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Colonization and reproduction of potential competitors with mountain pine beetle in baited logs of a new host for mountain pine beetle, jack pine

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ABSTRACT

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a bark beetle that is native to pine forests of western North America and the Black Hills of South Dakota. Recent eastward range expansion into stands of jack pine (*Pinus banksiana*) and associated hybrids with lodgepole pine (*Pinus contorta*) in western Canada has created concern that the insect will continue moving eastward. In the Great Lakes region, mountain pine beetle would encounter novel species of pines and associated insect fauna; interactions with which are largely unexplored. We baited logs of jack pine with lures for mountain pine beetle and *Ips grandicollis (*Eichhoff) alone and in combination in a 2 × 2 factorial design in the Black Hills of South Dakota. Both insects occur in this region, but not jack pine, a common species in the Great Lakes region of North America at risk of invasion by mountain pine beetle. We measured attraction and reproduction of insects that colonized the logs. *Ips grandicollis* were significantly more attracted to logs of jack pine baited with their aggregation pheromone, ipsenol, than unbaited logs or those baited with pheromones of mountain pine beetle and myrcene, a host volatile. Colonization by I. *grandicollis* was inhibited by the presence of lures for mountain pine beetle. We also found larvae of longhorn borers, likely - *Monochamus* spp., infesting logs. These borers, which act as competitors and facultative predators of bark beetles, were significantly attracted to logs baited with ipsenol over those baited with lures for mountain pine beetle. Our results suggest that if mountain pine beetle were to invade the Great Lakes Region, common bark and wood-boring species such as *I. grandicollis* and longhorn borers would not compete with mountain pine beetles at tree-colonizing stages, and thus could pose little resistance to invasion.

1. Introduction

In forested ecosystems, bark beetles (Coleoptera: Curculionidae) provide critical ecosystem services and impact carbon dynamics by promoting wood deterioration, nutrient cycling, and biodiversity (Wood, 1982; Kurz et al., 2008; Mikkelson et al., 2013; Beudert, et al., 2014). Most species of bark beetles are termed “secondary” as they are innocuous and infest dying or stressed trees, where they consume the phloem tissues (Wood, 1982; Lindgren and Raffa 2013). Conversely, a minority of bark beetle species are capable of killing mature, live trees at landscape scales. As natural components of disturbance regimes, these “primary” species can alter successional trajectories of biomes (Taylor and Carroll, 2003; Raffa, et al., 2008).

Several environmental requirements must be met for tree-killing species of bark beetles to reach outbreak levels. The first condition is favorable climate. Depending on the species, conditions may include landscape-scale drought that stress host trees or warm minimum winter temperatures that foster brood survival (Safranyik, 1978; Carroll et al., 2004; Klutsch et al., 2017). The second requirement is an abundant supply of susceptible host trees (Safranyik, 1978). Forestry practices such as overstocking or under thinning can increase the likelihood of bark beetle outbreaks (Fettig et al. 2007). Finally, population growth of outbreaking species must exceed that of predators, parasitoids and other subcortical woodborers that compete for resources and exert regulatory effects. Each of these guilds may depress the reproductive capabilities of primary bark beetles at endemic levels (Rankin and Borden, 1991; Lindgren and Raffa, 2013; Aukema et al., 2016).

Competition may be especially pronounced among bark beetles as an endophytic feeding guild (Lindgren and Raffa, 2013), frequently mediating population dynamics between primary and secondary species

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(Rankin and Borden, 1991; Aukema et al., 2016). Often, several sympatric species of bark beetles simultaneously infest the same tree (Rankin and Borden, 1991; Byers, 1989a). The overlap in the subcortical layer elicits the need for resource partitioning (Byers, 1989a). Interspecific competition can be avoided in two ways: temporally (e.g., exploiting differences in phenology) and spatially (e.g., infesting different parts of the tree). Host procurement and resource partitioning is frequently mediated by semiochemicals. Aggregation pheromones attract conspecifics, while inhibitory allomones push heterospecifics toward other resources (Paine et al., 1981; Byers, 1989b; Ayres et al., 2001). *Ips pini* (Say), *I. paraconfusus* (Lanier), and *Dendroctonus brevicomis* (LeConte), for example, may simultaneously infest a ponderosa pine (*Pinus ponderosae*) but spatially separate themselves throughout the bole (Birch and Wood 1975; Paine et al., 1981; Byers, 1989a). Despite temporal and spatial partitioning strategies among species, however, a broad range of overlap can still exist (Paine et al., 1981; Byers, 1989a; Ayres et al, 2001).

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), is a bark beetle native to North America west of the Rocky Mountains and the Black Hills of South Dakota and Wyoming, USA (Safranyik and Carroll, 2006). While mountain pine beetle is a generalist, feeding on most species of sympatric pines in these regions, its principal hosts have historically been ponderosa pine (*Pinus ponderosae* Dougl. ex Laws) and lodgepole pine (*Pinus contorta* Dougl. ex Loud) (Safranyik and Carroll, 2006; Raffa et al, 2008). Outbreaks of mountain pine beetle can lead to landscape-level mortality of mature pines over many thousands of hectares (Safranyik and Carroll, 2006; Bentz et al., 2010; Hicke et al., 2012). While populations of mountain pine beetle were historically restricted in their northern range due to climatic and geological barriers, ameliorating winter temperatures have permitted northward range shifts (Cudmore et al., 2010, Cullingham et al., 2011). In recent years, British Columbia, Canada has experienced the largest outbreak of *D. ponderosae* in recorded history (Aukema et al., 2006), expanding the insect's range over the geoclimatic barrier of the Rocky Mountains into stands of jack pine (*Pinus banksiana* Lamb.) and its hybrids with lodgepole pine (*Pinus contorta* Douglas. ex Loud. Var. *latifolia* Engelm.) in northwestern Alberta (Kurz et al., 2008; Safranyik et al., 2010; Cullingham et al., 2011; De la Giroday et al., 2012; Lusebrink et al., 2013). Of emerging concern is potential range expansion of mountain pine beetle to the Great Lakes Region of North America with evolutionarily naïve host species that include jack pine, red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.), and naturalized Scots pine (*Pinus sylvestris* L.) (Cooke and Carroll, 2017; Rosenberger et al., 2017b). A recent study has shown that age classes and distributions of these species exist on the landscape in categories considered highly susceptible to this insect based on comparative studies with suitable and susceptible hosts in western North America (Windmuller-Campione, 2018). While little is known about susceptibility of live potential hosts in the threatened range, it is apparent that mountain pine beetle is able to colonize, tunnel, attract mates, and reproduce within cut logs of all four species of pine (Rosenberger et al., 2017b; Cale et al., 2017).

If mountain pine beetle were to arrive in the Great Lakes Region of North America, it may encounter species of secondary bark beetles and woodborers with which it shares no evolutionary history. This mixing would result in novel ecological interactions that may either facilitate or impede the invasion of mountain pine beetle. In regions where mountain pine beetle is endemic, for example, persistence of mountain pine beetle in the ecosystem is facilitated by species of secondary bark beetles that allow mountain pine beetle to co-colonize weakened trees in low numbers (Safranyik and Carroll, 2006; Smith et al., 2011; Burke and Carroll, 2016). When an environmental stress lowers stand resistance, increasing populations of mountain pine beetle begin partially or mass-attacking mature, live hosts in a population phase transition across the incipient-eruptive threshold (Safranyik and Carroll, 2006). At high levels, secondary species may then inhibit the population growth of mountain pine beetle. Rankin and Borden (1991), for example, showed that forcing a secondary bark beetle such as the pine engraver, *Ips pini* Say, to compete with mountain pine beetle in synchronously co-colonized logs resulted in fewer progeny for both species than if logs were infested independently.

The Great Lakes Region has several native species of secondary bark beetles such as the pine engraver, *I. pini*, the red turpentine beetle, *Dendroctonus valens* LeConte, and the eastern five-spined ips, *Ips grandicollis* Eichhoff. *Ips grandicollis* is an especially common, multivoltine secondary bark beetle native to the Great Lakes Region that typically infests dying or stressed pines (Erbilgin et al., 2002; Lombardero et al., 2006). It is unknown how mountain pine beetle and *I. grandicollis* might interact in the complex of naïve pine species if they were to become sympatric in the Great Lakes region. While pheromones of bark beetles of the genera *Dendroctonus* and *Ips* have been shown to inhibit each other's response in several cases (Rankin and Borden, 1991; Byers, 1989a; Symonds and Elgar, 2004), the responses of *I. grandicollis* and mountain pine beetle to each other's pheromones have never been studied. *Ips grandicollis* utilizes a species-specific aggregation pheromone, consisting mainly of ipsenol (2-methyl-6-methylideneoct-7-en-4-ol), to attract conspecifics and find mates (Witanachchi and Morgan, 1981). Mountain pine beetle uses both *trans*-verbenol and (±)-*exo*-brevicomin as its aggregation pheromones (Conn et al., 1983). In this study, we aim to elucidate how the colonization behavior of each species of bark beetle is affected by the presence of the other's aggregation pheromones in logs of jack pine. Further, we examine the patterns of reproduction of bark and woodboring beetles in logs baited with each type of pheromone. We hypothesize that there will be no cross attraction or inhibition between *I. grandicollis* and mountain pine beetle. Our goal is to understand whether cross attraction and thus competitive interactions might exist between *I. grandicollis* as a bark beetle native to the Great Lakes Region and the potential invader, mountain pine beetle.

2. Materials & methods

2.1. Host material

Jack pine was used as a representative novel species of pine native to the Great Lakes Region. Mountain pine beetle is known to colonize and reproduce in jack pine in western forests (Cullingham et al., 2011) and can similarly colonize and reproduce in cut logs of jack pine from Minnesota (Rosenberger et al., 2017a; Rosenberger et al., 2017b). Twelve trees of 25–27 cm in diameter at 1.4 m were harvested from a single-aged stand of jack pine approximately 40 years old at the University of Minnesota Cloquet Forestry Center (CFC) in Cloquet, Minnesota (46.704490° N, −92.525310° E) on 23 July 2018 and again on 22 July 2019. The site from which trees were harvested is classified as a fire dependent ecosystem in the Laurentian Mixed Forest province of the state, with a climate moderately modified by Lake Superior and lying within USDA Cold Hardiness Zone 4a (Reinikainen et al., 2015).

Harvested trees were visibly free of infestation of bark beetles or other insects. Each year, the twelve felled trees were cut into 48 sections approximately 56 cm in length. The ends of these logs were then immediately sealed with melted paraffin wax (Gulf Wax, Roswell, Georgia) to reduce the desiccation rate of the logs. Once the wax cooled, logs were enclosed in 13-gallon drawstring plastic bags and placed in the bed of a covered pickup truck to prevent unwanted infestation from pine-infesting insects. Each year, the logs were transported to the Black Hills National Forest near Rapid City, South Dakota (44.072086° N, −103.234799° E) where populations of mountain pine beetle and *I. grandicollis* currently exist sympatrically. The logs were deployed at 12 different sites in stands of mature ponderosa pine within 48 h of being felled. Sites were separated by at least 0.5 km. At each site, four logs were suspended at breast height using MIL-C-5040 Type III 550 lb. nylon paracord (Paracord Planet, Fargo, North Dakota) in a square formation at 25 m spacing between logs.

2.2. Experimental design

We utilized a 2x2 factorial design in each of the twelve sites each year as follows: each position within the square was randomly assigned a commercially available pheromone treatment (Alpha Scents, Inc., West Linn, Oregon). Two positions received *I. grandicollis* lure, while two did not. Two positions then also received lures for mountain pine beetle, while the other two did not, such that each site ended up with four treatments as follows: a mountain pine beetle lure (myrcene, 2-(2H-benzotriazol-2-yl)-4-methyl-phenol, butylated hydroxytoluene, *trans*-verbenol, and *exo*-brevicomin), an *I. grandicollis* lure containing ipsenol, both lure types, and a control with no lures in combination. Amounts and elution rates of lure compounds are shown in online supplementary material. Each lure packet was attached to the log using a nail through the outer bark.

Logs were exposed to field conditions from July 25-August 8 of the years 2018 and 2019 to correspond to the flight period of both mountain pine beetle (Safranyik and Carroll, 2006) and *I. grandicollis*, which is typically abundant throughout the summer (Erbilgin et al. 2002). Logs were then retrieved from the field and placed inside rearing tubes at the proximate Wheaton College Science Station (44.061693° N, −103.407476° E) under ambient temperature conditions where any colonizing insects were allowed to continue development undisturbed (Rosenberger et al, 2018).

For each annual replicate, we removed the logs from the rearing tubes and debarked them in two batches: one half after one month (i.e., mid-September), and the other half after one year (i.e., July of the following year) ($n = 24$ each time). Logs debarked in the first batch of each year were chosen by randomly selecting six of the twelve sites and then debarking all logs from that site to ensure equal sampling of treatments. We chose to debark logs at these two different time periods in order to elucidate differences in insect community composition and development after one month and after one year. Outer bark was removed with a wood chisel, exposing the internal larval galleries created by insects. All adults, larvae, and pupae of insects were counted from each gallery and placed in vials of 95% ethanol for identification. All bark beetle larvae found were assumed to be from the species that had constructed the parental gallery. After debarking, a clear plastic sheet was laid over the phloem layer of the peeled barked and markers of different colors were used to trace and color-code galleries of bark beetles, creating a map of subcortical utilization. A Scalex PlanWheel XL was used to measure the one-dimensional length of bark beetle parental galleries. In the second year of the study, most of the *I. grandicollis* brood in the initial set of peeled logs had matured to adults by the time logs were peeled in mid-September. Because we could not confidently distinguish initial colonizing beetles from new progeny that had reached adult life stages, we report total counts of bark beetles in each log for each year without assigning colonizer and brood status.

The remaining sets of logs ($n = 24$ each year) were peeled in July of the following year, approximately one year after field exposure to allow any univoltine species such as mountain pine beetle to complete development (Rosenberger et al., 2018). All insects were collected from within the tubes. Larval *Monochamus* spp. were found to have consumed most of the phloem resource, destroying most, if not all, of the bark beetle galleries within. Due to the amorphous nature of the cerambycid galleries we chose to use imageJ (Schneider et al., 2012) to measure the area of phloem consumed by cerambycids rather than gallery length. As such, data analyzed from logs left in rearing tubes for one year only includes the total area of phloem resource consumed by *Monochamus* spp. larvae. Larvae of different species of *Monochamus* cannot be identified to species, so were simply tallied as *Monochamus*.

2.3. Statistical analysis

For the logs peeled after six weeks of field exposure and incubation time each year, we constructed separate mixed effects models using response variables of the number of bark beetles, the number of galleries, the number of *Monochamus* spp. larvae and the total phloem surface area consumed. Each model used an ANOVA framework where the fixed effects incorporated the 2x2 factorial design (i.e., terms for mountain pine beetle pheromone lure, *I. grandicollis* pheromone lure, and their interaction) and a term for site was included as a random effect. A random effect term for year was also originally included in the models but low variation between years induced issues of model singularity, so the term for year was removed. Data from one site in the second year ($n = 4$ logs) was excluded from our analysis due to labeling error obscuring treatment. Square root transformations were used on the response variables to satisfy the assumptions of a normal distribution of residuals and homogenous variances. Assumptions were assessed by visual inspection of residual plots. Statistical significance was evaluated using $\alpha = 0.05$. All statistical analyses were conducted using R version 3.5.3 (R Core team, 2020).

3. Results

Ips grandicollis readily colonized the logs of jack pine in the field but numbers varied with lure type. The ipsenol treatment significantly enhanced colonization by *I. grandicollis* (Table 1). The two logs baited with ipsenol had a mean of 0.1 ± 0.3 SE ovipositional galleries of *I. grandicollis* per dm^2 per log compared to a mean of 0.001 ± 0.001 galleries/dm^2/log in the two logs without (Fig. 1A). Conversely, the presence of mountain pine beetle pheromone lures appeared to have a significant negative effect on the colonization behavior of *I. grandicollis* (Table 1). The two logs baited with myrcene and the aggregation pheromones of mountain pine beetle had a mean of 0.024 ± 0.006 ovipositional galleries of *I. grandicollis* per dm^2 log, compared to 0.078 ± 0.014 in the two logs without. There was a significant interaction effect between the two treatments (Table 1) as fewer ovipositional galleries of *I. grandicollis* were constructed in logs baited with both ipsenol and mountain pine beetle lures than would be expected if both main effects were additive (Fig. 1A). Thus, the presence of the mountain pine beetle lure inhibits the response of *I. grandicollis* to its own pheromone.

Unsurprisingly, the effect of pheromone treatments on the number of insects found under the bark was very similar to the effects noted on the number of ovipositional galleries found above (Table 1; Fig. 1B). We observed significantly more *I. grandicollis* inside logs baited with ipsenol with a mean of 3.0 ± 0.9/dm^2 compared to those logs without the pheromones. In contrast, very few *I. grandicollis* were found in logs baited with mountain pine beetle lures versus those without (Fig. 1B). Again, we observed a significant interaction effect between the two lure types: we found significantly fewer *I. grandicollis* in logs baited with both pheromones than would be expected with an additive effect of the two lures (Table 1; Fig. 1B). In these co-baited logs, we collected a mean of 0.70 ± 0.32 *I. grandicollis*/dm^2/log. These results confirm an aversive response from *I. grandicollis* to the pheromone lure of mountain pine beetle.

In logs left in rearing tubes for one month, significantly more

Table 1
Summary of 2 × 2 factorial statistical results from field experiments using logs of jack pine baited with *I. grandicollis* (IGR) × mountain pine beetle (MPB) lures, $n = 12$ sites of 4 treatments each in Black Hills of South Dakota, each of 2018 and 2019.

Response variable	IGR lure		MPB lure		IGR × MPB Interaction	
	$F_{1,31}$	P	$F_{1,31}$	P	$F_{1,31}$	P
I. grandicollis galleries	97.57	<0.001	12.23	<0.001	8.99	<0.005
I. grandicollis insects	42.73	<0.001	10.04	<0.001	5.62	0.024
Monochamus larvae	11.62	<0.001	0.77	0.370	8.41	0.007
Phloem area consumed	4.46	0.0420	1.18	0.290	2.76	0.110

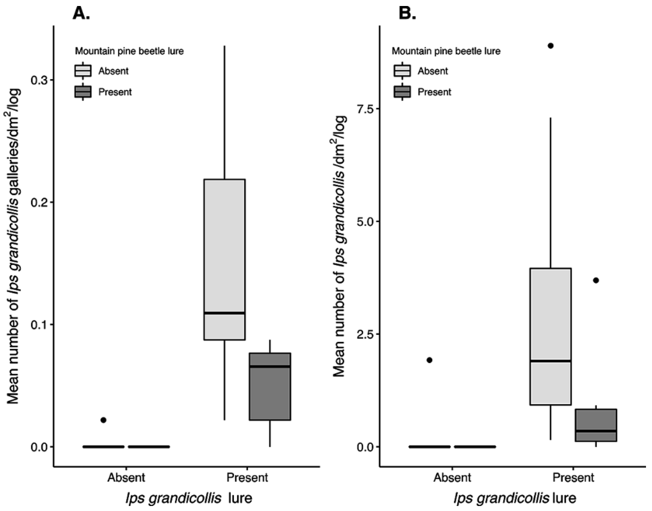

Fig. 1. Box and whisker plots of A) the number of galleries formed by *I. grandicollis* and B) the combined number of *I. grandicollis* adults, pupae, and larvae collected from logs baited with the different aggregation pheromones and peeled after thirty days in emergence tubes ($n = 44$ logs; mean surface area of a log was 45.74 dm^2). The upper whisker indicates the maximum value as the third quartile added to 1.5 times the interquartile range. The lower whisker represents the minimum value as the first quartile minus 1.5 times the interquartile range. The middle line of each box and whisker plot represents the median of the data set. Dots represent data points beyond plus or minus 1.5 times the interquartile range.

Monochamus beetle larvae were found in logs baited with ipsenol than those baited with mountain pine beetle aggregation pheromones (Table 1; Fig. 2). A mean of 0.42 ± 0.11 SE *Monochamus* larvae/dm^2 were found in logs baited with ipsenol compared to 0.31 ± 0.09 larvae/dm^2 found in logs without ipsenol. There was no overall effect of the mountain pine beetle lure on the numbers of *Monochamus* larvae (Table 1), with a mean of 0.28 ± 0.08 *Monochamus* larvae collected per dm^2. We did note a significant interaction effect between the two lure types (Table 1), with more longhorn borers in the logs with mountain pine beetle lure but no ipsenol than would be expected if the main effects were simply additive.

We did not find any mountain pine beetles in the logs peeled in the fall of each year or the sets that were allowed to develop for one year. Any potential colonizers may have been destroyed by *Monochamus*, however, as up to 90% of the surface area of the logs' phloem had been chewed apart by developing larvae. We noted small but statistically significant differences of phloem area consumed by *Monochamus* larvae between some lure treatments in logs left in rearing tubes for one year (Table 1; Fig. 3). In logs baited with ipsenol, *Monochamus* larvae consumed a mean of 2,015 ± 308 cm^2 which was significantly more than logs baited with no lures that had a mean area of 1,084 cm^2 ± 290 cm^2 of phloem consumed per log (IGR effect in Table 1). Logs baited with mountain pine beetle lures and those baited with both lures had 1733 cm^2 ± 262 cm^2 and 1,762 cm^2 ± 289 cm^2 of phloem consumed by *Monochamus* larvae respectively. Neither the effect of the MPB lure nor the interaction effect was significant (Table 1).

4. Discussion

Our results that the eastern five-spined pine engraver constructed fewer galleries and produced fewer offspring in logs that were baited with mountain pine beetle lures, even in the presence of their own aggregation pheromones, suggests that they will not compete directly mountain pine beetle if the latter were to arrive in the Great Lakes region. These two species have no historic sympatric association in the jack pine forests of Minnesota from where the logs originated. The aversive behavior of eastern five-spined pine engraver to pheromones of mountain pine beetle reflects long conserved traits unique to both genera, consistent with interaction between *Ips* spp. and *Dendroctonus* spp. elsewhere. For example, Byers and Wood (1980) demonstrated that *Ips paraconfusus* and *Dendroctonus brevicomis* are both captured in traps in smaller quantities when in the presence of logs infested by both species rather than just conspecifics. Additionally, response of mountain pine beetle to its aggregation pheromones has been shown in both laboratory and field bioassays to be inhibited by the addition of ipsdienol, a component of the aggregation pheromone produced by *I. pini* (Hunt and Borden, 1988). Similarly, response of *I. pini* to its pheromone component ipsdienol is inhibited by the presence of mountain pine beetle aggregation pheromones involving myrcene, *trans*-verbenol, and *exo*-brevicomin or some combination of the three (Hunt and Borden, 1988).

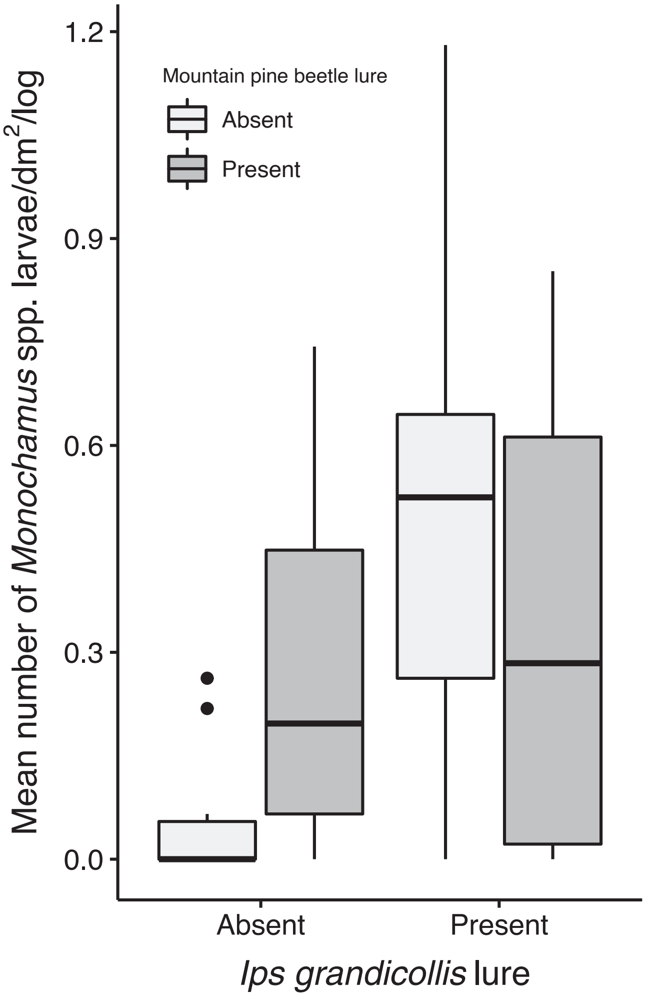

Fig. 2. Box and whisker plots of the number of cerambycid larvae collected from logs peeled after thirty days in emergence tubes of each treatment ($n = 44$ logs; mean surface area of a log was 45.74 dm^2). The upper whisker indicates the maximum value as the third quartile added to 1.5 times the interquartile range. The lower whisker represents the minimum value as the first quartile minus 1.5 times the interquartile range. The middle line of each box and whisker plot represents the median of the data set. Dots represent data points beyond plus or minus 1.5 times the interquartile range.

The aversion of bark beetles to aggregation pheromones of other species facilitates pheromone-mediated niche partitioning, regulating interspecific competition within the tree (Paine et al., 1981; Byers, 1989a). Several species of *Ips* in the southern United States compete with the southern pine beetle, *Dendroctonus frontalis* (Zimmerman), for example (Stephen, 2011). Typically arriving after *D. frontalis*, *I. avulsis*

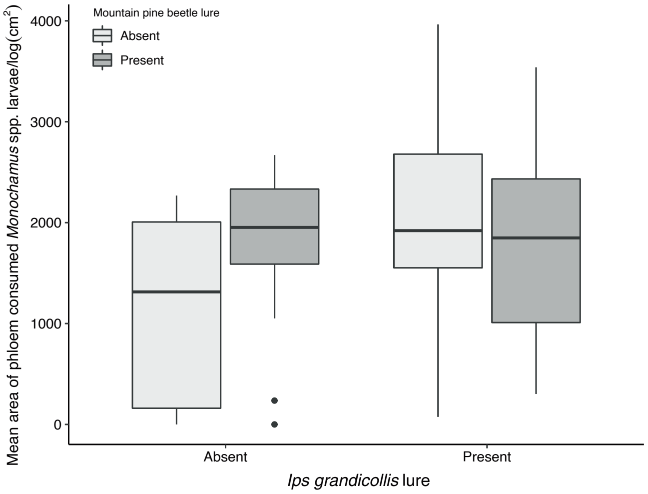

Fig. 3. Box and whisker plots of the area of phloem resource consumed by cerambycid larvae in logs of each treatment peeled after one year ($n = 48$ logs) in emergence tubes. Mean surface area of a log was 45.74 dm$^{2.}$ The upper whisker indicates the maximum value as the third quartile added to 1.5 times the interquartile range. The lower whisker represents the minimum value as the first quartile minus 1.5 times the interquartile range. The middle line of each box and whisker plot represents the median of the data set. Dots represent data points beyond plus or minus 1.5 times the interquartile range.

(Eichoff), *I. grandicollis,* and *I. calligraphus* (Germar) may all compete for resources within southern pine species, usually resulting in less phloem resource being consumed by each species when simultaneously infesting a tree than if they were individually infesting that tree (Stephen, 2011). While *D. frontalis* has been shown to be unresponsive to the pheromones produced by the southern *Ips* spp. complex, each of the *Ips* species in this system respond to pheromones of others *Ips* with only *I. grandicollis* responding to pheromones produced by *D. frontalis* (Svihra et al., 1980; Stephen, 2011). Interestingly, the response of *I. grandicollis* to pheromones of *D. frontalis* described by Svihra and others (1980) was one of attraction, which contrasts with our results. This pattern could indicate that sympatric coevolution of *I. grandicollis* with *D. frontalis* has resulted in the attraction of *I. grandicollis* to its pheromones while the lack thereof with mountain pine beetle has maintained its inhibitory response.

Most studies of pheromone responses in bark beetles have been conducted in areas of high populations, which may obscure responses to semiochemicals that vary with population density (Wallin and Raffa, 2004). Responses of both *I. pini* and *Ips latidens* (LeConte) to their respective aggregation pheromones, for example, are interrupted by verbenone, the anti-aggregation pheromone of mountain pine beetle, with increasing levels of interruption with increasing verbenone release rates (Borden et al., 1992; Miller et al., 1995). These examples of niche separation occur with bark beetles at high population levels. It is possible that facilitative interactions may emerge when at endemic population levels. Previous infestation of pines by *Pseudips mexicanus* Hopkins, for example, has been shown to create more suitable resources for mountain pine beetle when mountain pine beetle is in endemic population sizes. Mountain pine beetle was found to be attacking in higher densities while excavating similar sized galleries in trees previously infested by *P. mexicanus* rather than those not previously infested (Smith et al, 2011).

Species of *Monochamus* exist naturally in the Black Hills National Forest as well as the Great Lakes Region. *Monochamus clamator* is the most abundant sawyer beetle found in the Black Hills, SD and we suspect most larvae were of this species. Larvae of *Monochamus* beetles infest and feed on the phloem and xylem of pines. *Monochamus* spp. are thus potential subcortical competitors with mountain pine beetle and *I. grandicollis* as well as facultative predators (Dodds et al., 2001; Schenk and Benjamin, 1969; Schoeller et al., 2012). These findings are consistent with previous field and laboratory studies indicating that beetles in the *Monochamus* genus are kairomonally responsive to aggregation pheromones of *Ips* species (Rassati et al. 2012; Pajares et al. 2017; Chase et al. 2018) but not those of *Dendroctonus* (Dodds et al., 2001; Allison et al., 2003). These findings further indicate that species of *Monochamus* may also not act as significant agents of competition or predation on mountain pine beetle if it were to arrive in the Great Lakes Region but may instead compete more with native species of *Ips*.

While we noted aversion of *I. grandicollis* to mountain pine beetle lures, a lack of mountain pine beetles colonizing the logs precludes ability to make conclusions concerning the response of mountain pine beetle to pheromones of *I. grandicollis*. We also know little about potential responses of natural enemies of bark beetles to pheromones of mountain pine beetle in the Great Lakes Region (Pfammatter et al., 2015). It is possible that lack of coevolution with mountain pine beetle will correspond to a lack of response to the native complex of bark beetle predators and parasitoids, functionally releasing invasive populations of mountain pine beetle from the pressures of natural enemies. Additionally, our results suggest that insects such as the *I. grandicollis* may avoid trees being mass attacked by mountain pine beetle.

This research adds to existing bodies of literature of competition and interspecific pheromonal response of primary vs. secondary bark beetles as well as the response of Cerambycid beetles to the aggregation pheromones of bark beetles. Future work should focus on the kairomonal and/or allomonal responses of the diverse bark beetle predators as well as other potential competitors native to the Great Lakes Region to the aggregation pheromones produced by mountain pine beetle (Smith, 2021). Future work should also focus on testing and characterizing direct under-bark interactions where they exist, as neutral, facilitatory, or competitive interactions between bark beetle species mediate persistence at endemic levels and can influence population phase transitions (Rankin and Borden, 1991; Safranyik and Carroll, 2006; Smith et al, 2011). Understanding these interactions is especially important given the emerging threat to eastern North America by mountain pine beetle (Cudmore et al., 2010; Cullingham et al., 2011; Rosenberger et al., 2017b; Rosenberger et al., 2018).

CRediT authorship contribution statement

Zach M. Smith: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Supervision. **Kevin D. Chase:** Conceptualization, Methodology, Investigation, Writing - review & editing, Funding acquisition. **Etsuro Takagi:** Methodology, Investigation, Writing - review & editing. **Aubree M. Kees:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Project administration. **Brian H. Aukema:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119455.

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