest a wide
572 array of hosts in addition to aspen (Crouch et al. 2021) and perhaps even by historical
573 transportation of infested apple stock by Euro-American settlers or more recent movement of
574 infested nursery stock. However, our ability to determine how other host species facilitate OSS
575 invasions of aspen ecosystems is limited due to the lack of fine-scale mapping of where apples
576 were historically planted and where other OSS host species occur, particularly understory hosts
577 such as *Ceanothus* spp. In contrast to the North Kaibab and White Mountains, aspen
578 ecosystems on the Coronado tend to occur on relatively warmer, drier sites (Supplementary
579 table 1), but OSS may have been absent in our Coronado study plots because all the plots we
580 sampled were in areas burned the previous year by the 2020 Bighorn Fire. Importantly, our
581 sampling was not exhaustive and was restricted to aspen ecosystems, so OSS may occur in the
582 North Kaibab, White Mountains, and Coronado. More extensive monitoring in these areas,
583 including on hosts other than aspen, is warranted.

584 Prescott had the highest rates of OSS infestation of the seven major areas we studied,
585 with all 17 plots and 60.3% of live aspen in the region being infested. This is concerning because
586 Prescott also had the highest levels of sustainable aspen recruitment (Crouch et al. In revision),
587 so OSS outbreaks in this area might eventually counteract successful recruitment. One reason
588 why there is so much aspen recruitment in Prescott is because elk populations, which
589 significantly inhibit aspen recruitment (Beschta and Ripple 2010; Fairweather et al. 2014;
590 Crouch et al. 2023, In revision), do not occur in the area. Therefore, ungulate exclosures, which
591 do not exist in the area, do not facilitate OSS invasions of aspen ecosystems in Prescott as they
592 seem to do in other areas of Arizona. Instead, Prescott may have more OSS than other areas
593 because it has been present in the area for longer. The earliest report of OSS occurring on
594 wildland aspen in Arizona was in Prescott approximately 30 years before our study occurred
595 (Fairweather 1992). Another possible explanation for why OSS is so abundant in Prescott is
596 because aspen sites in this area tend to experience warmer temperatures than aspen in other
597 parts of Arizona (Supplementary table 1). As we discuss below, warmer temperatures are a
598 significant driver favoring OSS.

599

600 *OSS impacts*

601 OSS negatively affected aspen health at both the tree and stand levels. Aspen trees infested
602 with OSS had significantly lower crown ratios and higher dieback, indicating reduced stem
603 health. As OSS infestations became more severe, crown ratio significantly decreased, and
604 dieback significantly increased (Table 3). This crown damage was likely caused by the feeding
605 behavior of OSS, which extracts fluid from the host plant's non-vascular cells (Griswold 1925;

606 Beardsley and Gonzalez 1975), but the exact mechanism that causes damage remains unknown
607 and represents an important research need. For example, aspen bark is photosynthetic (Jones
608 and DeByle 1985), so OSS feeding might reduce the tree's photosynthetic capacity.
609 Alternatively, OSS feeding may compromise stem health by causing trees to allocate resources
610 from growth to defense (Cope et al. 2021). At the stand level, plots with more stems infested by
611 OSS had significantly greater dead aspen basal area, with a 10% increase in OSS abundance
612 equating to an increase of $0.57 \text{ m}^2 \text{ ha}^{-1}$ in dead aspen basal area (Table 4). Although density of
613 total dead aspen stems and density of dead stems in each of the four size classes had
614 insignificant relationships with OSS abundance, the models for dead tall regeneration and
615 saplings approached significance, suggesting that OSS may have an outsized influence on these
616 intermediate-sized, recruiting stems (Crouch et al. In revision).

617 Density of aspen saplings and saplings of all host species were significantly associated
618 with increased plot-level OSS abundance (Table 5), providing additional evidence that
619 intermediate-sized, recruiting stems seem to be most susceptible to OSS infestation. At the tree
620 level, OSS infestations were more severe on tall regeneration and saplings and were associated
621 with taller and thinner stems (Table 6). We hypothesize that short regeneration had such low
622 infestation rates because these stems remain shorter than 1.37 m for only a few years (Jones
623 and Schier 1985), which reduces the likelihood of OSS finding them before they grow into taller
624 size classes. Short regeneration may also be more likely to evade OSS because they are smaller
625 targets. We hypothesize that overstory trees had lower OSS severity than tall regeneration and
626 saplings because overstory trees tend to have thicker bark, which may inhibit OSS's ability to
627 insert their stylet and feed on larger aspen stems. On the other hand, overstory trees may have

628 had lower OSS severity than intermediate-sized stems because the OSS severity rating system
629 does not assess OSS above 6 m in height. The mechanisms underlying OSS's outsized impacts
630 on intermediate-sized, recruiting stems merit further research, but the potential impacts of this
631 finding are clear. Recruiting stems are critical indicators of aspen community resilience (Rogers
632 and Mittanck 2014; Rogers 2017), and increased mortality of these stems from OSS poses a
633 major threat to sustainability of aspen ecosystems (Crouch et al. 2023, In revision).

634

635 *Factors influencing OSS abundance*

636 Climate was the most important factor driving OSS invasions of aspen ecosystems in Arizona.
637 According to random forests, seven of the top 10 and 15 of the top 25 factors influencing OSS
638 abundance were climate variables. Moreover, SEM indicated that climate variables, namely
639 autumn evaporation and maximum winter temperature, had the strongest direct effect on OSS
640 abundance. Generally, warmer and drier conditions were associated with increased OSS
641 abundance. For example, greater OSS abundance was associated with fewer degree-days below
642 0°C and more degree-days between 10°C and 40°C, with warmer temperatures in winter,
643 spring, and summer, with less winter precipitation and annual snowfall, and with greater spring
644 climate moisture deficit (CMD) and winter evaporation (Table 5). The strong relationship
645 between climate and OSS abundance is not surprising because of the well-established influence
646 of climate on development of armored scale insects (Beardsley and Gonzalez 1975).
647 Alternatively, the relationship between climate and OSS might be mediated through host stress
648 (Crouch et al. 2021). The plant stress hypothesis would suggest that drought not only weakens
649 aspen defenses but also increases nutritional quality, leading to increased OSS fitness and

650 abundance (White 1984; Dale and Frank 2017). In support of this hypothesis, the optimal host
651 for sap-feeding herbivores is one that has experienced long-term, intermediate drought stress
652 punctuated by temporary releases from that stress (Kolb et al. 2016). Our findings seem to align
653 with this hypothesis because, although arid conditions in general were associated with more
654 OSS, we found that wetter conditions in autumn (e.g., reduced evaporation and increased
655 precipitation) were associated with increased OSS abundance. Therefore, we hypothesize that
656 OSS thrives when conditions are consistently arid with temporary releases from drought in
657 autumn. Further research is needed to assess this hypothesis and elucidate the mechanisms
658 underlying climate's influence on OSS.

659 Although previous research has indicated that elevation is an important limiting factor
660 for OSS (Crouch et al. 2021, In revision), our study revealed that climate drives this relationship.
661 Based on SEM, elevation did not have a significant direct effect on plot-level OSS abundance
662 when climate was accounted for in the model. Instead, climate variables had significant direct
663 effects on OSS abundance and were significantly correlated with elevation. A clear elevation
664 threshold was observed in our study, in which no OSS was found above 2545 m (Fig. 6a).
665 However, thresholds were also observed for climate variables (Fig. 6b–f), indicating that there
666 are cooler, wetter climatic conditions which are currently unsuitable for OSS, and these
667 conditions happen to coincide with elevation. We suspect that these thresholds, particularly
668 the elevation threshold, will change as the climate continues to warm (Seager et al. 2007);
669 however, repeated measurements of study plots will be required to confirm this hypothesis.

670 Given OSS's hypothesized role as a sleeper species and the strong influence of climate
671 on OSS abundance, our study suggests that climate change caused OSS population sizes to

672 rapidly increase and to transition from an innocuous pest to a high-impact invasive species. We
673 have shown that OSS is associated with more arid conditions. Therefore, we hypothesize that
674 prolonged, record drought and warmer temperatures over the past 10–20 years (Williams et al.
675 2022) caused OSS populations in Arizona to awaken. Climate is generally considered the most
676 common cause of sleeper species awakenings (Bradley et al. 2018; Frank and Just 2020),
677 although other possible explanations exist, such a new mutualism, loss of a predator or
678 parasite, evolution, or introduction of a new genetic strain (Lockwood et al. 2005; Borden and
679 Flory 2021; Spear et al. 2021). A new mutualism is unlikely because there are no documented
680 mutualists associated with OSS (Griswold 1925; Miller and Davidson 2005), whereas the other
681 explanations are conceivable and represent fruitful areas for future research. For example,
682 armored scale populations are susceptible to suppression by natural enemies (Edmunds 1973;
683 Raupp et al. 2010; Frank 2020), so release from one or more natural enemies could lead to OSS
684 population growth. Interestingly, climate change can cause such a release by creating
685 asynchrony between phenology of scale insects and their natural enemies (Frank 2020).
686 Research on OSS genetics is needed to determine whether evolution or introduction of a new
687 genetic strain of OSS may have influenced awakening of OSS populations. Because of the strong
688 relationship between climate and OSS, we have serious concerns that OSS populations in other
689 areas will continue awakening with continued climate warming (Seager et al. 2007), as has
690 recently been observed in Utah, Nevada, and Idaho (Williams 2021; Grady et al. 2022).

691 In addition to climate, fire had a strong influence on OSS abundance. Fire strata was the
692 third most important direct influence on OSS abundance based on SEM. Less recent fire
693 resulted in significantly more OSS, suggesting that fire can be an important strategy for

694 managing OSS. Of the 31 study plots that experienced fire in the two years prior to sampling,
695 only two plots were infested with OSS, and OSS abundance in these two plots was low, with
696 only 1.7% and 7.3% of aspen stems infested. In contrast, 40 of the 139 plots that had not
697 experienced fire in the preceding 20 years were infested with OSS. Fire may be an important
698 limiting factor for OSS because it kills OSS both directly and indirectly, by killing hosts upon
699 which OSS is dependent (Crouch et al. 2021). Aspen has thin bark, making it highly susceptible
700 to fire mortality, so even low severity fire can kill overstory aspen (Jones and DeByle 1985;
701 Stoddard et al. 2018) and, in turn, the OSS feeding on aspen. Alternatively, lack of OSS in areas
702 of recent fire might simply be due to timing. It might take two or more years after a fire for
703 stands of recruiting stems, which we know are susceptible to OSS infestation, to develop.

704 We also found that ungulate management strategies, which primarily consisted of
705 fenced exclosures, resulted in significantly more OSS (Fig. 5). Although exclosures are highly
706 effective at promoting aspen recruitment (Crouch et al. In revision), this study supports
707 previous evidence that OSS is more prevalent in areas of ungulate management (Crouch et al.
708 2021, In revision). We hypothesize that ungulate exclosures promote OSS by directly increasing
709 aspen density and, potentially, by indirectly reducing host vigor. Dense aspen stands provide
710 more available host material and feeding sites for OSS and might facilitate OSS spread. High
711 densities might also reduce host vigor through increased inter-tree competition (Ashton and
712 Kelty 2018), thereby making individual aspen stems more susceptible to OSS. In support of this
713 hypothesis, we found that aspen inside areas of ungulate management had greater height-to-
714 diameter ratios compared to aspen outside these areas. Dense stands produce stems with
715 greater height-to-diameter ratios (i.e., increased slenderness) (Wang et al. 1998; Frey et al.

716 2004), likely because trees prioritize height growth over diameter growth to compete with their
717 neighbors for sunlight. We expect that this is especially true for shade-intolerant species such
718 as aspen (Perala 1990). Frey et al. (2004) hypothesized that slender aspen in dense stands are
719 more susceptible to stressors because they have more difficulty with hydraulic conductivity and
720 may be more vulnerable to water stress and reduced photosynthesis as the stand naturally self-
721 thins. In our study, aspen with greater height-to-diameter ratios (i.e., taller, thinner stems)
722 were significantly associated with increased OSS presence and severity (Table 6), indicating that
723 slender stems with reduced vigor may be more susceptible to OSS. Research is needed to
724 determine which of these mechanisms explains why more OSS is found inside ungulate
725 exclosures. For example, Lindroth et al. (2023) found reduced levels of phenolic glycosides,
726 which is aspen's primary chemical defense against ungulate and insect herbivory, in unbrowsed
727 aspen found inside exclosures, so perhaps exclosures alter growth-defense trade-offs in aspen
728 in a way that increases susceptibility to OSS.

729

730 **Management implications**

731 OSS is already widespread across several states in the Interior West, including Arizona, so
732 management tactics intended to eradicate this pest are unlikely to succeed. Eradication is
733 further complicated by OSS's ability to infest an array of different host species and by the fact
734 that small populations are exceedingly difficult to detect due to OSS's small size and cryptic
735 coloring (Crouch et al. 2021). Instead of eradication, management resources may be better
736 spent suppressing OSS population sizes, mitigating damage to native ecosystems through
737 integrated pest management, and developing slow-the-spread tactics (Sharov et al. 2002).

738 Robust monitoring to assess a species' extent and impacts is a critical first step to managing any
739 invasive species. Continued monitoring in areas of Arizona where we did not find OSS (e.g.,
740 southern Arizona, North Kaibab, and White Mountains) is necessary, as is continued monitoring
741 of areas where OSS already occurs to document potential changes to the species' range (i.e.,
742 will OSS migrate to higher elevations in the future?). We also recommend monitoring of OSS in
743 nursery stock of all host species, in urban areas that contain aspen, in riparian areas that
744 connect urban and wildland aspen populations, and in wildland aspen ecosystems, all of which
745 may harbor sleeper populations of OSS (Frank and Just 2020; Crouch et al. 2021). Our findings
746 can help managers identify stands at risk and prioritize which aspen ecosystems to monitor. For
747 example, OSS is most likely to occur on warmer, drier sites, in areas that have not recently
748 experienced fire, and in stands that have dense recruitment, such as those inside fenced
749 ungulate exclosures. Specifically, the climatic and elevation thresholds we identified (Fig. 6) can
750 guide monitoring efforts. Although elevation is the easiest metric for managers to consider
751 when searching for OSS, the 2545 m threshold is liable to change across aspen's expansive
752 range. Instead, the climate thresholds are likely to be more consistent outside our study area,
753 though we anticipate such climate-based thresholds will shift as warming continues. These
754 climate data can be easily obtained via ClimateNA (<https://climatena.ca/>).

755 Our findings can also be used to guide management that seeks to suppress OSS
756 populations and mitigate damage to aspen ecosystems. Our study indicates that three
757 strategies might help to suppress OSS populations: (1) increasing application of fire at the
758 landscape scale, (2) reducing reliance on ungulate exclosures, and (3) decreasing aspen stand
759 density. Fire has a negative influence on OSS, and although frequency and size of wildfires will

760 likely continue to increase as climate warming continues (Seager et al. 2007; Singleton et al.
761 2019), managers may consider implementing prescribed fire to suppress OSS infestations in
762 individual aspen stands. Frequent, low-severity fire may be detrimental to aspen stands,
763 especially in the presence of chronic ungulate browse (Crouch et al. 2023), so fire should be
764 implemented with caution and infrequency when managing for OSS. Advantages of fire as an
765 OSS management strategy include low cost of implementation, the ability to kill OSS on
766 multiple host species including understory plants, and the fact that fire is a natural component
767 of aspen ecosystems (Crouch et al. 2021). Prescribed fire may also be an effective strategy for
768 slowing the spread of OSS from newly discovered invasion sites.

769 Another strategy managers may consider is reducing use of fenced ungulate exclosures.
770 Reducing reliance on exclosures should help reduce OSS population sizes, although this will
771 require finding other ways to overcome chronic ungulate browse that threatens aspen
772 ecosystem resilience, adaptive capacity, and sustainability (Rogers 2017; Crouch et al. 2023, In
773 revision). Dense stands with abundant recruiting stems are the structure that seems most
774 favorable for OSS population growth. However, it remains unclear whether the relationship
775 between aspen stand density and OSS is due to increased host availability, facilitated spread
776 among densely growing stems, and/or decreased host vigor in more slender stems. Further
777 research is needed to determine how stand density and growth versus defense trade-offs
778 influence aspen susceptibility to OSS at different spatial scales.

779 A third strategy managers may consider for suppressing OSS populations is reducing
780 aspen stand densities via thinning. Thinning might also promote aspen resistance to drought, as
781 reduced growth rates which occur in dense stands are associated with increased mortality

782 during drought (Kane and Kolb 2014; Ireland et al. 2014, 2020; Crouch et al. 2023). However,
783 thinning must be implemented with care in aspen stands because aspen is sensitive to
784 mechanical damage from logging equipment and susceptible to subsequent infection by
785 canker-causing fungi and decay diseases (Walters et al. 1982; Jones and Shepperd 1985).
786 Another potential drawback to thinning is that sudden, direct exposure of aspen stems to
787 sunlight may cause sunscald (Krasnow et al. 2012), creating potential infection courts for
788 pathogens. Before we can wholeheartedly recommend use of prescribed fire or silvicultural
789 strategies like thinning to manage OSS, long-term experimental research is needed to assess
790 the efficacy of these strategies for suppressing OSS populations and mitigating damage to
791 aspen ecosystems. Research is also needed to assess the efficacy of other forms of
792 management, such as application of systemic insecticides, that will be critical components of an
793 integrated pest management program for OSS. Our future work seeks to address these needs
794 by assessing OSS and aspen responses to various suppression strategies.

795

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815

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