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Susceptibility of Eurasian Scots pine, *Pinus sylvestris* L., to the aggressive North American mountain pine beetle, *Dendroctonus ponderosae* Hopkins

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ABSTRACT

Introductions of alien forest insects can exert substantial ecological and economic impacts on natural forest systems. The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, an aggressive bark beetle native to western North America, kills mature pines at outbreak levels and is currently expanding its geographic, altitudinal and host ranges across the continent. Its oligophagous feeding behavior and its ability to kill novel hosts in newly invaded areas of Alberta, Canada suggest that this insect could threaten pine forests in other regions of the world. Little is known of the susceptibility of Scots pine, *Pinus sylvestris* L., to mountain pine beetle. Scots pine is a potential novel host common to forests across Eurasia and introduced to North America. Laboratory studies indicate the insects can colonize and reproduce in harvested logs of the host. We measured outcomes of an outbreak by mountain pine beetle in mixed stands of mature Scots pine and ponderosa pine, *P. ponderosa* Dougl. ex. Laws. var. *scopulorum* Engelm., a historical host for the insect, in the Black Hills of South Dakota, U.S.A. We conducted a retrospective assessment of beetle attack and tree mortality of 165 trees (54 Scots pine and 111 ponderosa pine) of similar size and proximity that experienced high beetle pressure for three to four years ending in 2015. Our results show that mountain pine beetle can detect and attack live trees of Scots pine. Notably, we found that nearly 90% of Scots pines showed signs of attack, while no evidence of attack was found on the historical host in mixed stands. However, we found that Scots pines received half the attack density and demonstrated fifteen fold less likelihood of mortality in one year's time relative to ponderosa pine in nearby stands. These results are important for assessing the potential for mountain pine beetle to kill trees in Eurasia and North America in Scots pine stands.

1. Introduction

Western North American bark beetles (Curculionidae; Scolytinae) are globally some of the most destructive native forest pests (Lindgren and Raffa, 2013). During outbreaks, some aggressive species kill vigorous, large diameter, healthy trees at landscape scales, exerting biome-level influences (Raffa et al., 2008; Meddens et al., 2012). Members of the genus *Dendroctonus* are among the most destructive species, causing extensive mortality among conifers (Meddens et al., 2012; Reeve et al., 2012; Six and Bracewell, 2015). *Dendroctonus* spp. are thought to have evolved in North America (Wood, 1982) with only two species present in the Old World (*D. micans* and *D. armandi*). Consequently, with the exception of *Ips typographus* in Eurasia, landscape scale outbreaks of native tree-killing bark beetles are largely restricted to North American forests (Lindgren and Raffa, 2013). The putative absence of selective pressure for resistance to aggressive bark beetles and their associated fungi thus suggests the possibility of defense-free space in other regions of the world for aggressive bark beetles, should they inadvertently be introduced in such locales (Desurmont et al., 2011; Flø et al., 2013; Burke et al., 2017).

Many forests pests, including bark beetles, have been accidently introduced worldwide (Haack, 2001, 2006; Brockerhoff et al., 2006; Aukema et al., 2010), causing significant ecological and economic impacts (Gandhi and Herms, 2010; Aukema et al., 2011). Establishment of these insects requires selection of and reproduction within suitable hosts, as well as the ability to overcome mate-finding Allee effects (Liebhold and Tobin, 2008). Mountain pine beetle (*D. ponderosae* Hopkins), an aggressive bark beetle native to western North America, has been intercepted in international trade in the past (Brockerhoff et al., 2006), and some evidence suggests that outbreaks can be

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initiated from small founder populations (Schaupp et al., 1993). In recent years, mountain pine beetle and the southern pine beetle (*D. frontalis*) have expanded their ranges north within North America due to warming climates (Carroll et al., 2004; Lesk et al., 2017) and now are colonizing and killing novel hosts (Cullingham et al., 2011; Weed et al., 2013). Such phenomena raise the spectre of continent-wide range expansions (Safranyik et al., 2010), and the potential to inflict landscape-scale mortality in new global regions if established.

Mountain pine beetle is an oligophagous feeder, specialized on large mature hosts, attacking and killing most pine species within its range when at outbreak levels (Wood, 1982). Tree killing behavior requires a stepwise process of initial attraction, bark and phloem entry, aggregation pheromone production, and fungal inoculation (Wood, 1982; Rosenberger et al., 2017). Synergisms between aggregation pheromones from pioneering females and host kairomones trigger mass attacks by conspecifics. Constitutive physical and chemical defenses such as outer bark and resin may be effective in initially deterring colonization (Krokene, 2015) but once colonized, induced defenses such as increasing localized monoterpene concentrations in the phloem are critical to deterring further colonization by conspecifics and their symbionts, and for reducing brood production if beetles establish (Klepzig et al., 1996; Boone et al., 2011; Cale et al., 2017). Successful attacks generally result in rapid host mortality within a year, and broods emerge as adults the following summer.

While some work has tested the susceptibility of North American conifers to the aggressive Eurasian bark beetle *Ips typographus* (Bertheau et al., 2009; Økland et al., 2011; Schroeder and Cocoş, 2017), little is known about how conifers would fare with the introduction of a novel aggressive North American bark beetle like mountain pine beetle to Europe or Asia. Recently, urban plantings of more than 100 Scots pine (*Pinus sylvestris*), a pine species native to Eurasia, were killed during a mountain pine beetle outbreak surrounding Fort Collins, Colorado, U.S.A. (Negrón and Cain, 2018). Very young trees of this species were attacked at higher frequencies than a nearby native pine planting of the same age in British Columbia (Fries, 2017). Scots pine, another Eurasian pine, Austrian pine (*P. nigra*), and two Asian pines - Chir pine (*P. roxburghii*) and Japanese red pine (*P. densiflora*) - were previously attacked and killed by mountain pine beetle in North American arboretums (Furniss and Schenk, 1969; Smith et al., 1981). Scots pine, in particular, was most commonly attacked in an arboretum in Idaho in the 1960s, although not the most susceptible, as approximately half of the attacked trees survived (Furniss and Schenk, 1969). However, due to the artificial nature of an arboretum environment, the lack of many historical hosts in the proximity to compare attacks, and distance from proximate outbreaks to fuel beetle pressure, gaining systemic inferences for attraction and susceptibility have posed challenges.

Here, we report results from assessments of nearly 100 attacked trees of uniform diameter in a feral mixed stand of mature Scots and ponderosa pine in the otherwise homogenous ponderosa pine forests of the Black Hills, South Dakota, U.S.A. The susceptibility of Scots pine to attack by mountain pine beetle, the pine's vulnerability to mortality after attack, and attack intensity on Scots pine relative to ponderosa pine are reported. Based on our previous work with cut logs showing similar attraction of mountain pine beetles to infested logs of both Scots and ponderosa pines (Rosenberger et al., 2017), we hypothesized that Scots pine would be equally attractive to mountain pine beetle as the historical host. However, due to previous reports of colonization in arboreta (Furniss and Schenk, 1969; Smith et al., 1981), we hypothesized that Scots pine would demonstrate low vulnerability to mortality from mountain pine beetle attacks.

2. Methods

2.1. Susceptibility to attack

In mid-August 2015, immediately following the peak seasonal flight of mountain pine beetle, we established three 50 × 50 m plots in an approximately 8 ha mixed stand of mature feral Scots and native Ponderosa pines (el. approx. 1660 m, south facing aspect) in the Black Hills of South Dakota, USA (latitude, longitude: 44.264767, −103.622783; 44.265933, −103.623350; 44.266033, −103.622500). The origin of the mixed stand was unclear but is unique, particularly due to its relatively remote location in otherwise homogenous native ponderosa pine forest in the region. Cores from several of the largest Scots pines indicated the stand was approximately 80 years of age. In each plot, we measured the diameter at breast height (DBH, at 1.4 m above ground) of each tree to assess stand basal area. We then censused each tree, inspecting the bottom and mid bole (to approximately 4 m) for attacks by mountain pine beetle. Attack type was categorized as a strip attack, in which just a portion of the bole or just one side of the bole was attacked (pitch tubes present), or mass attack when the entire bole was attacked (Bleiker et al., 2014). Year of attack was determined by the condition of pitch tubes and foliage. Soft, fresh pitch tubes and green needles were rated as same-year (2015) attacks. Pitch tubes that were still intact and/or needles that were red were assessed as 2014 attacks. Pitch tubes that were hard and crumbly and/or had few to no red needles remaining on branches were assessed as attacked in 2013 or before. Trees with green needles and any of the previous pitch tube types were assessed as unsuccessful attacks. Thus, we were able to identify at least three years of attack history, with many Scots pines displaying more than one year of attack. Trees with pitch tubes and all red needles or partial to total needle shed were deemed to have been killed by mountain pine beetle.

2.2. Attack density

Attack density was assessed on Scots and ponderosa pines that had been attacked the previous year. Twelve Scots pines were selected from the mixed Scots and ponderosa stand, and 12 ponderosa pines were selected from nearby pure ponderosa stands. A 40 cm (width) × 60 cm (height) area at breast height was assessed on the north and south side of each tree. Pitch tubes were counted by year of attack as described above. The DBH of each tree was also measured.

2.3. Vulnerability to mortality

To assess vulnerability of Scots compared to a historical host, we established two 50 × 50 m plots in ponderosa stands adjacent (100–150 m away) to the mixed stands. These stands had undergone attack in recent years as determined by the condition of pitch tubes and foliage. Each tree was assessed as above to determine DBH, attack type, and year of attack.

2.4. Analysis

Generalized linear models with a binomial distribution (lme4 package in R) were used to assess the effects of plot and pine species on proportion of trees in the mixed plots showing signs of attack from 2015, 2014, or prior, and proportion of trees killed by attacks in 2014. The proportion all of trees attacked was not affected by plot before ($\chi^2 = 3.48$, df = 2, $P = 0.18$) or after ($\chi^2 = 1.70$, df = 2, $P = 0.43$) accounting for species in 2015, and the proportion of trees killed in mixed stands in 2014 were similarly not affected by plot ($\chi^2 = 2.54$, df = 2, $P = 0.28$), so we pooled data across plots. We used ANOVA to determine if there were differences in DBH between pine species. In order to determine whether the size-specific attack rate varied between species logistic regression (ANCOVA) models were used to examine proportion of Scots pine attacked (strip or mass attack) and ponderosa pine in the pure ponderosa stands attacked as a function of tree diameter, species, and their interaction. We used ANOVA to determine if attack density (pitch tubes per m^2) varied with pine species. Attack density did not differ between north and south sides of the trees

Table 1
Stand and tree characteristics at the five stands measured in the Black Hills, SD in 2015.

Stand	Stand Basal Area (m^2/ha)	Type	Species	Stems	Diameter at breast height (± SE) (cm)
A	9.0	Pure	Ponderosa	26	32.5 (1.3)
B	9.7	Pure	Ponderosa	46	24.5 (1.2)
C	9.4	Mixed	Ponderosa	19	27.4 (1.9)
			Scots	15	30.0 (2.2)
D	10.6	Mixed	Ponderosa	10	33.2 (3.4)
			Scots	21	30.6 (2.2)
E	11.3	Mixed	Ponderosa	10	29.4 (2.9)
			Scots	18	36.3 (3.0)

($F_{1,46}$ = 0.41, P = 0.52), so north and south measurements were averaged to derive attack density per tree.

3. Results

3.1. Susceptibility to attack

We assessed a total of 93 trees (54 Scots and 39 ponderosa) in the three mixed plots (Table 1) to determine attack preference. Results of the attack census revealed a total of 50.5% of trees in mixed stands showed signs of attack by mountain pine beetle by the end of the flight period in 2015. All attacked trees were Scots pine (87% of total Scots pines), with no ponderosa pine attacked in these sites (χ^2 = 87.26, df = 1, P < 0.0001).

We could not attribute attack preferences to size differences between species, as diameter at breast height did not significantly differ ($F_{1,91}$ = 1.86, P = 0.18) between ponderosa (29.4 ± 1.5 cm; mean ± SE) and Scots (32.3 ± 1.5) pines. Mountain pine beetles preferentially attacked larger trees, as the likelihood of attack increased with tree size among Scots pine in mixed stands (χ^2 = 4.83, df = 1, P = 0.028) and ponderosa pines in pure stands (χ^2 = 12.27, df = 1, P = 0.0005) (Fig. 1). The slope of each line in the logistic regression models for likelihood of attack vs. size was similar (χ^2 = 0.0001, df = 1, P = 0.99) indicating that the likelihood of being attacked for each species increased by similar amounts per unit increase in DBH. The intercepts differed, however (χ^2 = 6.14, df = 1, P = 0.013) (Fig. 1), indicating a greater likelihood of attack at smaller diameters among

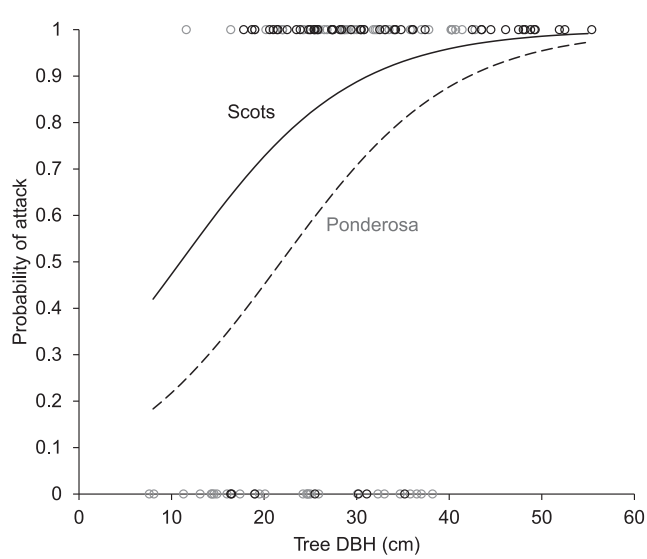

Fig. 1. Relationship between tree diameter and proportion of ponderosa pines (dashed lines and gray circles) and Scots pines (black lines and circles) attacked in the Black Hills of South Dakota over at least a 3 year period (≤2013–2015). Circles indicate raw data (n = 126).

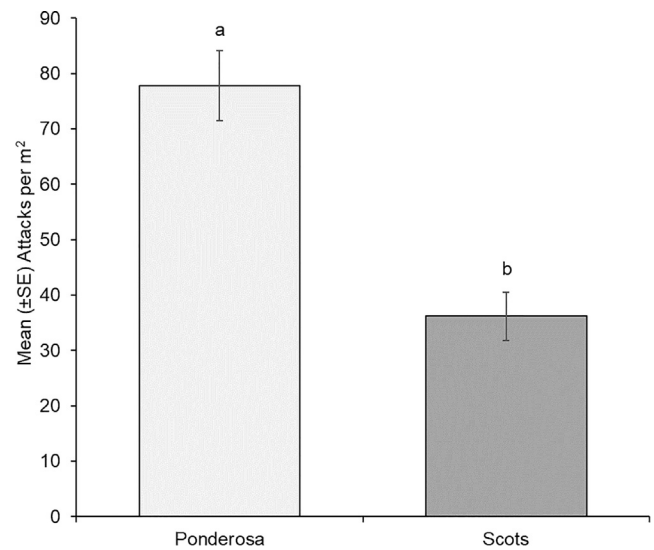

Fig. 2. Mean attacks (± SE) m^{2-2} as measured by the average number of the pitch tubes on the north and south side of each tree created one year prior (2014) by attacking mountain pine beetles (n = 24 total pines). Different letters indicate statistically significant differences (P < 0.05).

Scots pine compared to ponderosa pine.

Assessment of pitch tubes from attacks the previous year showed that ponderosa pine in pure stands had over twice as many attacks per square meter as did Scots pine in mixed stands ($F_{1,22}$ = 29.40, P < 0.0001) (Fig. 2). There was no relationship between attack density and tree size (DBH) after accounting for species ($F_{1,21}$ = 0.184, P = 0.67).

3.2. Vulnerability to mortality

Ponderosa pine trees assessed for mountain pine beetle-caused mortality in 2015 in nearby homogenous stands, with similar basal area to that of the mixed stands (Table 1), showed 15.5 times more mortality among trees mass attacked the previous year than Scots pines (χ^2 = 59.3, df = 1, P < 0.0001) (Fig. 3). Strip attacks were relatively uncommon in the ponderosa stand, occurring on 6% of the trees during the outbreak in the stand in 2014, vs. over 50% of trees suffering mass attacks (Table 2). Mass attacks on ponderosa pines frequently resulted in mortality the following year (Fig. 3). In contrast, among Scots pines, both strip and mass attacks were common in 2015, 2014 and prior, with one third to one half of the trees being attacked each year (Table 2). In contrast to ponderosa pines, mortality in Scots pines was less likely immediately following attacks, as only 5% of trees died (Fig. 3). Scots pines appeared to succumb to mountain pine beetle over longer periods, however (Table 2). Of the 22 Scots pines that showed signs of attacks in 2013 or prior, 13 (59.1%) were dead in 2015. Six Scots pines were attacked two years in a row; two of which were dead in 2015. Three were attacked at least three years in a row; two of which were dead in 2015.

4. Discussion

Our results demonstrate that a novel pine species, Scots pine, a species both geographically and phylogenetically distant from historical hosts (Bertheau et al., 2010), can be mass attacked (Table 2) and killed (Fig. 3) by mountain pine beetle during natural outbreaks. These results suggest that Eurasian Scots pine forests are at risk should the insect be inadvertently introduced. However, our results also suggest that these naïve trees do not represent defense-free space, despite their lack of coevolution. Indeed, attack success, defined here as a mass attack resulting in tree mortality, and rate of tree morality was lower in Scots

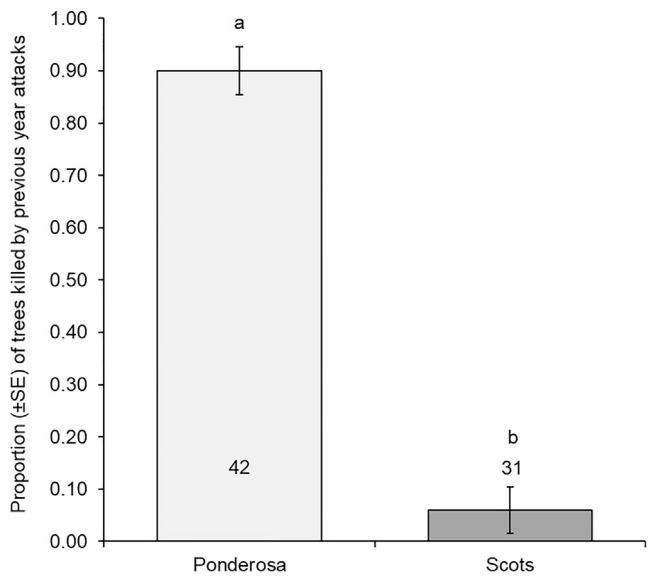

Fig. 3. Proportion (± SE) of trees from three mixed ponderosa and Scots stands and two pure ponderosa stands that were killed (red needles) after sustaining mountain pine beetle attacks the previous year in the Black Hills, SD. Numbers on bars indicate sample size. Different letters indicate a statistically significant difference ($P < 0.05$).

Table 2
Proportion of trees attacked in each stand type per year. Proportions indicate attacks on Scots trees in the mixed Scots and ponderosa pine stands ($n = 54$ trees) and ponderosa trees ($n = 72$ trees) in the homogenous ponderosa stands. Attack types include strip attacks (on just one side of the tree) or mass attacks (on all sides) in the Black Hills of South Dakota, USA. Note that no ponderosa pines were attacked in the mixed stands containing Scots pine. Stands were censused in August 2015.

Species and Attack Type	Proportion of trees attacked each year (*n*, proportion of those attacked trees that that been attacked previously)*		
	≤2013	2014	2015
Scots ($n = 54$)			
Strip	0.09	0.22	0.13
	(5, na)	(12, 0.08)	(7, 1.00)
Mass	0.31	0.35	0.19
	(17, na)	(19, 0.26)	(10, 1.00)
Ponderosa ($n = 72$)			
Strip	0.00	0.06	0.03
	(0, na)	(4, 0.00)	(2, 0.00)
Mass	0.01	0.53	0.01
	(1, na)	(38, 0.00)	(1, 1.00)

na, not applicable.
* Proportion of attacked trees previously attacked were not assessed for 2013 due to inability to distinguish exact year of attack with certainty prior to 2014.

pine than in a common native host (Fig. 3).

The apparently complete preference for the novel Scots pine in mixed stands was contrary to our hypothesis of similar attraction between these two species. Indeed, ponderosa pine is one of the most attractive historical hosts to foraging beetles in various host choice tests (Richmond, 1933; West et al., 2014, 2015; Rosenberger et al., 2017). A preference by mountain pine beetle for Scots pine over native hosts has been noted on a smaller scale previously. At the Shattuck Arboretum at the University of Idaho in the 1960s mountain pine beetle attacked Scots pines and other exotic pines growing in a common garden environment, with no concurrent attacks on ponderosa and western white pines (*P. monticola*) (Furniss and Schenk, 1969). A recent wave of attacks circa 2015 (Cook and Martinez, 2018) at the arboretum further revealed that Scots pines were attacked at least one year before any other species of pines although ponderosa pines are no longer present (Rosenberger, 2016). Negrón and Cain, (2018) further report that most trees attacked in Fort Collins, CO between 2008 and 2013 were Scots pines, and Fries (2017) reported 1.7–2.5 times greater attack rates on Scots pine than on lodgepole pine, another historical host on young trees in British Columbia Canada. The absence of attacks by mountain pine beetle on ponderosa pine in mixed stands is further surprising, as ponderosa pine contains higher concentrations of pheromone synergists such as myrcene and 3-carene that enhance attraction to colonized trees than does Scots pine (Rosenberger et al., 2017).

While preference for one host over another has been shown previously (Bentz et al., 2015; Raffa et al., 2013; Richmond, 1933), the absence of attacks by mountain pine beetle on a species of pine in mixed pine stands has been shown in one other system to date. Recent studies have indicated that Great Basin bristlecone pine (*P. longaeva* Bailey) also remains unattacked in mixed stands (Gray et al., 2015; Bentz et al., 2017). Great Basin bristlecone pine is a native non-host however, remaining unattacked even in homogenous stands (Gray et al., 2015), likely due to long co-evolutionary history with mountain pine beetle that has selected for resistant trees (Eidson et al., 2017, 2018) without reciprocal adaptation (Raffa and Berryman, 1987). It is possible that tree defenses could have been greater among ponderosa pines in our mixed stand, with weaker cohorts of trees being successively culled in previous years. However, we did not find any pitch tubes visible on the boles of ponderosa pines in the mixed stands, nor any evidence of previous tree-killing activity on ponderosa pines. Further inter-plot scouting in 2015 revealed only one attacked ponderosa pine. Because high proportions of ponderosa pines were attacked and killed in proximate homogenous stands, we see no evidence of higher resistance in ponderosa pine vs. Scots pine in general.

It is unclear what accounts for such strong host discrimination to the point of excluding another host during foraging. Several factors have been suggested for host discrimination for mountain pine beetle such as visual cues (Shepherd, 1966), random landing with post-landing gustatory assessment (Hynum and Berryman, 1980; Raffa and Berryman, 1982; Pureswaran and Borden, 2005), and bark and foliage volatile cues (Moeck and Simmons, 1991; Gray et al., 2015; Eidson et al., 2017). We believe that visual discrimination is an unlikely driver of host attraction as Scots pine and ponderosa pine were similar in size (Table 1) and color. Here, gustatory cues in the outer bark (Eidson et al., 2017) and/or volatile cues (Gray et al., 2015) are likely important. It is unclear whether beetles were deterred by gustatory discrimination after landing, as we were not able to measure landing rates. Gustatory deterrence of phloem (Raffa and Berryman, 1982) alone is unlikely, as ponderosa pine is known to be a highly acceptable host (West et al., 2014; 2015; Rosenberger et al., 2017) and no pitch tubes were observed on ponderosa pine. However, some repellency from outer bark (Eidson et al., 2017) in combination with attractive volatiles from nearby Scots pine could explain stronger relative attraction. Indeed, the deterrent 4-allylanisole is present in much higher concentrations in ponderosa pine and other historical hosts (Bentz et al., 2015, 2016; Keefover-Ring et al., 2016; Rosenberger et al., 2017) than in Scots pine (Rosenberger et al., 2017).

While Scots pines were more likely to be attacked than ponderosa pine, they were over 15 fold less likely to be dead by the following year than ponderosa trees in nearby stands (Fig. 3). Reduced vulnerability to successful attack was suggested by previous work on colonization success using harvested logs, which indicated that Scots pine would have a lower proportion of beetles boring into the bark, accepting the phloem, and initiating brood galleries than ponderosa pine (Rosenberger et al., 2017). Similar to native pines, induced defenses of Scots pine in response to fungal associates likely further deter beetles from establishing brood (Lieutier et al., 1989). Gradual but extensive accumulation of monoterpenes in Scots pine has been shown previously in response to Ophiostomoid fungi in Eurasia (Lieutier et al., 1989). This defensive

response may be responsible for increased likelihood of tree survival, although trees respond differently to different fungi (Lieutier et al., 1989; Raffa and Smalley, 1995), and the response of Scots pine to specific fungal associates of mountain pine beetle such as *Grosmania clavigera* and *Ophiostoma montium* remains unknown.

Extended survival of trees may also be due to a lower attack density on Scots pine vs. ponderosa pine (Fig. 2), similar to that observed on attacked but surviving Scots pines in California (11–43 pitch tubes m^{-2}) (Smith et al., 1981). In lodgepole pine, the optimum attack density for beetle survival is around 62 attacks m^{-2} (Raffa and Berryman, 1983), which is lower than the 77.8 attacks m^{-2} observed on our ponderosa pine but much higher than the 36.2 attacks m^{-2} observed on our surviving Scots pines (Fig. 2). Low attack density despite apparently strong attraction supports the preference-performance hypothesis where parents will choose hosts that best support larval development (Gripenberg et al., 2010). Indeed, in our previous work in cut logs, significantly fewer adults are produced in Scots than in ponderosa pine (Rosenberger et al., 2018). Thus, lower pitch tube densities may suggest that more beetles rejected the host after cues from a gustatory assessment of the periderm or secondary phloem (Krokene, 2015).

While the results of this study strongly suggest that Scots pine is highly attractive to mountain pine beetle, ultimate vulnerability to mortality in outbreaks remains uncertain for several reasons. First, absolute population estimates of beetle abundance were not available. Thus, it is unclear whether low attack densities on Scots pine were due to unsaturating numbers of beetles present in the stands, or due to few beetles choosing to continue boring into Scots pine and producing pitch tubes to be counted the following year. The latter is more likely as we observed 11 separate red-attacked pockets of ponderosa pine within 300 m of the mixed Scots pine stand, suggesting high populations of beetles on the landscape in 2014 despite few dead Scots pines. We did not reassess the stands in 2016 due to harvesting operations in the area, so are unable to determine if the trees did indeed succumb to the beetle/fungal complex, or if they survived the attack. However, nearly 71% of Scots attacked before 2013 were dead by 2015. This pattern suggests that attacked trees may succumb after two or more years possibly due to continued growth of Ophiostomoid fungi or attack by secondary bark beetles. The vulnerability of Scots pine to mountain pine beetle and/or its associated fungi was also noted by Fries (2017) who reported 70–90% mortality of Scots pine among young attacked trees, although time to mortality from initial attack was not reported.

This study shows that mountain pine beetle is attracted to Scots pine and able to mass attack live trees, thus putatively demonstrating the ability to produce aggregation pheromones. However, whether establishment is possible if introduced to Scots pine stands in Eurasia remains uncertain. Establishment requires successful reproduction, which was not measured in this study. As such, it is unknown whether an outbreak can be maintained in Scots pine, or whether these trees will serve as sinks or ecological traps, producing fewer insects than are required to procure the host (Pearse et al., 2013). Other observations of relatively low reproductive success in live Scots pines in Idaho, and our previous work with cut logs suggests Scots pine may be a poor host in this regard (Cook and Martinez, 2018; Furniss and Schenk, 1969; Rosenberger et al., 2018). While eradication of introduced insects is often difficult (Brockerhoff et al., 2010), a highly attractive host serving as a sink could assist in eradication efforts should the insect be introduced to Scots pine forests. Further, in North America, where Scots pine is planted extensively, highly attractive Scots pine may have utility as a sentinel tree, indicating the presence of mountain pine beetle in a stand (Poland and Rassati, 2019). Indeed, in a recent outbreak in Shattuck Arboretum in Idaho, 7 Scots pines were attacked at least one year prior to the seven other species that were subsequently attacked (Cook and Martinez, 2018; Rosenberger, 2016). In the absence of additional tests on live trees, the apparent ability of Scots pine to resist rapid mortality common to other pine hosts attacked by mountain pine beetle (Fig. 3; Furniss and Schenk, 1969; Smith et al., 1981) suggests that the likelihood of sustained outbreaks in Scots pine forests may be less than that of native North American forests.

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Declarations of interest

None.

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