

Article

Suitability of a Historical, Novel, and Occasional Host for Mountain Pine Beetle (Coleoptera: Curculionidae)

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Abstract: The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), recently underwent a notable range-expansion event in western Canada, resulting in access to the novel host jack pine, *Pinus banksiana* Lamb. We assessed the suitability of jack pine for mountain pine beetle, as well as the historic host lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm., and the non-*Pinus* host white spruce, *Picea glauca* (Moench) Voss, to help inform an assessment of the risk of future spread into Canada's boreal forest and to further our understanding of host use in bark beetles. Several performance traits we measured were similar between lodgepole pine and jack pine, but gallery length and productivity indicated that lodgepole pine was the more suitable host. Development appeared to be faster in jack pine; however, in contrast to previous studies, we attribute it to oviposition arresting earlier in the novel host compared to the other hosts and not a difference in development rate. Initial productivity was surprisingly high in spruce, but we found evidence of a delayed negative effect that manifested as reduced cold tolerance, delayed development, and high mortality of late-instar larvae. Although jack pine is a suitable host for the mountain pine beetle, our results indicate that the beetle's eruptive potential could be lower in jack pine compared to lodgepole pine, given all other factors are equal. Other factors that may also affect mountain pine beetle population dynamics require additional research and include the composition and structure of jack pine forests, environmental conditions, and biotic interactions.

Keywords: host suitability; range expansion; novel host; development rate; cold tolerance



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1. Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Curculionidae), is an interesting example of an insect that recently underwent a notable range-expansion event earlier this century when it breached a major biogeoclimatic barrier and invaded a new ecosystem. The mountain pine beetle is native to western coniferous forests in North America, where periodic eruptions lead to significant tree mortality and ecological impacts. The last major outbreak in British Columbia, Canada, started in the mid-1990s, impacted 18 M ha of forest, and killed 54% of the merchantable pine volume in the province by the time it subsided [1]. The historical (pre-2000) range of mountain pine beetle extends from northern Mexico to central British Columbia and from the West Coast to the Rocky Mountains. There are isolated populations in pockets of forest on the Great Plains, most notably in the Black Hills in North Dakota, United States of America, and in the Cypress Hills on the Alberta–Saskatchewan border, Canada. Cold temperatures limit the northern extent of the beetle's range, which occurs around the $-40\text{ }^{\circ}\text{C}$ isotherm in central British Columbia [2,3]. The Rocky Mountains, which cut across northern British Columbia, have served as a biogeoclimatic barrier preventing mountain pine beetle from accessing the boreal forest, which extends from the east into central and northern Alberta [4]. Cold winters and cool summers have likely restricted mountain pine beetle populations in southern Alberta from spreading north along the eastern slopes of the Rockies and into

the boreal forest in central Alberta. Thus, a notable range-expansion event occurred when large numbers of mountain pine beetles from the epidemic in central British Columbia cited above were carried on upper atmospheric winds across the Rocky Mountains and deposited in northeastern British Columbia and western Alberta multiple times during the 2000s (e.g., [4,5]). Despite the harsh continental winters east of the Rocky Mountains, mountain pine beetle managed to establish and spread where it is proximate to Canada's vast boreal forest (e.g., [6–8]).

The mountain pine beetle is a specialist in the genus *Pinus* but a generalist within this genus. Lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm. is the most abundant host in western coniferous forests, but most *Pinus* spp. endemic to the beetle's historic range in western North America are attacked, including western white pine, *P. monticola* Douglas ex D. Don, ponderosa pine, *P. ponderosa* C. Lawson, whitebark pine, *P. albicaulis* Engelm., limber pine, *P. flexilis*, and sugar pine, *P. lambertiana* Douglas: only Jeffrey pine, *P. jeffreyi* Balf., and Great Basin bristlecone pine, *P. longaeva* D.K. Bailey, have been described as unsuitable hosts [6,9–12]. Successful attack or reproduction has also been reported on eastern North American pine species, including red pine, *P. resinosa* Ait.; eastern white pine, *P. strobus* L.; pitch pine, *P. rigida* Mill.; and jack pine, *P. banksiana* Lamb. [13–20]. The ranges of lodgepole pine, which extends from the west, and jack pine, which occurs in the boreal forest and extends from the east, overlap in central Alberta, where the two species hybridize and introgress [21,22]. Since the mountain pine beetle crossed the Rocky Mountains and was established in western Alberta, concern has been growing over its potential to spread across the boreal forest in jack pine (e.g., [6,8]).

Here, we assess the suitability of the common historic host lodgepole pine, the novel host jack pine, and the non-*Pinus* host white spruce, *Picea glauca* (Moench) Voss. We included white spruce, hereafter called spruce, because the mountain pine beetle occasionally attacks and even reproduces in such non-*Pinus* hosts during outbreaks [9,23–26]. Host suitability was inferred from measures of development, productivity, sex ratio, and cold tolerance of insects reared in each tree species under controlled conditions in the laboratory. Our results contribute to a growing body of knowledge aimed at informing assessments of habitats at risk of mountain pine beetle invasion and may further our understanding of host use and shifts in *Dendroctonus* (e.g., [13,24,26,27]).

2. Materials and Methods

2.1. Insect and Host Tree Source

Mountain pine beetles were sourced from logs cut from attacked lodgepole pine trees at a site near Wit'at (a.k.a. Fort Babine) in central British Columbia (55.44° N, 126.68° W; elevation: 800 m). Populations crashed several years ago in the new range, making it challenging to obtain beetles from central Alberta. We sourced beetles from an active infestation near Wit'at because the beetles that invaded central Alberta originated from outbreak populations in central British Columbia (e.g., [4,5,8]), and beetles from this area show genetic similarities to beetles proximate to the boreal forest in central Alberta [28]. Trees were 30 and 40 cm in diameter at 1.4 m and felled on 15 September 2021, when most broods were in the larval stage. The infested portion of the bole was cut into short logs approximately 35 cm long so that they could be safely carried by the field crew out of the forest and transported to the Pacific Forestry Centre in Victoria, British Columbia. Mountain pine beetle readily infests and reproduces in logs of this size. We coated the cut ends with hot paraffin wax to prevent desiccation and hung the logs in mesh emergence cages at 20.5 °C. Emergence of adult beetles peaked in late October and early November, during which time beetles were collected daily and their sex determined using the characteristic of the seventh abdominal tergite under magnification [23]. Beetles were held at 5 °C on moist filter paper in Petri dishes for up to 5 day until the required number of beetles was obtained, and then they were introduced into logs (see below). We sourced host material from a lodgepole pine and spruce tree at a site southeast of Edson in central Alberta (53.61° N, 116.09° W; elevation: 884 m) on 18 September 2021 and from a jack pine tree northwest

of Quebec City in southern Quebec, Canada (50.58° N, 71.83° W; elevation: 220 m) on 23 September 2021. Due to logistical constraints associated with shipping wood and obtaining permission to fall mature trees, one tree of each species was included in the study: other studies have also used the same approach (e.g., [12,24]). Although host tree defensive chemistry can vary among trees (or families) within a species (e.g., [29]), interspecific differences in chemistry, including relative ratios of defensive compounds, is greater than intraspecific variation (e.g., [10,30,31]). The logs in our study ranged between 25 and 30 cm in diameter. The cut ends were sealed with paraffin wax to reduce desiccation, and logs were stored at 1.5 °C until use.

2.2. Productivity and Development

Pairs of beetles were introduced to logs of each species on 5 November 2021. We used a 3/16" drill bit to make 2-cm-long tunnels in the phloem at 7- to 10-cm increments around the bottom of logs (Figure 1). A total of 26, 35, and 22 pairs of beetles were introduced to lodgepole pine, jack pine, and spruce, respectively. One female beetle followed by one male beetle was inserted into each hole, and a small square of mesh was stapled over the area. Insects were reared at 20.5 °C for 40 day before the bark was carefully removed with a mallet and chisel, and each pair of beetles was classified as either: unsuccessful, no brood produced, or successful, with one or more brood produced. We measured the entire length of each egg gallery, including where beetles continued gallery construction downwards after approaching the top of the log. The number of broods (including eggs) produced per centimeter of gallery was calculated. Larval instar was assigned based on the width of the head capsule using the cut points reported in Bleiker and Régnière [32]. A developmental index for each gallery was determined by multiplying the number of individuals in each life stage by a corresponding classification number (egg = 0, larval instar 1 = 1, L2 = 2, L3 = 3, L4 = 4, pupa = 5, brood adult = 6) and dividing the sum by the total number of brood.



Figure 1. Examples of vertical egg (adult) galleries (black arrows) and horizontal larval galleries (white arrows) produced by mountain pine beetle after 40 day of development at 20.5 °C under the bark of lodgepole pine (a), jack pine (b), and spruce (c) logs.

2.3. Larval Cold Tolerance, Adult Size, and Sex Ratio

Pairs of beetles were introduced to each tree species on 1 November 2021, as described above, and held at 20.5 °C. After 27 day, the supercooling points (SCPs) of 10–12 third-instar larvae and 10–12 fourth-instar larvae from each tree species were determined using the method described below. Insects were then acclimated at 0.5 °C for a total of 70 day, and SCPs of larvae were determined after 50 day and 70 day at 0.5 °C. After 70 day at 0.5 °C, insects were maintained at 20.5 °C, emergent beetles were counted, and the sex and pronotal width were determined.

2.4. Phloem Thickness and Moisture Content

We measured phloem thickness and phloem and sapwood moisture content on three samples taken from around the circumference of the top, middle, and bottom third of each log 27 day after beetles were introduced when late-instar larvae were present. Phloem thickness was measured for intact phloem, which had not yet been impacted by adults or larvae constructing galleries. A 14-mm-diameter arch punch was used to excise an unconsumed sample of phloem and the outer 3 mm of sapwood. Phloem thickness was measured at 10× magnification, and the wet weights of the phloem and sapwood were measured before and after drying for 72 h at 60 °C. Percent phloem and sapwood moisture were calculated as a percent of oven dry weight ((wet weight – dry weight)/dry weight × 100). Percentages over 100 mean that there is more water by weight than dried tree tissue.

2.5. Supercooling Points

Supercooling points were determined using the methods of Bleiker and Smith [33]. In brief, each larva was secured with vacuum grease to an AWG30 Type T thermocouple inserted in a shell vial secured in a 13-mm × 100-mm test tube. The test tubes were immersed in a Glacier G50 ethanol bath controlled by a Haake PC200 circulator (Thermo Fisher Scientific, Waltham, MA, USA). The bath was cooled at a rate of 1 °C per minute starting from 15 °C or 5 °C for insects originating from 20.5 °C or 0.5 °C treatments, respectively. The temperature of each larva was recorded every second by a USB TC-08 data logger (Pico Technology, Cambridgeshire, UK). The SCP was taken as the lowest temperature preceding the exothermic reaction associated with the heat of crystallization [34–36].

2.6. Statistical Analyses

We used logistic regression to test if the likelihood of successful gallery establishment varied with tree species. One-way analysis of variance (ANOVA) tests were used to assess the effect of host species on the following dependent variables: gallery length, brood per gallery, brood per centimeter of the gallery, development index, supercooling capacity, phloem thickness and moisture, and sapwood moisture. Given there was no expectation of a within-tree log effect for logs cut from the main portion of a tree trunk and data were collected for each beetle pair, the beetle pair formed the experimental unit [16,17,24,25]. We also performed an analysis of covariance (ANCOVA) to test for an effect of host species on the index of mountain pine beetle development while controlling for gallery length. Female beetles lay eggs as they extend the gallery; thus, gallery length and ovipositional period are positively correlated, and the length of the ovipositional period will affect the distribution of life stages. A two-way ANOVA was used to test for an effect of host species and sex on adult beetle size; the interaction between host species and sex was not significant, and the reduced model was presented. Significant tests were followed by Tukey's honestly significant difference test. Variation in adult sex ratio among host tree species was tested using a binomial generalized linear model. Significance was set at 0.05 for all tests. The two-way ANOVA was performed in JMP Software (Version 15.0, SAS Institute, Cary, NC, USA), and all other analyses were conducted using R (Version 4.1.2, R Core Team, Vienna, Austria, [37]), using *ggplot2* [38] for visual assessments of data.

3. Results

3.1. Gallery Success and Productivity

We found that approximately half of the beetle pairs produced offspring, and host species had no effect on the likelihood of a gallery being successful ($\chi^2 = 0.35$, $df = 2$, 82, $p = 0.84$) (Table 1). For the unsuccessful pairs that failed to produce offspring, half exited the bark without initiating a gallery, and the other half constructed galleries less than 5 cm long and then exited the bark. Females in successful galleries usually laid the first egg within 3 to 6 cm of the start of the gallery. The length of successful galleries varied with tree species ($F = 13.0$, $df = 2$, 38, $p < 0.0001$). Beetles constructed longer egg galleries in lodgepole pine than in jack pine and spruce ($p \leq 0.05$) (Table 1). The number of broods

per successful gallery varied with host species ($F = 6.4$, $df = 2, 38$, $p = 0.004$), with a lower number of broods per gallery produced in jack pine compared to either spruce or lodgepole pine ($p \leq 0.05$). Similarly, the number of brood per centimeter of gallery varied with host species ($F = 8.7$, $df = 2, 38$, $p < 0.001$), and more brood were produced per centimeter of the gallery in spruce compared to either lodgepole pine or jack pine ($p \leq 0.05$).

Table 1. Summary of performance measures used to assess the suitability of lodgepole pine, jack pine, and spruce for mountain pine beetle.

Host Species	No. Pairs	Successful Galleries (%) ¹	Average (SE) Gallery Length (cm) ²	Average (SE) No. Brood/Gallery ²	Average (SE) No. Brood/cm of Gallery ²	Average (SE) Pronotal Width of Brood Adults (mm)
						Female/Male
Lodgepole pine	26	54	38.2 (5.1) a	38.4 (6.1)	1.0 (0.1) a	1.97 (0.02)/1.76 (0.04) a
Jack pine	35	49	11.3 (2.4) b	15.1 (5.0)	1.1 (0.2) a	2.01 (0.01)/1.82 (0.02) a
Spruce	22	45	22.8 (4.5) b	50.3 (11.8)	2.1 (0.3) b	1.90 (0.02)/1.69 (0.05) b

Means in the same column with different letters are significantly different (ANOVA, followed by Tukey's honestly significant difference test, $p \leq 0.05$). ¹ A successful gallery is one in which one or more offspring are produced by the introduced pair of beetles; performance measures in this table refer to successful galleries. ² Determined after 40 day at 20.5 °C. See text.

3.2. Development

After 40 day at 20.5 °C, the most common life stage was pupae in jack pine but fourth-instar larvae in lodgepole pine and spruce (Figure 2). While controlling for gallery length, the development index of the mountain pine beetle differed among host species ($F = 28.9$, $df = 2, 38$, $p < 0.001$); the interaction between host species and gallery length was not significant ($F = 1.0$, $df = 2, 35$, $p = 0.40$). We simplified the model by combining the two pine species and found no reduction in the explanatory power of the simplified model ($F = 2.9$, $df = 2, 38$, $p = 0.10$). This supports a similar rate of mountain pine beetle development in lodgepole pine and jack pine and slower development in spruce (Figure 3). Interestingly, we noted greater discoloration of tree tissues around galleries in lodgepole pine and jack pine compared to in spruce, but the amount of discoloration was not quantified (Figure 1).

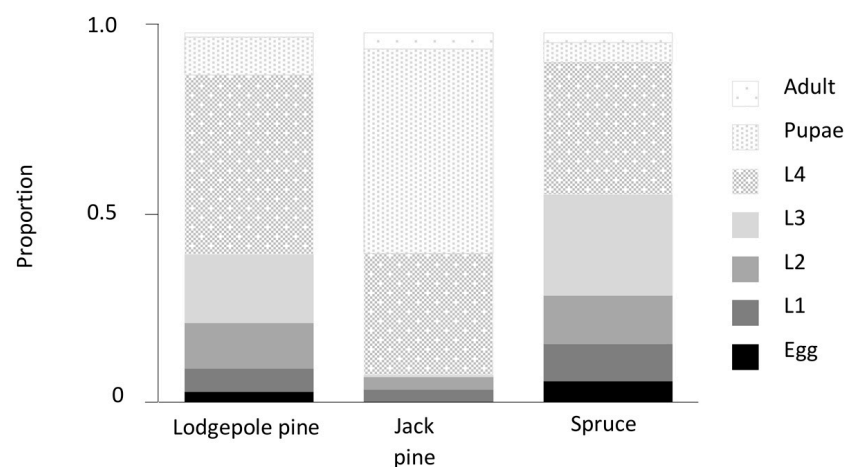


Figure 2. Proportion of mountain pine beetles in each life stage after developing for 40 day at 20.5 °C in lodgepole pine, jack pine, and spruce logs.

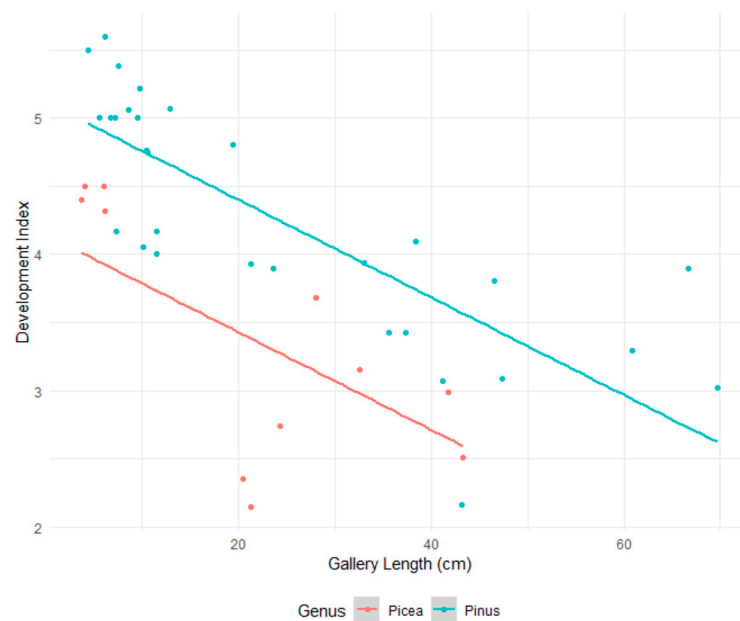


Figure 3. Development index of mountain pine beetle as a function of gallery length and host genus after 40 day or development at 20.5 °C.

3.3. Cold Tolerance of Larvae

The SCP of late-instar larvae reared for 27 day at 20.5 °C did not vary by host species ($F = 2.1$, $df = 2, 62$, $p = 0.13$) and ranged from a mean (\pm SE) of -12.7 °C (± 0.1) in lodgepole pine to -13.5 °C (± 0.4) in jack pine. After acclimating at 0.5 °C for 50 day, the SCP of larvae varied by host species ($F = 10.0$, $df = 2, 55$, $p < 0.001$). The SCP of larvae reared in spruce (-14.3 °C [± 0.5]) was warmer than for larvae reared in either lodgepole pine (-16.6 °C [± 0.5]) or jack pine (-17.4 °C [± 0.05]) ($p \leq 0.05$). Similarly, after 70 day at 0.5 °C, the SCP of larvae varied by host species ($F = 10.0$, $df = 2, 34$, $p < 0.001$), with the SCP of larvae reared in lodgepole pine (-18.0 °C [± 0.5]) and jack pine (-17.3 °C [± 0.5]) being similar ($p > 0.05$) and lower than for larvae reared in spruce (-14.0 °C [± 0.3]) ($p \leq 0.05$). Mortality throughout the experiment was negligible in lodgepole pine and jack pine; however, after 70 day at 0.5 °C, we noted low survival of late-instar larvae in spruce. While collecting 16 living late-instar larvae from spruce for SCP determination, we counted 95 dead late-instar larvae.

3.4. Adult Size and Sex Ratio

Adult beetle size varied among all three host species, with jack pine producing the largest beetles, followed by lodgepole pine and then spruce ($F = 19.6$, $df = 2, 414$, $p < 0.001$) (Table 1). Female beetles were larger than males ($F = 132.2$, $df = 1, 414$, $p < 0.001$). For beetles that emerged, the ratio of females to males was 1:1 in lodgepole pine and spruce but 1:0.6 in jack pine, with the effect of host species approaching significance ($\chi^2 = 5.7$, $df = 2, 415$, $p = 0.06$).

3.5. Phloem Thickness and Moisture Content

Phloem thickness varied among tree species ($F = 23.4$, $df = 2, 6$, $p = 0.001$) and was thicker in spruce compared to either lodgepole pine or jack pine ($p \leq 0.05$). The mean (\pm SE) phloem thickness of spruce, lodgepole pine, and jack pine used in our study was 4.7 mm (± 0.6), 1.3 mm (± 0.3), and 1.6 mm (± 0.1), respectively. Phloem moisture content also varied with the host ($F = 19.2$, $df = 2, 6$, $p = 0.002$), being lower in spruce compared to either lodgepole pine or jack pine ($p \leq 0.05$). The mean (\pm SE) phloem moisture content of spruce, lodgepole pine, and jack pine was 170% (5), 221% (± 10), and 241% (± 9), respectively. Finally, sapwood moisture content also varied with the host ($F = 24.3$, $df = 2, 6$, $p = 0.001$) and was lower in jack pine compared to either lodgepole pine or spruce ($p \leq 0.05$). Mean

(\pm SE) sapwood moisture content for jack pine, lodgepole pine, and spruce was 124% (± 3), 172% (± 11), and 187% (± 4), respectively.

4. Discussion

Mountain pine beetle successfully completed development in all three tree species, but our results indicate that lodgepole pine was likely overall the most suitable host. The chemical and physical properties of trees affect their suitability as hosts for bark beetles. Dispersing beetles use tree volatiles to locate potential hosts, and initial beetles that arrest on trees may further assess their suitability using gustatory cues (e.g., [39,40]). Trees have constitutive resin defenses to resist attack by bark beetles and their microbial symbionts, as well as an induced response that includes the formation of traumatic resin ducts and secondary resinosis. The density of attack needed to overwhelm host resistance is positively correlated with host vigor (e.g., [41]). Furthermore, some chemical components of the resin defense systems, e.g., terpenes, serve as precursors or synergists for the beetle's semiochemical communication system [31]. Beetles also carry a suite of associated microorganisms, including ophiostomatoid fungi (Ophiostomatales: Sordariomycetidae, Microascales: Hypocreomycetidae), into host trees [42]. Blue-staining fungi may play a role in the host colonization process, neutralizing host defensive chemistry and promoting semiochemical communication, in addition to providing nutritional benefits to developing broods (e.g., [43–52]). Host suitability is also affected by the characteristics of the phloem and sapwood. Mountain pine beetle preferentially attacks large-diameter trees because they tend to have relatively thick phloem and a higher volume of sapwood, which helps retain moisture over the life cycle of the beetle [reviewed in 39]. The egg lay per centimeter of the gallery, adult size, and other fitness metrics are positively related to phloem thickness in lodgepole pine, and female beetles will abandon trees if they become too dry or the phloem is too thin.

Performance measures for mountain pine beetle developing in lodgepole pine and jack pine were similar, with two exceptions, which indicated that lodgepole pine was the superior host. First, productivity per female was higher in lodgepole pine than in jack pine because egg galleries were three times longer in the historical host. Second, the sex ratio of emerging adults was balanced in lodgepole pine but tended towards favoring females in jack pine, and a female-biased sex ratio is indicative of a stressed population [39]. The rate of development appeared to be faster in jack pine than in lodgepole; however, there was no difference once the effect of gallery length was considered, indicating that an earlier end to the ovipositional period in jack pine led to a higher proportion of older life stages. Previous studies reported that the suitability of lodgepole pine and jack pine was either similar for mountain pine beetle or that lodgepole pine was more suitable [16,17,19,20,53]. Rosenberger et al. [19,53] reported faster development in novel hosts compared to historical hosts; however, the effect of gallery length (ovipositional period) on development rate was not considered. Our results indicate that what initially appears to be faster development in the novel host can be attributed to a shorter ovipositional period. The reasons for reduced performance on jack pine are unknown; tree defenses should be largely negated in cut logs, but we cannot rule out latent effects related to tree chemistry. Lodgepole and jack pine are closely related species with similar chemical components, but the amount and ratios of the various compounds vary (e.g., [31,54,55]). We also noted that the phloem and sapwood were stained darker in jack pine than in lodgepole pine (Figure 1), suggesting a difference in colonization by microbial symbionts. The color of the lodgepole pine was more typical of what we have observed in logs and naturally attacked trees in the past; however, we did not sample the microbes in tree tissues. There is evidence from experiments using monoterpene-amended media or small squares of phloem that differences in tree chemistry can affect the growth of mountain pine beetle's microbial associates, which may affect beetle performance [49,52].

We attribute the surprisingly high number of eggs laid per centimeter of the gallery in spruce to its thick phloem. However, there was evidence of a latent negative effect for

insects developing in spruce that may be due to the chemical or physical properties of spruce. During outbreaks, mountain pine beetle occasionally attacks non-*Pinus* species within the Pinaceae, e.g., Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; true firs, *Abies* spp.; larch, *Larix* spp.; and spruce, *Picea* spp., when they are proximate to pine hosts undergoing a simultaneous mass attack, but infestations are not maintained in these species (e.g., [13,14,23,25,26,56]). Attack on non-*Pinus* spp. is thought to occur due to high levels and local diffusion of aggregation pheromones caused by high-density mass attacks on nearby pine hosts that lead to some responding beetles arresting on, and attacking, adjacent non-*Pinus* trees (e.g., [13,39]). Attack and reproduction on non-*Pinus* spp. are rare, but there are several notable reports for *Picea* spp. [13,14,23,25,26,56]. The ability of mountain pine beetle to reproduce in spruce may be due to similarities in chemistry, given they are in the Pinaceae (see [26] and references therein). There is also evidence that mountain pine beetle may benefit from both lower intraspecific [26] and interspecific competition [25] by attacking spruce. In fact, Huber et al. [26] reported higher productivity in two naturally-infested spruce trees compared to two nearby pine trees due to the latter having extraordinarily high attack densities and intraspecific competition. However, when pairs of spruce and pine trees were baited with mountain pine beetle's aggregation pheromones, beetles only successfully reproduced on the pine, causing the authors to posit that spruce is avoided due in part to challenges related to overwhelming its defenses. Cut logs have compromised defenses, which would explain why introduced beetles initiated galleries on spruce [57]. Chemical and nutritional characteristics of spruce phloem may have accrued over time, resulting in lower cold tolerance, high mortality (~83%) at a benign temperature (0.5 °C), and smaller brood adults. Some ophiostomatoid fungal associates of mountain pine beetle are known to provide nutritional benefits to developing beetles, e.g., nitrogen and ergosterols, which can be important for growth, metamorphosis, and cold survival (e.g., [46,47,51]). Interestingly, there was limited discoloration of tree tissues around mountain pine beetle galleries in spruce after 40 d, suggesting a potential lack of microbial symbionts (Figure 3). We know that the main ophiostomatoid fungal associates of mountain pine beetle are capable of colonizing spruce trees because they have been recovered from phloem and sapwood tissues near Lac le Jeune, British Columbia, the year following the attack (K.P. Bleiker, unpub. data). However, the rate at which spruce tissues are colonized by microbes after the attack is unknown, and we hypothesize that it may be delayed in spruce, affecting insect development.

5. Conclusions

Our results contribute to a growing body of knowledge that will help assess the threat of mountain pine beetle expanding its range eastwards in jack pine through Canada's boreal forest. Results from *Pinus* and non-*Pinus* hosts help to further our understanding of host use and limitations in bark beetles that may lead to speciation events within the genus *Dendroctonus*. We demonstrate that the putatively faster development of mountain pine beetle in the novel host jack pine is likely due to a negative interaction with the host and early cessation of oviposition rather than a faster rate of development. The chemical and physical characteristics of different tree species can vary over space and time, yet most assessments (but see [17]) of host suitability for mountain pine beetle have been limited to one to several trees per species from one population at one point in time. However, each study provides an incremental increase in knowledge and, taken together, helps to move our understanding forward. There is substantive evidence that jack pine is a suitable host for the mountain pine beetle; however, there is emerging evidence and growing uncertainty if the mountain pine beetle's reproductive potential will be as high in this novel host as in lodgepole pine.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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