

β -Pinene + ethanol attracts more red turpentine beetles than carene + ethanol, with or without traces of frontalin, at prescribed burn or thinned sites

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Abstract

1. Red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Curculionidae: Scolytinae), previously responded more strongly to (–)- β -pinene + ethanol than (+)-3-carene + ethanol lures at sites burned the prior year by wildfire in Oregon and northeastern California, whereas at a thinned-unburned Arizona site (+)-3-carene + ethanol was the stronger attractant. This discrepancy was further examined to tease apart whether *D. valens* attraction varies by region or previous forest disturbance types.
2. Here, (–)- β -pinene + ethanol and (+)-3-carene + ethanol lures were tested in pine stands at two Oregon sites disturbed the previous year by a prescribed burn or thinning only. Both lures were tested also with or without trace amounts of the pheromone frontalin, as its presence enhanced attractions in China but had not been tested in North America.
3. At both sites, regardless of prior forest disturbance, (–)- β -pinene + ethanol lures attracted the most beetles. Lures releasing trace frontalin attracted more beetles than their corresponding lures without it at both sites, except in one case.
4. Overall, previous year disturbances from disparate management treatments had minimal influence on lure attraction to *D. valens*. For detection, monitoring or management (–)- β -pinene + ethanol + frontalin in trace amounts attracts the most beetles of lures tested to date in Pacific Northwest pine forests.

KEYWORDS

(–)- β -pinene, (+)-3-carene, *Dendroctonus valens*, ethanol, frontalin, lures, prescribed burn, thinning

INTRODUCTION

The need for a lure to monitor or manage *Dendroctonus valens* LeConte (Coleoptera: Curculionidae: Scolytinae) did not arise until after its invasion in China in the early 1980's and subsequent outbreak with aggressive behaviour toward *Pinus tabulaeformis* in the late 1990's (Sun et al., 2013; Yan et al., 2005). This sharply contrasts with its non-aggressive colonization of stressed, dying or recently dead pines throughout its native range in North and Central America

(Owen et al., 2010). The aggressive behaviour trait in China has been aided by the activity of vectored symbionts, including changes in pathogenicity and shifts of microbial communities from those carried by *D. valens* in North American forests (Cheng et al., 2016, 2018; F. Liu et al., 2020; M. Lu et al., 2010, 2011; Q. Lu, Decock et al., 2009; M. Lu, Zhou, et al., 2009; Taerum et al., 2013; L. T. Xu et al., 2016). The microbial changes create a latent risk to North American pine forests, should any of these *D. valens* return with new or more virulent forest pathogens.

Although a *D. valens* re-introduction from China has low probability because of phytosanitary standards to reduce forest pest transport by world trade and movement of people (Haack & Petrice, 2009; Meurisse et al., 2019), the risk is bolstered by two changes since 1980. First, the multifold expansion in maritime trade (UNCTAD, 2021), the most likely route for re-introductions (Meurisse et al., 2019), and second, a dramatic increase in the availability of susceptible host trees for colonization in western US forests, especially those stressed by fire. This results from increases in large wildfire numbers, fire severity and area burned driven in part by climate change (Abatzoglou & Williams, 2016; Littell et al., 2009, 2016; Singleton et al., 2019; Westerling, 2016; Williams et al., 2019). Furthermore, the availability of fire-injured trees will likely remain high or increase in western landscapes based on future projections for climate and fire activity (Barbero et al., 2015; Peterson & Littell, 2014; Williams et al., 2019), and enhanced use of prescribed fire to manage fuel loads (Kolden, 2019; Melvin, 2020). Burned trees are quickly attacked by *D. valens* (Ganz et al., 2003; Kelsey & Westlind, 2017) with a rapid population density increase the following year, capable of spreading any newly introduced exotic pathogens. In addition, although Southern Hemisphere pine plantations remain free of *D. valens*, this is one of the species with the highest invasion risk there from among 64 North American Scolytinae bark beetle species evaluated (Lantschner et al., 2017). Thus, developing a strong lure contributes to a second-level defence (National Invasive Species Council, 2008; Rabaglia et al., 2019) to rapidly detect unwanted movement of *D. valens* from North America or China to other pine forests around the world should phytosanitation efforts fail. It is also a tool for beetle management within both continents.

Lures for *D. valens* with pine kairomones have focused on (–)- α -pinene, (+)- α -pinene, (–)- β -pinene and (+)-3-carene, the major resin components in ponderosa pine, *Pinus ponderosa* (Smith, 1977). Comparison tests have shown (+)-3-carene to be the strongest attractant in China, California, Wisconsin, Pennsylvania, Mexico (Erbilgin et al., 2007; Sun et al., 2004) and Arizona (Kelsey et al., 2023), whereas (–)- β -pinene attracted more beetles than (+)-3-carene in central Oregon and northeastern California (Hobson et al., 1993; Kelsey et al., 2023). When each of these terpenes was released with ethanol in Pacific Northwest (PNW) and Arizona forests their attraction strength often increased substantially (Kelsey et al., 2023; Kelsey & Westlind, 2020). All of the PNW test sites were disturbed the previous year by prescribed burns or wildfire and (–)- β -pinene + ethanol attracted more beetles than (+)-3-carene + ethanol. In contrast, at an Arizona test site disturbed the previous year by thinning rather than fire, (+)-3-carene + ethanol was a stronger lure than (–)- β -pinene + ethanol (Kelsey et al., 2023). This raised the question of what impact did dissimilar disturbances or management, and their remaining stressed host materials, have on the divergent responses of *D. valens* in Arizona compared to the PNW. Similar geographic variability in lure attraction was noted with (–)- α -pinene, ethanol and (–)- α -pinene + ethanol in southeastern forests for wood-boring beetles (D. M. Miller, 2006) and several conifer bark beetles (D. R. Miller & Rabaglia, 2009). The latter authors proposed influencing factors could include dissimilar primary host species among test

sites, other competing sources of ethanol or α -pinene, local weather, or associated vegetation dampening of lure emissions. To address such effects on *D. valens*, our first objective was to compare their attraction consistency for (–)- β -pinene + ethanol and (+)-3-carene + ethanol at two relatively close geographic sites in Oregon, one disturbed the previous year by prescribed fire and the other disturbed by thinning.

Frontalin is produced and released by *D. valens* females and serves as a dual function sex- and aggregation-pheromone, with males responding to a wider concentration range than females (Z. Liu et al., 2013; Luxová et al., 2007). In China, lures with (+)-3-carene + trace frontalin mixed in at 0.005 or 0.05 ng/ μ L each caught more *D. valens* of both sexes than (+)-3-carene lures, with the latter frontalin mix attracting the most beetles (Z. Liu et al., 2013). Other lures with higher frontalin levels, albeit still trace amounts, showed a similar trend, (+)-3-carene + frontalin (11 ng/ μ L) was the strongest, followed by (+)-3-carene + frontalin (1.1 ng/ μ L) and finally (+)-3-carene the least attractive. However, (+)-3-carene + high release frontalin at 3 mg/d decreased the *D. valens* catch by more than half the number trapped by (+)-3-carene alone in China (Zhang et al., 2009). And, in central Oregon (–)- β -pinene + ethanol + frontalin at a 1.5 mg/d high dose attracted beetle numbers similar to (–)- β -pinene + ethanol lures (Kelsey & Westlind, 2022). In North American forests, the attraction of lures with trace levels of frontalin mixed with (–)- β -pinene or (+)-3-carene have not been investigated. Hence, our second objective was to test the attraction of *D. valens* to (–)- β -pinene + ethanol + frontalin and (+)-carene + ethanol + frontalin mixed at 11 ng/ μ L of terpene as used in China (Z. Liu et al., 2013), for comparison with one another, and their corresponding lures without frontalin, at the sites burned or thinned the previous year.

MATERIALS AND METHODS

Lures

Four lures were tested, (–)- β -pinene + ethanol, (+)-3-carene + ethanol, plus both of them with trace frontalin mixed at 11 ng/ μ L monoterpene. (+)-3-Carene (>90.0%), and (–)- β -pinene ($\geq$ 97%) were purchased from Sigma Aldrich (St. Louis, Missouri); their optical designation was omitted from here forward. Ethanol (95%) pouches and racemic frontalin ($\geq$ 95%) were from Synergy Semiochemicals Corp., Burnaby, Canada. Carene, β -pinene and their frontalin mixes were dispensed from low-density polyethylene (LDPE) bottles (15 mL, The Cary Company, Addison, IL) similar to earlier tests (Erbilgin et al., 2007; Kelsey et al., 2023; Kelsey & Westlind, 2020, 2021, 2022; Z. Liu et al., 2013; Sun et al., 2004). Bottles for each lure type were filled to the neck leaving a small air bubble under the cap, then sealed in two 3 mil plastic bags and held in separate coolers at room temperature for 5 days to allow bottle saturation (Kelsey & Westlind, 2020) before storing in a 5°C cold room. Bottles were weighed initially after a brief adjustment to room temperature, then immediately held in the cold room for a few hours until further

TABLE 1 Oregon field test locations, prior year disturbances and tree metrics.^a

Site	Species status	BA (m ² /ha)	Trees/ha	Tree means (range)		
				Diameter (cm)	Height (m)	Age
La Pine, burned 21–22 April 2021	PP-live	9.4	77.3	45.6 (24.9–68.0)	25.0 (20.9–33.4)	119 (70–202)
43°39.465' N; 121°24.360' W	PP-dead	2.1	36.8	34.0 (23.1–40.3)	19.0 (14.0–22.4)	–
Elevation (m): 1384	LPP-dead	0.2	5.6	22.8 (NA)	26.4 (NA)	–
	Total	11.7	119.7			
Crescent, thinned June–September, 2021	PP-live	9.9	39.4	65.1 (20.4–99.0)	31.4 (14.9–44.8)	232 (133–330)
43°26.854' N; 121°54.762' W	DF-live	0.2	0.2	110.1 (NA)	33.8 (NA)	179+
Elevation (m): 1503	Total	10.1	39.6			

Abbreviations: BA, basal area; DF, Douglas-fir = *Pseudotsuga menziesii* (Mirb.) Franco; LPP, lodgepole pine = *Pinus contorta* Douglas ex Loudon; PP, ponderosa pine = *Pinus ponderosa*, Douglas ex P. Lawson & C. Lawson.

^aTree metrics are means (ranges) obtained from 10 systematically positioned variable radius plots overlapping the study area using a 10 basal area factor prism. All trees within each plot were measured for diameter at 1.4 m, and height using an Impulse laser range finder (Laser Technology Inc., Englewood, CO). An estimate of the overstory age was obtained from the largest diameter live tree on each plot cored to the pith at 1.4 m with a 5 mm diameter increment borer and growth rings counted in the field at Crescent and in the lab for La Pine. Only six trees were aged at the Crescent site because of rot or excessive size.

processed. Ethanol pouches were not weighed for these trials as their release rates among lures within sites have remained similar as demonstrated repeatedly (Kelsey et al., 2023; Kelsey & Westlind, 2022).

To simulate mixing of ethanol and monoterpenes vapours from stressed conifer tissues (Gara et al., 1993), the ethanol pouches and weighed monoterpene bottles were combined in a wide mouth, high-density polyethylene jar (9.3 × 9.7 cm, D × L cap on, 473 mL, Uline, Pleasant Prairie, WI) with five equally spaced ventilation holes in an X pattern drilled in the bottom (0.79 cm dia.) and screw cap (0.95 cm dia., Kelsey et al., 2023; Kelsey & Westlind, 2020, 2021). A screen inside the cap prevented insects from entering the top holes, and the outside jar wall was wrapped with aluminium foil to reduce solar heating. Site temperatures were monitored with one ibutton temperature data logger (model 1922L, Maxim Integrated Corp. San Jose, CA) secured with tape inside the wall of three randomly selected jars for each lure type, providing one ibutton per block of traps.

Each mixing jar received one ethanol pouch wrapped around the inside wall leaving a center opening for one 3-carene or 3-carene + frontalin bottle, whereas two β-pinene or β-pinene + frontalin bottles were added to provide similar release rates (Kelsey & Westlind, 2020). Loaded mixing jars were sealed in plastic bags by lure type and stored in separate coolers at 5°C overnight. The following morning these coolers were packed with ice and transported to the study sites where lure jars were attached to Lindgren style 16-unit funnel traps at the 6th funnel above the catch cup containing automotive antifreeze (Prestone®, ethylene glycol with diethylene glycol mix, Prestone Products Corp., Alsip, IL) to kill and preserve beetles.

Study sites and trial designs

The La Pine trial was located about 6 km east of La Pine, Oregon in an uneven-aged ponderosa pine stand prescribed burned the previous April to reduce woody surface fuels and understory shrub and small tree ladder

fuels (see Table 1 for stand metrics). Traps were setup in a randomised complete block design with 12 blocks each having four randomly assigned lures, carene + ethanol, carene + ethanol + frontalin, β-pinene + ethanol, β-pinene + ethanol + frontalin. Traps within blocks were separated a minimum of 50 m, and at least 3 m from potential host trees. Blocks were a minimum of 50 m apart. Traps were secured to a metal rod stand, with catch cup bottoms 10–30 cm above the forest floor. On the last day of trap sampling, beetles and lures were collected simultaneously from pairs of adjacent blocks with lures immediately regrouped by type in sealed plastic bags in separate coolers with ice and returned to the 5°C cold room later in the day. The following morning LDPE bottles were adjusted briefly to room temperature and reweighed for calculating release rates. Lures were attached to La Pine traps on 11 May 2022, with beetles collected on 25 May, 8 and 23 June, 43 days total.

The Crescent site was located about 17 km west of Crescent, Oregon and about 47 linear km southwest of the La Pine site, in a mixed stand of ponderosa and lodgepole pine, *Pinus contorta*. It was commercially thinned starting early summer 2021 to promote ponderosa by removing all lodgepoles, but temporarily halted during fire season from late July to late September and completed in fall. This was followed by the removal of small diameter understory trees, primarily lodgepole pine. Unusable large stem or branch pieces and small trees were gathered into piles positioned across the site and remained throughout the entire trap period. This produced an uneven-aged ponderosa pine stand with no lodgepole larger than seedlings (see Table 1 for stand metrics). The lures, their processing, and field trial design were the same as described for La Pine, above. Lures were attached to traps on 19 May, with beetle collections on 2, 16 and 29 June, 41 days total.

Statistical analysis

At the thinned Crescent site, elk (*Cervus canadensis*) activity knocked traps to the ground or dislodged catch cups just prior to the final

collection day (traps checked 5 days earlier were undamaged). A total of 17 were damaged, seven carene + ethanol + frontalin, five β -pinene + ethanol + frontalin, three β -pinene + ethanol, and two carene + ethanol replicates. Thus, the summed 2 and 16 May total beetle catch per trap were analysed. The total trap catch summed for all three collection dates was also analysed to evaluate how the 17 missing replicates from the 26 June collection may have changed the lure catch relationships. At La Pine, one catch cup was found dislodged on the first collection date and its value was estimated by calculating that lure catch as a proportion of the catch by the other three lures combined, using its comparable proportion in each of the two nearest blocks averaged.

Data from each site were analysed separately using SAS software, version 9.4 (SAS, 2014). During analysis, the data sets were checked for normality and equal variance through quantile-quantile and residual versus predicted plots, respectively. When these assumptions were not met the data were natural log transformed with the resulting means and 95% confidence limits back-transformed for presentation. Means for all analyses were compared by Fisher's protected ($\alpha \leq 0.05$) least significant difference and considered significantly different at $p \leq 0.05$, but most were lower and reported in the graph legend.

β -pinene, β -pinene + frontalin, carene and carene + frontalin daily release rates within each site were analysed as a randomised complete block analysis of variance (ANOVA) using the mixed model procedure (proc MIXED). Block was modelled as a random effect, and lure as a fixed effect, with no data transformation required. Ethanol release rates were not checked as they have proven consistent among lures within sites (Kelsey et al., 2023; Kelsey & Westlind, 2022). Daily lure jar average, minimum, and maximum temperature values for each lure type were analysed within sites separately also using proc MIXED, with no transformations necessary.

Total beetle catch for each trap was summed over the entire trapping period and then analysed by lure type for each site separately with a generalised mixed model ANOVA (proc GLIMMIX) using a Poisson distribution for count data and a log link function to meet model assumptions for normality and equal variance. Block was modelled as a random effect and lure as a fixed effect.

RESULTS

The 24-h release rates from both carene lure types were statistically greater than the two β -pinene lures by 1.3 to 1.5 times at each site, while the releases for each monoterpene pair with and without frontalin were not statistically different, except for the carene pair at La Pine where carene + ethanol + frontalin was lower than carene + ethanol (Figure 1a,b). Each Crescent lure type had a higher release rate than corresponding lures at La Pine because Crescent lure jars experienced 1 to 2°C higher mean average, maximum, and minimum temperatures (Figure 1a,b), although between site differences in release rates or temperature values were not compared statistically. Within each site, none of the lure jar temperatures were different among the four lure types; La Pine mean average ($F_{3,8} = 0.80$,

$p = 0.529$), maximum ($F_{3,8} = 0.55$, $p = 0.661$), minimum ($F_{3,8} = 0.40$, $p = 0.757$), and at Crescent mean average ($F_{3,8} = 1.19$, $p = 0.374$), maximum ($F_{3,8} = 2.06$, $p = 0.184$), minimum ($F_{3,8} = 0.29$, $p = 0.829$).

At the burned La Pine site, 28,983 beetles were captured in total, with β -pinene + ethanol + frontalin attracting the most beetles, followed by β -pinene + ethanol > carene + ethanol + frontalin > carene + ethanol, and all statistically different from one another (Figure 1c). At the thinned Crescent site, the total catch was 1417 *D. valens* through the second collection date with the highest number also attracted to β -pinene + ethanol + frontalin, followed by β -pinene + ethanol > carene + ethanol + frontalin = carene + ethanol, and all differences statistically significant except the latter two carene lures (Figure 1d). Although the third collection date had a substantial number of missing lure replicates the total catch was 3259 *D. valens* with the same order of lure attraction and statistical differences observed at the second collection (data not shown). Had traps not been damaged, the Crescent catch by carene + ethanol + frontalin would likely have been statistically higher than carene + ethanol, as observed at La Pine.

DISCUSSION

Responses of *D. valens* to the four lures were nearly identical at both sites, β -pinene + ethanol + frontalin > β -pinene + ethanol > carene + ethanol + frontalin $\geq$ carene + ethanol, with just the latter two showing slight site differences. Yet the release rates for the two carene lures were 1.3 to 1.5 times higher than the two β -pinene lures at each site. Lures with trace frontalin attracted more beetles than corresponding lures without it at both sites, except for carene lures at Crescent. The increased catch for β -pinene + ethanol + frontalin over β -pinene + ethanol was 1.6 and 1.1 times higher at Crescent and La Pine, respectively, while the increase for carene + ethanol + frontalin over carene + ethanol was 1.2 times at La Pine, and no change in Crescent. The frontalin influence with carene + ethanol was limited compared to China where carene + frontalin attracted 1.7 times more beetles than carene alone, using the same frontalin concentration tested here (Z. Liu et al., 2013). One possibility is that the presence of ethanol may have dampened the frontalin impact, but this requires further testing. In China, the *D. valens* response increased as the trace frontalin levels rose from 0.005 to 11 ng/ μ L in the carene mix (Z. Liu et al., 2013). The 11 ng/ μ L mix is the highest trace frontalin level tested here and in China; and thus, the concentration providing optimum attraction in North America or across ecosystems worldwide remains to be determined.

Although the two test sites received dissimilar management treatments the previous year, they both left uneven-aged ponderosa pine stands with comparable overstory basal areas, but different tree densities. At La Pine there were three times more trees/ha, shorter, younger and thinner than at Crescent serving as the main influence on lure vapour plumes or beetle movement because fire consumed woody and herbaceous surface fuels, shrubs and small understory trees. At Crescent, there was more open space among trees with shrubs scattered individually or in patches throughout the stand left intentionally

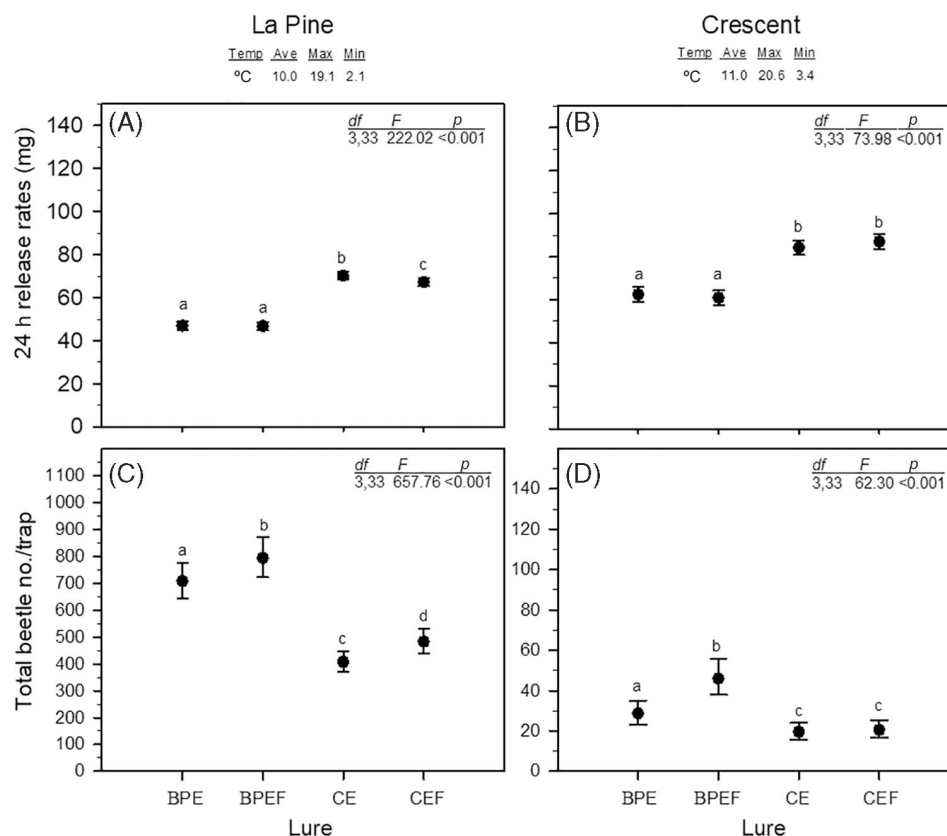


FIGURE 1 Lure release rates (means $\pm$ 95% confidence interval [CI]) and *Dendroctonus valens* total beetle number/trap (means $\pm$ 95% CI) at the La Pine prescribed burn and Crescent thinned site in Oregon. Lure components, β P, β -pinene; E, ethanol; F, frontalin; C, carene. The analysis of variance table for each graph data analysis is inserted near the top. (a) Symbols with different letters indicate significant statistical differences (SSD) at $p \leq 0.001$ for all comparisons, except CE versus CEF where $p \leq 0.016$, and those with the same letter, $p = 0.921$. (b) Symbols with different letters indicate SSD at $p \leq 0.001$ for all comparisons, and those with the same letters are not different at $p \geq 0.230$. (c) Symbols with different letters indicate SSD at $p \leq 0.001$ for all comparisons. (d) Symbols with different letters indicate SSD at $p \leq 0.001$ for all comparisons, and those with the same letters are not different at $p = 0.564$. Temperatures listed below site names are the mean daily average, maximum, and minimum measured across the four lure types within each site.

for wildlife cover. But a more important difference most likely was the type of host resources remaining available for colonization.

Host resources at La Pine were the base of stems and roots of fire-injured and dying ponderosa pine with char on the outer bark as indicated by gallery entrance resin tubes (Kelsey & Westlind, 2017). Larvae and callow adults developing in these tissues would be exposed to high carene levels (37%–64%), the dominant oleoresin component in PNW ponderosa pine, and lower amounts of β -pinene ranging from 9% to 29% (Hobson et al., 1993; Kelsey & Westlind, 2020, tab. S3; Smith, 1977; Sturgeon, 1979). Ethanol would also be present in attacked trees with concentrations increasing with the severity of fire injury (Kelsey & Joseph, 2003; Kelsey & Westlind, 2017).

In contrast, the Crescent host materials were stumps and below-ground roots of ponderosa and lodgepole pine, or their woody stem and branch segments gathered into large slash piles. The species proportions for these resources and their colonization rates are unknown, although visual observations suggested a limited number of ponderosa stumps relative to lodgepole, as the thinning prescription favoured

the removal of lodgepole and retention of ponderosa. Any larvae and callow adults living in lodgepole pine tissues would be exposed to β -phellandrene (56.7%–77.7%), with β -pinene (3.8%–22.4%) being comparable or in some instances more abundant than carene (4.6%–11.7%), based on trees sampled across its range in western US and Canadian forests (Clark et al., 2014; Smith, 2000). Ponderosa pine tissues would have the same monoterpene content as mentioned above. Neither pine host contains β -pinene as the most abundant monoterpene. Some ethanol may have been present in stumps and roots with variable concentrations depending on the tissue, environmental parameters and time since harvest (Kelsey & Joseph, 1999; von Sydow & Birgersson, 1997). Despite the dissimilarities in stand structures and host resources the relative attractiveness of the different lures remained comparable.

Stronger β -pinene + ethanol attraction than carene + ethanol in the burned La Pine and thinned Crescent stands was similar to beetle responses observed in five other ponderosa pine stands burned the previous year by wildfire or prescribed burns at locations across the PNW from northern Washington near the Canadian border, through

central Oregon into northeastern California (Kelsey et al., 2023; Kelsey & Westlind, 2020). The strong β -pinene + ethanol attraction at the thinned Crescent site contrasts with behaviour in a thinned Arizona ponderosa pine stand where carene + ethanol attracted the most beetles. The Arizona overstory basal area post-thinning was higher than both sites here, with cut stem and branch debris stacked in piles like Crescent (Kelsey et al., 2023). The xylem oleoresin would be different in Arizona as ponderosa pine near that test site is usually dominated by α -pinene (43%–50%), carene (27%–35%) and β -pinene (5%–6%, Smith, 1977), with similar proportions in the phloem (Kolb et al., 2019). These results indicate that the type of management disturbance or host resin chemistry is unlikely the cause for *D. valens* response differences observed between thinned ponderosa pine forests in the PNW and Arizona (Kelsey et al., 2023), shifting the focus to regional genetic differences in these beetle populations.

Based on *D. valens* microsatellite markers, four genetically and geographically distinct population groups have been identified (Taerum et al., 2016); West (Washington, Idaho, Montana, Oregon, California, and Arizona), Central (Wisconsin), Northeast (New Hampshire, Vermont and Massachusetts) and Mexico (Durango and Hidalgo). Populations in the West group clustered together in the Principal Components plots, with Arizona beetles being most distant from the others. Exclusion of Arizona *D. valens* from the West group is further supported by chromosome-level assembly and population genomic analysis showing them more closely aligned with Colorado beetles than with West group beetles collected in northern California, and west central Montana (Z. Liu et al., 2022). Additional experiments can expand the level of genetic differences between the Arizona and PNW beetle populations.

The North American source of *D. valens* transported to China may have come from one or more locations, but most likely within the West group and possibly the PNW based on genetic studies (Cai et al., 2008; Cognato et al., 2005; Z. Liu et al., 2022; Taerum et al., 2016), while origination from Central or Northeast populations is suggested by symbiont community analyses (Q. Lu, Decock et al., 2009; M. Lu, Zhou, et al., 2009; Taerum et al., 2013, 2016). Further refinement of the North American source(s) invading China may be provided by population's primary attraction responses to β -pinene or carene. In China, carene attracts more beetles than β -pinene (Sun et al., 2004), and in PNW populations β -pinene attracts more beetles than carene (Hobson et al., 1993) even when both are released with ethanol or ethanol + frontalin (Kelsey et al., 2023; Kelsey & Westlind, 2020; here). Had these PNW populations been the invasive source, their primary attraction response would need to change from β -pinene to carene after establishment in China. Yet, *P. tabuliformis* resin contains very little 3-carene, with α -pinene and β -pinene being the most abundant terpenes (Z. Liu et al., 2011; B.-B. Xu et al., 2014). Such a change seems unlikely as it is unclear what advantage this would provide to pioneering beetles for host selection or colonization. Therefore, populations we have tested in Washington, Oregon and northeastern California, where β -pinene produces the strongest response, can be removed from the source pool. Genomic analyses show northeastern California and western Montana populations to more closely align with beetles in China than US populations from Arizona-Colorado, or Wisconsin-

Minnesota (Z. Liu et al., 2022). The California collection site for Z. Liu et al. (2022) is in a general area where some *D. valens* populations respond more strongly to carene than β -pinene (Erbilgin et al., 2007), while no comparison tests for these two kairomones have been conducted in Montana. Further testing of β -pinene + ethanol and carene + ethanol, with and without a trace frontalin mix, is worthwhile within the West group range including Montana, Idaho, other California and Arizona sites, in addition to populations within the distinct Central, Northeast and Mexico genetic groups (Taerum et al., 2016).

D. valens can be captured with α -pinene + ethanol lures as demonstrated in surveys designed to catch a broad array of taxa over extensive areas (D. R. Miller, 2020; Rabaglia et al., 2019). However, any survey targeting *D. valens* specifically may attract more beetles with β -pinene + ethanol or carene + ethanol depending on the geographic area covered and the survey's objectives. β -pinene + ethanol has consistently been a stronger lure than β -pinene in tests across all PNW and Arizona test sites (Kelsey et al., 2023; Kelsey & Westlind, 2020), whereas carene + ethanol has not been consistently stronger than carene at all these sites (Kelsey et al., 2023). Based on current evidence, β -pinene + ethanol lures, with or without trace frontalin, are best suited for monitoring or managing *D. valens* in Washington, Oregon and northeastern California forests. Carene or carene + ethanol, with or without trace frontalin, will provide better efficacy for monitoring or managing beetles in China, and other US locations. In novel environments, such as the Southern Hemisphere, the sensitivity and efficacy of early detection surveys will depend on the beetle's origin and lure selection.

AUTHOR CONTRIBUTIONS

Rick G Kelsey: Conceptualization; data curation; investigation; methodology; writing – original draft. **Douglas J. Westlind:** Formal analysis; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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