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RESEARCH ARTICLE

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Development of an aggressive bark beetle on novel hosts: Implications for outbreaks in an invaded range

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Abstract

1. Some subcortical insects have devastating effects on native tree communities in new ranges, despite benign interactions with their historical hosts. Examples of how insects, aggressive in their native habitat might respond in novel host environs are less common. One aggressive tree-killing insect undergoing a dramatic range shift is the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Ongoing eastward expansion by the mountain pine beetle through the previously climatically unsuitable Canadian boreal forest may have large-scale impacts on north eastern North American pine forests.
2. No systematic studies have been conducted on potential reproduction of mountain pine beetle on pines common to north eastern North America. We report reproduction of mountain pine beetle in logs of novel pine species (jack, *Pinus banksiana* Lamb; red, *Pinus resinosa* Ait.; eastern white, *Pinus strobus* L.; and Scots *Pinus sylvestris* L.) compared to the two most common pine hosts in its historical range (ponderosa, *Pinus ponderosa* Dougl. ex. Laws. var. *scopulorum* Engelm. and lodgepole *Pinus contorta* Dougl. var. *latifolia* Engelm.) in a two year study.
3. Successful reproduction of mountain pine beetle occurred in all novel hosts, demonstrating that constitutive defences pose no barrier to further range expansion. Despite the number of progeny in novel hosts on par with that of historical hosts, a greater number of adult brood in novel hosts died prior to emergence.
4. Brood mortality was correlated with the number of brood that developed to adulthood prior to winter, particularly in red pine. Brood developed more rapidly in novel vs. historical pine hosts and, the summer after a warm fall, exhibited less synchronized emergence in novel hosts.
5. *Synthesis and applications*. Outbreaks by an aggressive bark beetle may be possible outside its historical host range, but constrained by an interaction between host and seasonality. Our results suggest that pines common to north eastern North America are suitable hosts for mountain pine beetle and highlight the value of monitoring efforts and response preparations as the insect moves eastward.

KEYWORDS

bark beetle, *Dendroctonus ponderosae*, development, insect, invasive species, mountain pine beetle, novel host, pine, range expansion, reproduction

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1 | INTRODUCTION

Range expansions and invasions of insect herbivores have been facilitated by human movement of infested materials (Brockerhoff, Bain, Kimberley, & Knížek, 2006) and by increasingly suitable climates (Carroll, Taylor, Régnière, & Safranyik, 2004; Sambaraju et al., 2012). Climate may facilitate or hinder invasion success (Raffa et al., 2015), although success is first and foremost dependent upon the ability of the herbivore to utilize novel hosts (Bertheau, Brockerhoff, Roux-Morabito, Lieutier, & Jactel, 2010; Branco, Brockerhoff, Castagneyrol, Orazio, & Jactel, 2015). Highly suitable hosts can result in major shifts in the population dynamics of an invader, often to the detriment of natural communities (Gandhi & Herms, 2010).

Some of the most common and destructive invaders of forests are subcortical bark and wood boring beetles (Aukema et al., 2010). While few introductions of non-native insects result in establishments, select inadvertent introductions have resulted in billions of dollars in damages (Aukema et al., 2011). These destructive invaders are often insects with narrow host ranges that attack species phylogenetically similar to their historical hosts (Bertheau et al., 2010; Pearse & Altermatt, 2013). Damages can be especially unexpected when the invader is a benign or minor pest in its historical range (e.g. *Agrilus planipennis* Fairmaire, *Dendroctonus valens* LeConte, *Ips grandicollis* (Eichhoff), and *Xyleborus glabratus* Eichhoff). There are relatively few examples of historically aggressive subcortical insects that have been introduced to novel ranges. Thus, it is unclear how aggressive subcortical forest insects may respond to novel hosts, particularly when exogenous factors such as climate play crucial roles in mediating key life-history events such as host procurement (Powell, Jenkins, Logan, & Bentz, 2000).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an aggressive bark beetle that can colonize and kill large diameter and vigorous pines (*Pinus* spp.) during outbreaks. Outbreaks have affected tens of millions of hectares in the beetle's native range of western North America over the past two decades (Aukema et al., 2006; Meddens, Hicke, & Ferguson, 2012), modifying forest resilience (Karst et al., 2015), carbon cycles (Hicke et al., 2012; Moore et al., 2013) and even weather (Maness, Kushner, & Fung, 2012). The mountain pine beetle's primary hosts in its native range include lodgepole (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and ponderosa (*Pinus ponderosa* Dougl. ex. C. Laws.) pines. While the insect's northern distribution in British Columbia has historically been restricted by cold temperatures (Safranyik, Shrimpton, & Whitney, 1975), an increasingly suitable climate has facilitated northward range expansion (Carroll et al., 2004) and subsequent breach of the geoclimatic barrier of the northern Rocky Mountains in Alberta over the past decade (De la Giroday,

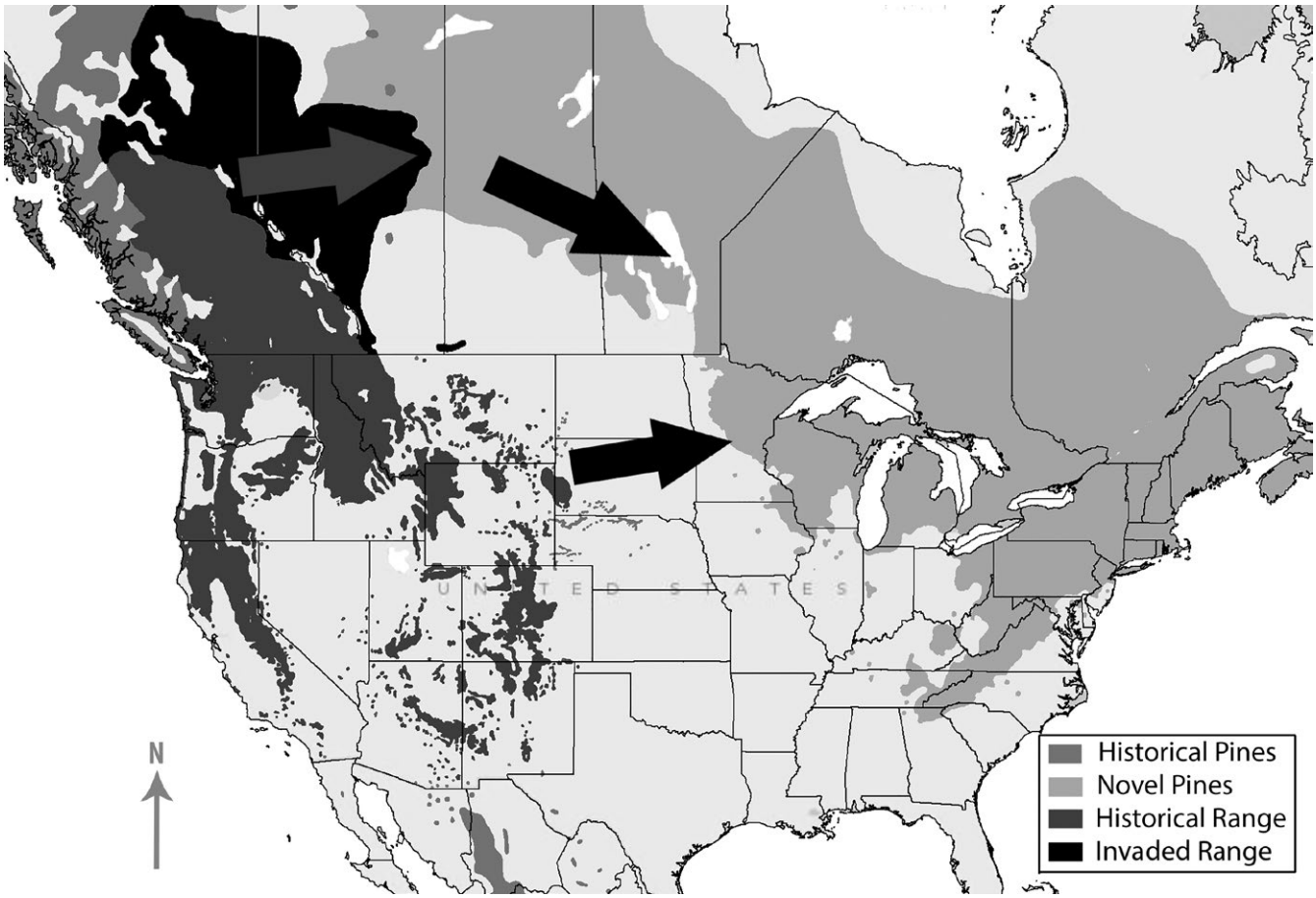

FIGURE 1 Range expansion of mountain pine beetle. The light grey arrow denotes current range expansion and pathways to eastern forests are denoted by dashed arrows. Redrawn from Rosenberger, Venette, Maddox, et al. (2017)

Carroll, & Aukema, 2012). Mountain pine beetle has spread into the hybrid zone of lodgepole × jack (*Pinus banksiana* Lamb.) pines in the Canadian boreal forest, expanding eastward into stands of pure jack pines, which constitute novel host pools (Cullingham et al., 2011). The insect continues to spread through the jack pine of the Canadian boreal forest eastward towards more evolutionarily naïve forests containing jack, red (*Pinus resinosa* Ait.), eastern white (*Pinus strobus* L.), and Scots (*Pinus sylvestris* L.) pines of the western Great Lakes region (Figure 1).

Mountain pine beetle reproduction occurs in the subcortical tissues of the tree. The insect is typically univoltine, and a synchronized peak emergence period of 2–3 weeks in late summer provides the population densities needed to procure hosts (Logan & Bentz, 1999). Mountain pine beetles colonize hosts via pheromone-mediated mass attacks when at outbreak levels. These attacks, in concert with vectored micro-organisms, can collectively overwhelm host defences. Female beetles bore under the bark, attract males, construct vertical egg galleries in the phloem, and lay eggs. Larvae hatch and mine the phloem tissues in larval galleries emanating from the egg gallery. Variations in lower developmental thresholds at different life stages synchronize developing brood. Later instars exhibit higher temperature developmental thresholds than earlier instars (Bentz, Logan, & Amman, 1991; Régnière, Powell, Bentz, & Nealis, 2012), such that late instars arrest development in the fall with onset of cooler temperatures, while early instars continue development (Powell & Logan, 2005). In the spring, synchronized populations resume development through pupal and teneral adult life stages, which are less cold tolerant (Cerezke, 1995; Rosenberger, Aukema, & Venette, 2017). Adults then emerge collectively in late July to seek new hosts.

Although mountain pine beetle's primary hosts are lodgepole and ponderosa pines in western North America, the insect is classified as a feeding generalist on pines (Wood, 1982). For this reason, potential range expansion mediated by "naïve" or "novel" host pools has been identified as a critical emerging threat. The insect has successfully expanded into higher elevations and semi-naïve whitebark pine (*Pinus albicaulis* Engelm.) populations in the Rocky Mountains of the USA, for example (Logan & Powell, 2001; Raffa, Powell, & Townsend, 2013). Several studies have investigated reproduction of mountain pine beetle on novel hosts. Reproduction is enhanced in northern populations of naïve lodgepole pine in British Columbia, for example (Cudmore, Björklund, Carroll, & Staffan Lindgren, 2010). Beetles seem to be less willing to accept jack pine than lodgepole pine when artificially introduced, however, and egg galleries tend to be shorter, resulting in fewer offspring per female (Cerezke, 1995; Erbilgin et al., 2014; Lusebrink, Erbilgin, & Evenden, 2016). The suitability of common north eastern pine species threatened by eastward range expansion is unclear, although these pines are likely susceptible to attack. In an arboretum, dozens of mature jack, red, eastern white and Scots pines were killed over several years (Furniss & Schenk, 1969). In lieu of a sustained outbreak far from stands of historical hosts, these pines appeared to be putatively suitable for reproduction, although comparative brood performance has never been reported.

The objective of this study was to determine the suitability of novel pines common in north eastern North American forests for mountain pine beetle development and reproduction to provide insight into further potential transcontinental range expansion. We hypothesized that mountain pine beetle would be able to reproduce in these evolutionarily naïve pines, although we expected that reproduction and development would vary, as has been observed among other hosts (Amman, 1982; Cerezke, 1995; Langor, 1989; Safranyik & Linton, 1983).

2 | MATERIALS AND METHODS

We compared reproduction and development parameters of mountain pine beetle in a common garden environment with cut logs following established protocols (e.g. Bentz, Bracewell, Mock, & Pfrender, 2011; Cale et al., 2015; Langor, 1989; Safranyik & Linton, 1983; West, Briggs, Jacobi, & Negrón, 2015). In total, eight trees of each of the following species were utilized; jack (*P. banksiana* Lamb), red (*P. resinosa* Ait.), eastern white (*P. strobus* L.), Scots (*P. sylvestris* L.), lodgepole (*P. contorta* Dougl. var. *latifolia* Engelm.) and ponderosa (*P. ponderosa* Dougl. ex. Laws. var. *scopulorum* Engelm.) pine. All trees were *c.* 24 cm diameter at breast height (DBH, *c.* 1.3 m above ground) and free of visible signs of insect or disease. In 2013 and 2014, logs of common north eastern pines, jack, red, eastern white, and Scots pines were obtained from the Cloquet Forest Research Center, MN (Rosenberger, Venette, Maddox, & Aukema, 2017). The historical hosts, lodgepole and ponderosa pine, were obtained from the Big Horn Mountains in Wyoming and Black Hills in South Dakota respectively (Rosenberger, Venette, Maddox, et al., 2017).

Experiments were initiated twice each summer, 1 week apart, during the short flight period of mountain pine beetle. In 2013, two trees of each species were cut on 29–30 July and two more were cut 5–6 August. In 2014, two trees of each species were harvested on 4–5 August and 11–12 August. Boles were cut into 1 m sections and the ends were waxed to reduce desiccation. Logs were immediately placed in tarpaulin bags to exclude other insects (BP Medical Supplies, Brooklyn, NY, USA) after waxing before transport to a central location in the Black Hills within 24 hr of harvest.

Mountain pine beetles to seed the logs were caught in 12-funnel Lindgren funnel traps baited with commercial pheromone lures (Contech Enterprises Inc, Delta, BC) in ponderosa pine forest near Silver City, SD (Rosenberger, Venette, Maddox, et al., 2017). Beetles were collected daily and sexed with a repetitive audible method (Rosenberger, Venette, et al., 2016). Beetles were stored in separate Petri dishes on moist tissue paper at *c.* 5°C until use. All insects were used within 5 days of collection.

2.1 | Infesting logs

In each of the 2 weeks each year, six logs, 40 cm long, were cut from each of two trees of each of the six species, yielding 72 logs, the ends of which were sealed with hot paraffin wax. Females, followed by

males were introduced to logs within 24–48 hr of trees being harvested as outlined in previous work (Rosenberger, Aukema, et al., 2017). We designated the date of generation commencement as the date that males were introduced. All logs were colonized within 3 days of harvest.

Logs were sealed in charcoal-coloured aluminium screening (New York Wire, Hanover, PA) and moved to 12 locations in the central Black Hills for 6 days for conspecific attraction experiments (Rosenberger, Venette, Maddox, et al., 2017) before being stored outside on the north side of a building to overwinter. A temperature logger (HOBO, Onset Computer Corp., Bourne, MA) was suspended 30 cm from the ground among the logs to record air temperatures. In 2013, due to technical difficulties, temperature data were not recorded until 22 October, so late summer temperatures were obtained from a weather station within 5 km of the overwintering site. Because the entire procedure was repeated twice in 2013 and twice in 2014, we established a total of 288 infested logs, 48 of each of six pine species.

2.2 | Midwinter parameters

Development of mountain pine beetle ceases with winter, so midwinter brood examinations provide insight into development rate and reproductive potential. We debarked two logs chosen at random and stored below 0°C from each tree (eight from each species) in January of each year and tallied brood in each life stage. An additional log of ponderosa pine was also debarked both years and one of eastern white pine in 2014. The headcapsule widths of larvae and pronotal widths of brood adults were measured with a digital micrometer, and a mixed distribution analysis (mixtools in R) used to determine instar. A developmental index was devised by multiplying the number in each stage by a corresponding classification number (Larval instar 1 = 1, L2 = 2, L3 = 3, L4 = 4, pupae = 5, brood adult = 6) and dividing the result by the total number of brood in that log (Langor, 1989). A developmental index was calculated for each log. Brood adults were sexed using the morphology of the seventh abdominal tergite (Lyon, 1958).

Once logs were debarked, egg galleries were traced onto clear plastic sheets and measured using a mapwheel (Scalex Corp., Carlsbad, CA). Galleries were characterized as either paired (i.e. male joined female), unpaired introductions, or re-entries (i.e. galleries were constructed at points other than original introduction points). Galleries were classified as fertile if first instar larval galleries extended from the vertical egg gallery. In the second year, larval galleries were counted for each fertile egg gallery to obtain a measure of egg viability.

2.3 | Emergence

To determine reproduction and emergence rate, the remaining logs not debarked in winter (94 in 2014 and 95 in 2015) were removed from their screening and placed in rearing containers in an unheated building in mid-April. Beetles were allowed to emerge naturally and collected every 2–3 days commencing on 3 June in 2014 and 27 May in 2015. We terminated each experiment in mid to late August after allowing more than 365 days for brood development. Logs were debarked and all remaining live and dead adults were counted, sexed and measured. Egg galleries were then traced and measured.

2.4 | Statistical analysis

We used the sine-wave method (Allen, 1976) and minimum and maximum temperatures obtained from the data loggers and the weather station to calculate developmental degree days (DD) experienced by logs each year (base 5.6°C; Safranyik et al., 1975). We used analysis of variance in a mixed effects framework (nlme package in R) to analyse the effects of tree species (and/or pooled historical vs novel hosts) on variables of interest. These responses included development index, day to 50% emergence (E50), gallery length, fertile eggs per cm of gallery, brood density, midwinter brood per female, potential brood adults per female, emerged brood adult per female, and size of larvae and adults. All data except for size data were analysed at the log level, so a term for tree within species was included as a random effect. Because size data were at the beetle level, we included terms for log and log nested within tree as random effects. For the development index, we included a term for week of experiment replication as a random effect. Where significant treatment effects existed, means were compared using Tukey procedures. In addition to species-specific comparisons of E50 values, we also constructed 95% confidence intervals to examine which hosts facilitated mean generation times of less than 365 days. Simple linear regression was used to analyse the effect of number of midwinter adults versus post-winter adult mortality in the logs. Residual plots were visually inspected for all models to ensure model assumptions of homoscedasticity and normality of errors were met. Square root transformations of potential and emerged brood per female were needed. Because experiments were replicated across 2 years, we tested and combined years where there were no annual differences. Sex ratio data were analysed using logistic regression in a mixed effects framework (MASS package in R). Terms for tree and log were included as random effects.

3 | RESULTS

3.1 | Development index

When pooled by host type, brood developed more quickly by midwinter in novel versus historical hosts, although species differences were only pronounced in 2013–2014 (Table 1). Brood developed most rapidly in red pine, reaching pupal and adult stages by January of 2014 (Table 1), concomitant with warm fall temperatures. The fall of 2013 was warmer than 2014, with 1,006 DD versus 815 DD accumulated respectively by 1 January of the following year (Figure S1). In total, across all pines, 40% of brood reached the adult stage prior to January the first year, while less than 1% reached adulthood prior to January the second year. Beetles exhibited the lowest mean developmental

TABLE 1 Mean (*SE*) midwinter development index among pine species in 2013 and 2014 (1 = first instar, 2 = second instar, 3 = third instar, 4 = fourth instar, 5 = pupae, 6 = brood adult). Means followed by the same letter are not significantly different. *n* = 8 logs per species each year

	Winter 2013–2014	Winter 2014–2015
Species	***M* (*SE*)**	***M* (*SE*)**
Historical		
Ponderosa	4.74 (0.20)b	3.76 (0.07)
Lodgepole	4.65 (0.21)b	3.64 (0.11)
Novel		
Jack	4.94 (0.26)ab	3.79 (0.09)
Red	5.36 (0.20)a	3.89 (0.13)
Eastern white	4.87 (0.15)ab	3.86 (0.05)
Scots	4.85 (0.19)ab	3.85 (0.07)
$F_{5,17}$	3.57	1.32
p	.0218	.301
All historical	4.7 (0.14)a	3.70 (0.06)a
All novel	5.0 (0.10)b	3.85 (0.05)b
$F_{1,21}$	7.99	4.37
p	.0101	.0489

rates in lodgepole and ponderosa pines both years, although they were not statistically different than progeny developing in jack, eastern white or Scots pines (Table 1).

3.2 | Emergence

Insects successfully completed development in all species of novel and historical pines in both 2013–2014 and 2014–2015. Emergence of progeny commenced sooner in 2014 than 2015, particularly among novel pines (Figure 2). While only 2%–3% of emergence occurred among historical hosts before 1 July in both years, up to 45% of total emergence in 2014 and between 7% and 14% of total emergence in 2015 occurred prior to July among novel hosts. Beetles in red pine emerged particularly early, with 16% of emergence occurring by 3 June, the first day cages were checked in 2014. Emergence from novel hosts occurred steadily throughout the summer. In 2015, an extended emergence commenced in novel pines in mid-July (Figure 2c), coincident with variable rates of development among hosts (Figure 2d).

Clear peaks in emergence occurred in early August among historical pines both years. The number of days to 50% brood emergence, which was not significantly different between years after accounting for species ($F_{1,41}$ = 0.05, p = .82), was not significantly different than a 1 year generation time for both lodgepole and ponderosa pines, as demonstrated by 95% confidence intervals that overlap 365 days in Figure 3. However, insects in novel pines developed more rapidly than 1 year, with the most rapid development in red and Scots pines (Figure 3). In these logs, E50 occurred *c.* 3 weeks earlier than the 1 year mark (Figure 3).

3.3 | Fertile gallery length

Life histories were reconstructed when the bark was peeled from the logs after emergence. Of 2,280 ovipositional galleries we measured, 42% exhibited larval galleries. These fertile galleries were 25% longer in historical hosts (37.2 cm ± 0.79SE) than novel hosts (27.8 cm ± 0.54SE) ($F_{1,46}$ = 32.7, p < .0001). Females in ponderosa pine produced galleries 40% longer than those in jack pine (Table 2). Female beetles frequently abandoned galleries in jack pine, with 46% of females abandoning and re-entering jack pine compared to an average of 26% for all other pines.

3.4 | Fertility and brood density

The number of first instar galleries per ovipositional gallery (i.e. proxy for viable eggs, hereafter termed "fertility") was standardized by the length of the gallery. Total brood successfully developing up to winter in each log was standardized by the length (cm) of fertile ovipositional gallery per log. We observed the greatest fertility in eastern white pine where 1.73 larvae initiated galleries per cm of egg gallery, 33% more than in lodgepole or red pine (Table 2). Eastern white pine also exhibited 26%–95% more midwinter brood per cm than all other pine species. Relatively high first instar mortality (20%–40%; i.e. one minus proportion surviving, measured as midwinter brood density divided by initial egg viability per cm gallery) was observed in all hosts but red pine, which demonstrated only 8% first instar mortality (Table 2).

3.5 | Midwinter brood potential

We measured the number of brood found in January, and standardized by the number of fertile ovipositional galleries resulting from our introductions. This metric yielded brood potential per fertile female. We found an average of 30 brood per female across all pines. Brood potential varied by species, with females in eastern white and ponderosa pine producing 15%–43% more brood than the other four pines, particularly lodgepole and Scots pine (Table 2).

3.6 | Expected vs realized brood potential

Realized reproduction comprised all brood adults that emerged or were found alive in logs by late August (i.e. >365 days post introduction), standardized by the number of fertile ovipositional galleries. Expected reproduction was estimated by adding the number of fully developed but dead adults to the realized reproduction value. In both years, expected potential reproduction (alive and dead adults) was similar among species (2014:$F_{5,18}$ = 1.6, p = .21; 2015: $F_{5,18}$ = 1.28, p = .32) and classifications of co-evolutionary history (historical vs. novel) (2014: $F_{1,22}$ = 1.17, p = .29; 2015: $F_{1,22}$ = .52, p = .48; Figure 4).

Realized reproduction, however, which comprised only live adults, was much less than expected reproduction, particularly among novel pines, where over half of all brood that reached adulthood died prior to emerging both years (Figure 4b,d). Only half as many brood per

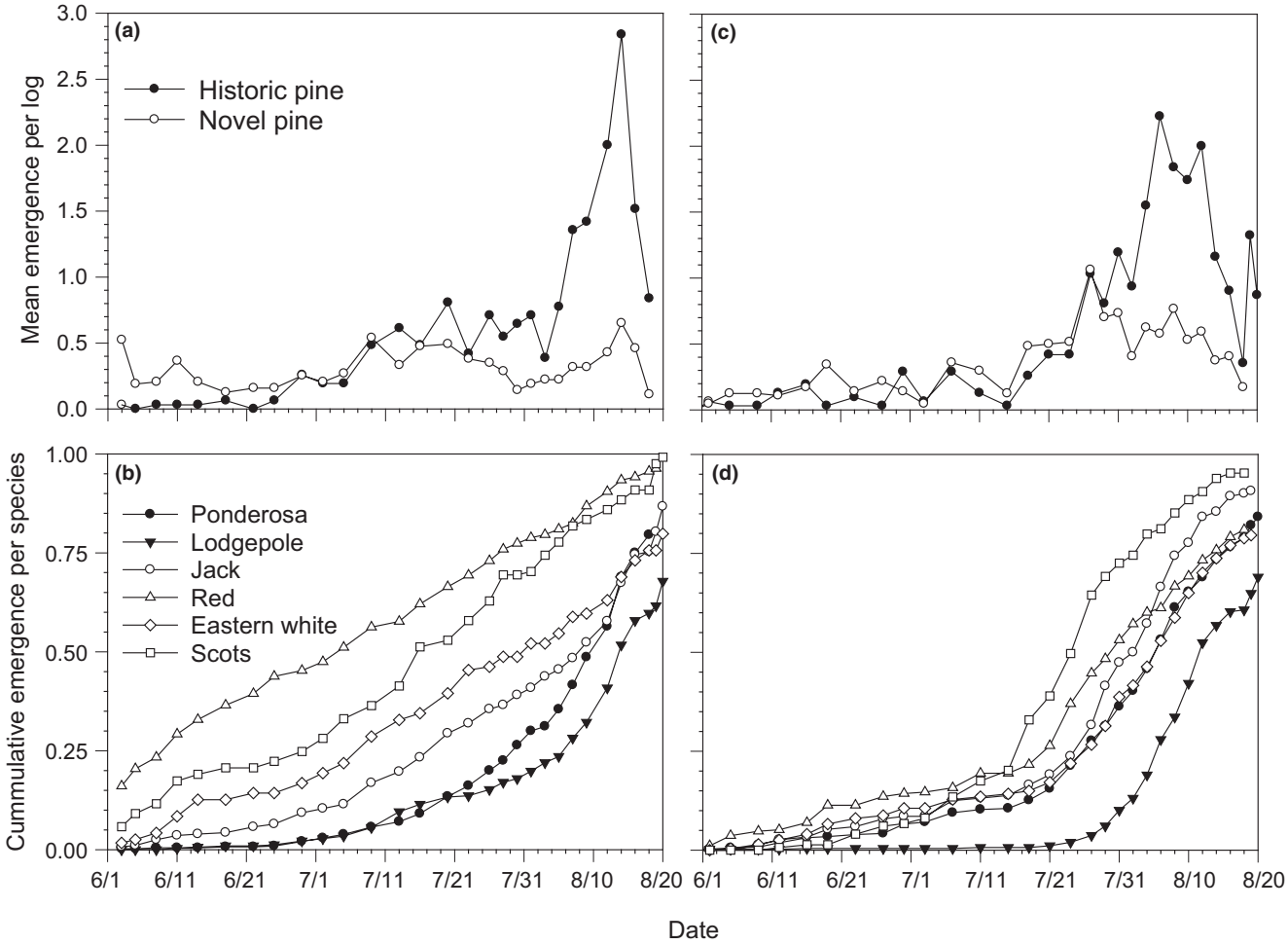

FIGURE 2 Mean emergence per log per collection among historical and novel hosts in Black Hills, *SD* in summer 2014 (a) and summer 2015 (c), and cumulative emergence among six pines hosts in summer 2014 (b) and summer 2015 (d). *n* = 15–16 logs per species each annual replication in a common garden environment. Cumulative emergence is calculated by dividing total emerged at a collection point from total emerged and unemerged (found after debarking) live adults

female emerged from novel pines vs historical hosts across both years ($F_{1,46}$ = 9.85, p = .003), although statistical differences were more clear in 2014 ($F_{1,22}$ = 6.5, p = .02) than 2015 ($F_{1,22}$ = 3.43, p = .078). Similarly, we observed a significant effect of species on realized reproduction in the first year of our experiments ($F_{5,18}$ = 3.5, p = .02), with three of the four novel hosts producing one-third as many adults as ponderosa pine. No significant difference was observed at the species level in 2015 ($F_{5,18}$ = 1.45, p = .25; Figure 4c).

Many adults entered the winter, particularly among novel pines in January 2014, and many dead adults were found in the novel host logs when debarked that summer. Adults per female by midwinter (January) was positively correlated with dead adults per female in the following summer ($F_{1,46}$ = 29.42, p < .0001; Figure 5).

3.7 | Sex ratio and insect size

We observed more females than males in both years overall (mean sex ratios across all pines 59F:41M and 56F:44M respectively). These ratios were similar across all species of pines (χ^2 = 5.03, df = 5, p = .41; Table 2). Sex-specific larval winter mortality likely did not contribute significantly to the female-biased sex ratio as we also found no difference in sex ratio between beetles that reached adulthood prior to January 2014 (60F:40M), compared to those from the same generation that emerged in the summer (57F:43M; χ^2 = 1.11, df = 1, p = .29). Among larvae, the largest progeny occurred in red pine, with size differences from lodgepole pine beginning to emerge by the second instar both years (Table 3). Adult sizes were similar across all pines the second year (Table 3).

4 | DISCUSSION

This study demonstrates that constitutive defences pose no barrier to successful reproduction of mountain pine beetle in the four most common pines of north eastern North America. We show that mountain pine beetles developing in some novel pines have faster development and emergence rates, greater larval size (e.g. red pine; Tables 1 and 3, Figure 3) and higher reproductive potential

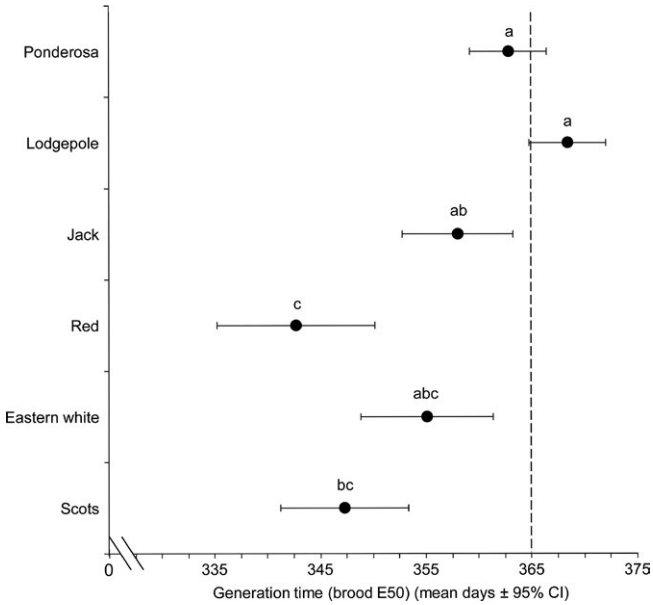

FIGURE 3 Effect of pine species on time to 50% emergence (E50) of mountain pine beetles in Black Hills, *SD* ($F_{5,42}$ = 8.6, p < .0001). Data represent logs with emerging beetles both years. 95% confidence intervals permit comparison to 1 year (dotted line) since brood initiation. Means followed by the same letter are not significantly different from each other. n = 22–29 logs per species

(e.g. white pine; Table 2), but may also suffer from higher mortality prior to emergence than beetles developing in historical hosts (Figure 3).

Some mortality in a novel host such as red pine can likely be attributed to rapid development to life stages that exhibit greater susceptibility to overwintering temperatures (Table 1, Figure 5; Cerezke, 1995; Rosenberger, Aukema, et al., 2017), which would be detrimental to eastward invasion success. However, rapid development to cold-susceptible life stages before midwinter does not fully account for the surprisingly high mortality observed in 2014–2015 (86%–91% in novel hosts), when most brood had achieved more cold tolerant larval overwintering stages by late fall. An early November 2014 cold snap may have killed many unacclimated larvae (Cerezke, 1995; Rosenberger, Aukema, et al., 2017). Overwintering mortality of up to 88% is not uncommon in historical hosts such as lodgepole pine (Cole, 1975). Late stage mortality could have also occurred from desiccation of the hosts, as novel hosts contained slightly thinner phloem than historical hosts in the second year of the study (Cerezke, 1995; Rosenberger, Aukema, et al., 2017). Mortality could have also been due to a lack of symbiotic micro-organisms or latent toxic effects of the host—important areas that require further study (Bentz & Six, 2006; Clark, Huber, & Carroll, 2012; McKee, Huber, & Aukema, 2013; Therrien et al., 2015).

4.1 | Three possible outcomes of desynchronized development

Development rate in the mountain pine beetle is an evolved adaptation (Bentz et al., 2014) under significant selective pressure due to the requirement for a univoltine life cycle that facilitates host procurement (Hicke, Logan, Powell, & Ojima, 2006; Logan & Powell, 2001). Subtle differences in climate in novel ranges vs the native range from which the insect is adapted may result in several disparate scenarios. First, if the climate in the invaded range is warmer than required to regulate univoltinism, fractional voltinism may occur (Reid, 1962). Brood in novel hosts could enter winter as adults, or brood emerging as adults in the fall could attack new trees, resulting in two emergence events in a single year. Such situations can be maladaptive if brood are unable to synchronize life stages to facilitate host procurement through mass attack (Bentz et al., 2010; Powell et al., 2000). Fractional voltinism has recently been observed in limber pine in Colorado (Bentz

TABLE 2 Performance traits of mountain pine beetles colonizing logs, 2013–2014 and 2014–2015. Means followed by the same letter within a column are not significantly different. n = 8 logs × 6 species each year for midwinter data

Species	*M* (*SE*) egg gallery length (cm)	*M* (*SE*) egg viability (first instar galleries/cm of egg gallery)[a]	*M* (*SE*) brood density (brood/cm of egg gallery)	*M* (*SE*) midwinter brood/female		Sex ratio (proportion female midwinter and summer)
Historical						
Ponderosa	39.6 (1.0)a	1.32 (0.11)ab	0.87 (0.08)b	37.6 (3.5)a		0.601
Lodgepole	34.2 (1.2)ab	1.17 (0.10)b	0.72 (0.06)b	22.9 (3.3)b		0.553
Novel						
Jack	24.6 (1.0)d	1.39 (0.12)ab	0.99 (0.11)b	27.8 (4.2)ab		0.549
Red	31.4 (1.1)bc	1.12 (0.09)b	1.03 (0.08)b	32.3 (2.7)ab		0.590
Eastern white	25.5 (0.9)cd	1.73 (0.14)a	1.40 (0.11)a	38.7 (4.1)a		0.576
Scots	30.7 (1.2)bcd	1.32 (0.14)ab	0.77 (0.10)b	21.8 (2.6)b		0.593
F	13.8	2.64	7.33	4.31	*n*	4,377
df	5,42	5,18	5,42	5,42	χ^2	5.02
p	<.001	.059	<.001	.003	*p*	.41

[a]Data from 2015.

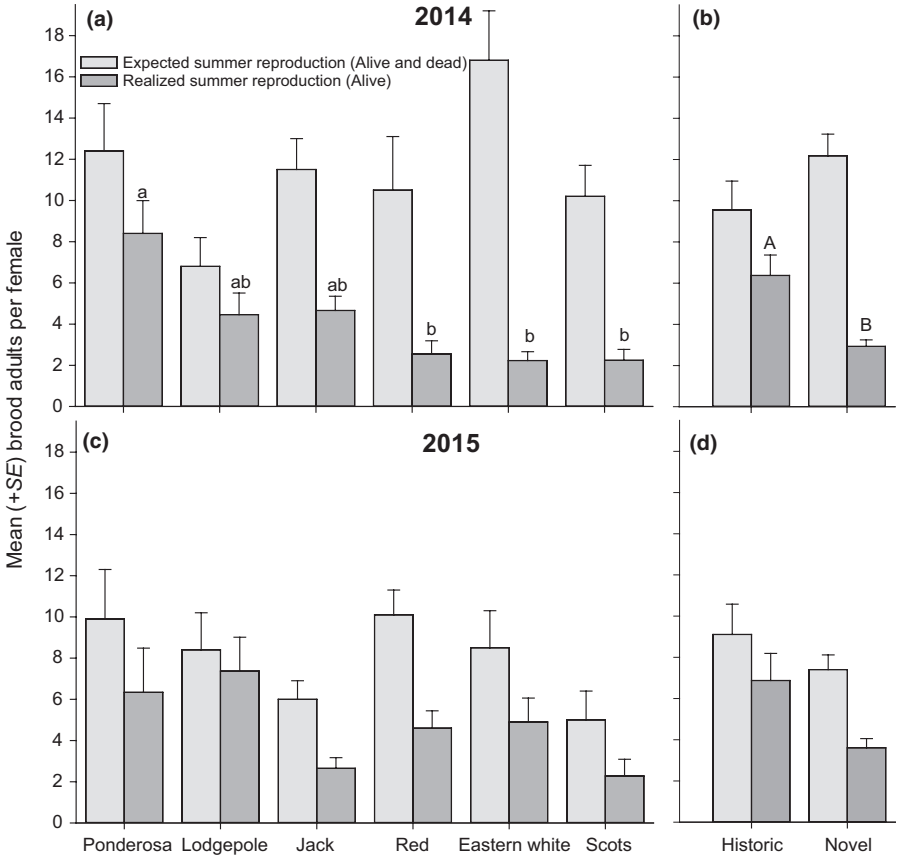

FIGURE 4 Mean (+*SE*) brood adults per female among six different pine hosts in summer 2014 (a) and summer 2015 (c) and among historical or novel pines in summer 2014 (b) and summer 2015 (d). Means with the same letter are not significantly different from each other; no letters indicate absence of global effect. *n* = 15–16 logs per species for each annual replication

& Powell, 2014; Mitton & Ferrenberg, 2012), possibly due to more rapid development in limber pine compared to other common hosts (Langor, 1989).

Second, if the climate in the invaded range is similar to climate experienced in the mountain pine beetle's historical range, development could be similar to what we observed in this study. That is, an extended peak emergence period may occur across novel hosts, even if populations are synchronized among hosts the previous fall, like we observed in the second year of this study (Table 1). If populations are sufficiently large for mass attacks to occur during this extended emergence period, an earlier peak emergence in July (Figure 2c) and more rapid development of the resulting brood in mid to late summer may result in brood overwintering at advanced life stages that are less cold hardy (Table 1; Cerezke, 1995; Rosenberger, Aukema, et al., 2017). Of the novel hosts, jack and eastern white pines are most similar in development rates to historical hosts (Figure 3), so these pines may be most adapted to climates similar to those of historical hosts.

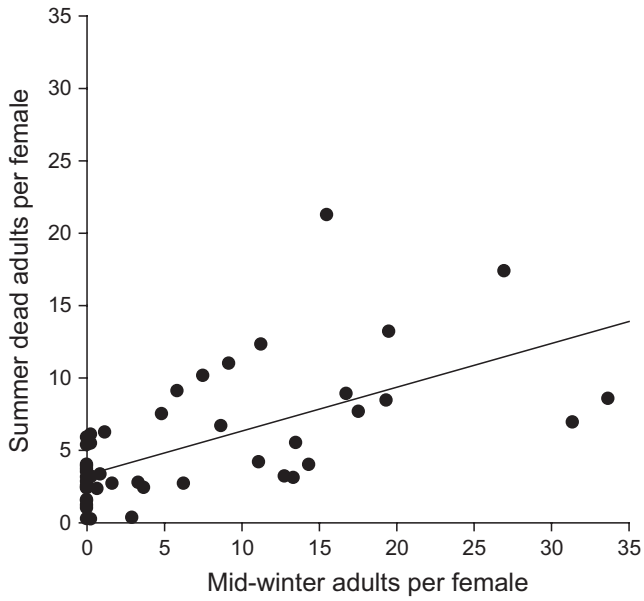

FIGURE 5 Comparison of mean adults per female in winter and mean dead brood in summer (*n* = 8 trees per species)

Finally, our results suggest that the most beneficial climate for mountain pine beetle developing in these novel hosts would be colder than its climate in the historical range. With fewer developmental DD per year, beetles would be more likely to synchronize development of the cold tolerant late instars (Powell & Logan, 2005). Indeed, slightly more rapid development may currently be benefiting beetles in the newly invaded jack pine of the cooler Canadian boreal forest (Safranyik et al., 2010).

Life-history traits and climate may also interact to affect mountain pine beetle persistence in new environments. Increased development rates in some novel hosts, an indicator of greater fitness, could desynchronize emergence, potentially reducing the ability of the insect to engage in cooperative mass-attack behaviour. Whether these novel hosts can be overcome by fewer beetles has not yet been studied.

Indeed, while our study contributes to assessments of relative differences in reproductive potential among hosts (Amman, 1982; Cerezke, 1995; Langor, Spence, & Pohl, 1990), it remains unclear how induced phytochemical defences may affect mountain pine beetle reproduction in eastern hosts as common garden studies with live trees are not possible in this system (Cale et al., 2015).

5 | CONCLUSIONS

Previous work (Furniss & Schenk, 1969; Rosenberger, Venette, Maddox, et al., 2017) has shown that mountain pine beetle will attack congeneric host material, despite substantial phylogenetic distances from historical hosts (e.g. red and Scots vs. ponderosa and lodgepole pine) and a lack of shared co-evolutionary history (Bertheau et al., 2010). Here, we further demonstrate that constitutive defences of novel and distantly related hosts do not preclude successful reproduction by the insect, although some life-history traits (e.g. size, development rate, brood size) may be affected. Colonization and reproduction within novel hosts across multiple *Pinus* clades portends susceptibility of other *Pinus* species not tested in this study (Bertheau et al., 2009), warranting future work.

Our work provides additional evidence that mountain pine beetle should be viewed as a critical, emerging threat to north eastern North American pine forests as the insect continues to expand its range east through the Canadian boreal forest. More rapid development in novel hosts could release insects from maladaptive semivoltine constraints in regions that were historically thought to be too cold (Bentz et al., 2010). Development of phenological models that can incorporate host-mediated development rates will help identify regions most at risk for range expansion. Such regions may include northern forests outside of North America, given the insect's successful reproduction in Scots pine. In Minnesota, state officials have implemented external quarantines on pine logs with bark attached transported from western states with active mountain pine beetle outbreaks. Such efforts, as well as continued management in the Canadian transition zone (De la Giroday et al., 2012) seem warranted to mitigate this threat.

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TABLE 3 Effect of pine species on *M* (*SE*) larval headcapsule size (midwinter) and adult pronotal width (midwinter and emerged adults), 2013–2014 and 2014–2015. Means followed by the same letter within a column are not significantly different. *n* = 8 logs per species each year

	M (*SE*) Larval headcapsule width (mm)					*M* (*SE*) Adult pronotal width (mm)			
Species	**Instar 1**	**Instar 2**	**Instar 3**	**Instar 4 (2014)**	**Instar 4 (2015)**	**Females 2014**	**Males 2014**	**Female 2015**	**Male 2015**
Historical									
Ponderosa	0.53 (0.007)	0.69 (0.004)b	0.96 (0.004)ab	1.31 (0.003)a	1.35 (0.002)ab	2.43 (0.01)ab	2.21 (0.01)ab	2.47 (0.01)	2.25 (0.01)
Lodgepole	0.53 (0.008)	0.69 (0.004)b	0.95 (0.004)b	1.28 (0.005)b	1.30 (0.004)c	2.36 (0.01)b	2.15 (0.01)b	2.46 (0.01)	2.22 (0.01)
Novel									
Jack	0.52 (0.008)	0.71 (0.006)b	0.98 (0.005)a	1.32 (0.004)a	1.35 (0.003)ab	2.40 (0.01)ab	2.21 (0.01)ab	2.40 (0.02)	2.11 (0.02)
Red	0.59 (0.015)	0.76 (0.009)a	0.99 (0.005)a	1.33 (0.005)a	1.39 (0.002)a	2.51 (0.01)a	2.27 (0.01)a	2.41 (0.01)	2.18 (0.02)
Eastern white	0.48 (0.009)	0.67 (0.010)b	0.97 (0.004)ab	1.31 (0.003)a	1.35 (0.002)ab	2.34 (0.01)b	2.15 (0.01)b	2.42 (0.01)	2.18 (0.01)
Scots	0.53 (0.007)	0.72 (0.007)ab	0.96 (0.004)ab	1.31 (0.005)a	1.32 (0.004)bc	2.46 (0.01)ab	2.23 (0.01)ab	2.35 (0.02)	2.08 (0.02)
F	1.99	6.25	2.62	4.48	8.57	4.43	4.62	0.075	1.8
df	5,10	5,32	5,41	5,18	5,18	5,18	5,18	5,18	5,18
p	.17	.0004	.04	.008	.0003	.0083	.0069	.6	.16
n	65	286	1,163	1,830	3,354	1,627	1,152	887	687

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AUTHORS' CONTRIBUTIONS

D.R., B.A. and R.V. conceived the ideas and designed the methodology; D.R. collected the data; D.R. and B.A. analysed the data. D.R., B.A. and R.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Data Repository for University of Minnesota (DRUM). https://doi.org/10.13020/d6nq3p (Rosenberger, Venette, & Aukema 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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