Consequences of distributional asymmetry in a warming environment: invasion of novel forests by the mountain pine beetle

JORDAN LEWIS BURKE1,†, JOERG BOHLMANN,1,2 AND ALLAN L. CARROLL1

1Department of Forest and Conservation Sciences, Faculty of Forestry, The University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada
2Michael Smith Laboratories, The University of British Columbia, 2185 East Mall, Vancouver, British Columbia V6T 1Z4 Canada

Citation: Burke, J. L., J. Bohlmann, and A. L. Carroll. 2017. Consequences of distributional asymmetry in a warming environment: invasion of novel forests by the mountain pine beetle. Ecosphere 8(4):e01778. 10.1002/ecs2.1778

Abstract. The range of many Holarctic forest insects does not comprise the entire range of their hosts, as they are often limited to more southern latitudes by the adverse effects of cold temperatures. Global climate warming has led to the increased potential for forest insects to invade novel habitats of native hosts within the same landmass. The mountain pine beetle (MPB; Dendroctonus ponderosae) has recently expanded into higher-latitude forests of the principal host, lodgepole pine (Pinus contorta var. latifolia), and the susceptibility of trees is greater in these systems compared to forests in the native range. We assessed the contribution of the induced defensive response of hosts to this elevated susceptibility, and whether these discrepancies are the result of coevolution with host populations within the historic native range of the insect. We challenged trees using paired treatments of a beetle-attack simulation and a generic defensive response elicitor (methyl jasmonate) to mitigate variability in the induced response among trees within and among populations, from within and outside the historic range of the beetle. We then assessed the production of monoterpenic chemicals by the trees in response to treatments using gas chromatography/mass spectrometry. The differential induction of monoterpenes in response to simulated beetle attack relative to the generic elicitor was highest in populations with the highest putative historic exposure to MPB. Elevated susceptibility and invasion potential of the beetle in novel systems is the proximate result of reduced defensive capacity, ultimately arising from a lack of coevolution with the beetle in novel systems. In forested systems with climate-driven herbivore–host distributional asymmetry, continued warming will potentially exacerbate the impacts of aggressive insect herbivores as they invade defensively naïve host populations.

Key words: climate change; invasion biology; lodgepole pine; mountain pine beetle; range expansion.

Received 6 March 2017; accepted 9 March 2017. Corresponding Editor: Debra P. C. Peters.
Copyright: © 2017 Burke et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: jordan.lewis.burke@gmail.com

INTRODUCTION

Introductions of invasive insect species have been increasing exponentially across the world as a consequence of anthropogenic climate change and globalization (Mattson et al. 1994, Liebhold et al. 1995, Hulme 2009, Ramsfield et al. 2016). Within climatically and geographically suitable habitats, the ability of an invasive insect herbivore to establish is influenced by interspecific interactions, host-plant defense potential, and biological traits of the invading species (Davis 2009, Cullingham et al. 2011, Liebhold et al. 2013, Rochlin et al. 2013, Raje et al. 2016). The invasive potential of insect herbivores is often enhanced in new habitats where they encounter both enemy- and defense-free space, resulting from a lack of coevolutionary association with those elements of the invaded habitats (Jeffries and Lawton 1984, Gandhi and Herms 2010). As a consequence of missing or ineffective population regulators, invasive arthropods can have devastating consequences on invaded
habitats and lead to cascading effects at multiple trophic levels (MacFarlane and Meyer 2005, Poland and McCullough 2005, Hanula et al. 2008, Gandhi and Herms 2010, Burke et al. 2011, Herms and McCullough 2014).

Global climate change has affected species from all taxonomic groups, often in the form of altered ranges (Parmesan and Yohe 2003, Parmesan 2006). Terrestrial ectothermic organisms are particularly susceptible to variations in weather and climate due to their sensitivity to temperature (Musolin 2007, Deutsch et al. 2008, Jönsson et al. 2009), and throughout the Holarctic region, the effects of climate warming on herbivorous insects have often resulted in range expansions into previously thermally unsuitable habitats (Parmesan et al. 1999, Carroll et al. 2004, Battisti et al. 2005, Hickling et al. 2005, 2006, Hagen et al. 2007). Rapid range expansion in response to climate change may result in novel herbivore–host interactions, potentially exacerbating herbivore impacts and accelerating range shifts due to weakly coevolved or evolutionarily naïve host defenses (Braschler and Hill 2007, Cudmore et al. 2010, Raffa et al. 2013).

Mountain pine beetle (Dendroctonus ponderosae Hopkins; MPB hereafter) is an exceptional example of climate-induced range expansion by an insect herbivore (Carroll et al. 2004, Sambaraju et al. 2011). Post-glacial recolonization of western North America by MPB and its principle host lodgepole pine (Pinus contorta var. latifolia Douglas) has led to significant distributional asymmetry between herbivore and host trees. The population genetic structure of MPB indicates a gradual expansion northward (Mock et al. 2007, Bentz et al. 2010), which lagged behind the earlier, post-glacial expansion of lodgepole pine (Wheeler and Guries 1982, MacDonald and Cwynnar 1985, Cwynar and MacDonald 1987). In recent history, MPB has been restricted to western North America south of 56° N (reviewed by Safranyik and Carroll 2006), whereas lodgepole pine stretches north to ~64° N and east of the Rocky Mountains to ~115° W (Farrar 1995). This suggests that forests north and/or east of the historic MPB range have been under no evolutionary selection pressure from beetle attacks and that the recent range expansion by MPB, both within the range of lodgepole pine and into novel host types, comprises an invasion of novel habitats.

Constitutive and induced defensive resin in novel lodgepole pine populations is different when compared to lodgepole pine trees in the native range (Clark et al. 2010, 2014), and reduced defensive capacity has been suggested as the proximate cause of higher MPB attack densities (Clark et al. 2010) and productivity (Cudmore et al. 2010), and higher rates of spread and impact by outbreak populations (Robinson 2015) in novel habitats. However, previous studies comparing the induced reactions of putatively experienced and naïve host populations (Clark et al. 2010, 2014, Raffa et al. 2013) have not explicitly tested whether the ultimate cause of reduced defensive capacity is a lack of coevolution with MPB, having not controlled for variation among individual trees and populations of trees arising from environmental conditions. Moreover, earlier studies have been further limited by either restricting their assessments to (1) simple wounding without simulating MPB attacks (Clark et al. 2010, 2014) or (2) a single population of host trees (Raffa et al. 2013).

Mountain pine beetle must kill all or part of their host to reproduce (Safranyik and Carroll 2006), and variation in the induction of monoterpane defenses has been shown to be the primary determinant of susceptibility to MPB-induced mortality for individual lodgepole pine trees (Raffa and Berryman 1982, Boone et al. 2011). Given the expectation of intense selective pressure by MPB on host trees, we conducted an extensive field study to critically evaluate the hypothesis that prolonged exposure to epidemic MPB has selected for a specific induced response to attack. If this hypothesis is correct, we predicted that the quantity of induced monoterpenes expressed in response to simulated MPB attack, relative to a generic defensive response elicitor, will increase in lodgepole pine populations with increasing historical exposure to epidemic MPB impacts.

**METHODS**

**Experimental sites**

Estimates of historic climatic conditions (Safranyik et al. 1975, Carroll et al. 2004) were used as a proxy for the degree of evolutionary association between MPB and populations of lodgepole pine. Classes of climatic suitability (very low, low, moderate, high, extreme) are derived from calculations of the joint likelihood of four conditions shown to
be critical to the establishment and persistence of MPB populations (Safranyik et al. 1975): a univoltine life cycle, temperatures favorable for overwinter survival, optimal emergence and dispersal conditions, and the quantity/variability of spring precipitation as an estimate of relative tree defensive capacity. Maps of historic climatic suitability classes (HCSCs) for western Canada were produced using BioSIM (Régnière 1996, Régnière et al. 2014), and historic weather records from the Environment Canada Meteorological Service for the period 1941–1970 (Carroll et al. 2004). This period precedes any significant change in climatic suitability associated with climate change (Carroll et al. 2004) while maximizing the number of available reporting weather stations for the calculation of HCSC.

In July of 2014, two stands from four populations of lodgepole pine in western Canada were selected representing the widest range of HCSC possible (eight total sites; Fig. 1, Table 1). Due to the magnitude of the recent MPB outbreak in western Canada (Safranyik et al. 2010) and subsequent salvage logging, usable stands that fell in the “extreme” HCSC (sensu Carroll et al. 2004) could not be located. In each population, two sites (i.e., stands) were selected that met the following criteria: ≥5 km from each other, >50% lodgepole pine in the overstory, at least 25 individuals >20 cm diameter at 1.3 m height, no current MPB
activity, and equivalent HCSC. The mensurational characteristics of each site (tree density, basal area, proportion basal area of lodgepole pine) were assessed using three randomly positioned, 100 m² fixed radius plots, in which all trees >7.5 cm diameter at 1.3 m were considered. In each stand, 11 lodgepole pine trees were selected for analysis (n = 88 total trees), with a clear, one-stem bole, and no apparent evidence of disturbance by biotic or abiotic stressors. Each tree was at least 2 m from another experimental tree, and none were selected near or adjacent to an edge.

**Experimental treatments**

Assessments of variation in tree defenses in response to subcortical challenges often encounter enormous inter-tree variability, making it difficult to isolate and identify treatment effects (Raffa and Smalley 1988, 1995, Miller et al. 2005, Clark et al. 2014). To control for inter-tree variation and allow direct comparison of treatment effects among sites, we exploited the propensity for *Pinus* species to respond to minor wounding through localized reactions, rather than systemic physiological alterations (Raffa and Smalley 1988, Wallin and Raffa 1999). Paired MPB-simulation and generic treatments were applied to each tree allowing the difference of the two to be assessed as the treatment effect, thereby equalizing the potential influences of inter-tree variation.

Mountain pine beetle-simulation comprised a mechanical wound combined with a single inoculation of the beetle’s fungal symbiont *Grosmannia clavigera* (Robinson-Jeffrey & R. W. Davidson), isolated from lodgepole pine trees harvested in Alberta, Canada, in 2011 near Grande Prairie (55.16 N, 118.80 W; D. Alayon and R. Hamelin, *unpublished data*). Application of this fungus as an analog for MPB attack is an established method which elicits a reaction similar to attacks by live beetles (Raffa and Berryman 1982, 1983a, Wallin and Raffa 1999, Boone et al. 2011). Fungus was propagated on petri plates in malt extract agar (Fisher-Scientific, Ottawa, Ontario, Canada) two weeks prior to field assays, and kept at 5°C until 24 h before use, at which time plates were removed from cold storage and stored at ambient temperature to allow growth to potentially resume.

Generic response treatments were achieved with a similar application of methyl jasmonate (MEJA), a phytohormone that is involved in the induced defensive response of all plants (Creelman and Mullet 1997) and has been used extensively to examine the defensive response of conifers (Francesschi et al. 2002, 2005, Martin et al. 2002, Hudgins et al. 2003,Zeneli et al. 2006, Graves et al. 2008, Krokene et al. 2008, Zulak and Bohlmann 2010). A MEJA solution was prepared by mixing MEJA (95% purity; Sigma-Aldrich) with Tween 20 (Sigma-Aldrich, St. Louis, Missouri, USA) in water both at 0.1% v/v concentration (Hudgins et al. 2003) and was stored at 5°C until use.

**Treatment application**

At each tree, a random cardinal direction was selected and MPB-simulation treatment was applied at breast height (1.3 m). Methyl jasmonate treatment was applied at the same time to the same tree at breast height on the opposite side of the bole. All treatments were applied with high-carbon steel tools sterilized and cleaned with 100% ethanol between each use. A 1-cm
round disk of outer bark and phloem was removed using a leather punch (C.S. Osborne, Harrison, New Jersey, USA). To apply the fungal treatment, a 1.0 cm² piece of agar from the petri dish was packed into the wound site. To apply MEJA treatment, a small piece of sterile dentist cotton was packed into the hole, and ~0.5 mL of MEJA solution was applied to the cotton using a syringe. During application, if discolored phloem or xylem tissue was discovered, a new punch was taken 10 cm to the right of the original, as this would be indicative of an existing lesion and unhealthy tissue, likely resulting from an infection. If clear, white phloem and xylem tissues were not found after three attempts, the tree was abandoned. The treatment areas were then wrapped tightly in plastic kitchen wrap and then again with cloth duct tape to keep the treatment materials in place and minimize the potential for contamination of the wound site. After four days, the plastic wrap and tape were removed. Samples from the treated trees were collected and handled using the methods of Raffa et al. (2013). Using a chisel, a 2 cm wide by 5 cm tall section of phloem was removed, with the center of the section being the wound site. Samples were placed on dry ice in the field, transported to the University of British Columbia in Vancouver, British Columbia, Canada, and stored at −35°C until processing.

**Chemical analyses**

Samples were removed from cold storage and prepared for chemical analysis. All tools and surfaces were cleaned and sterilized using 99.5% acetone (Fisher-Scientific) between every use. Using a razor blade, any outer bark was excised and discarded, and a portion of phloem directly above the wound site (closest to the crown) was removed. The dissected sample was sliced into ~1 mm thick strips, mixed, and then evenly distributed between three vials creating technical replicates. Each vial was filled with 1.3 mL of tert-butyl methyl ether (Fisher-Scientific), with 75 ppm isobutyl benzene (IBB; Sigma-Aldrich) as an internal standard. Vials were placed on a shaker table at room temperature for 24 h; then, 1 mL of each sample was transferred to a new vial containing 200 µL of 100 mmol/L ammonium carbonate aqueous solution and mixed to remove polar contaminants. Vials were centrifuged and stored at −35°C until GC/MS (gas chromatography/mass spectrometry) analysis. Monoterpene concentrations were calculated with an Agilent 6890 Gas Chromatograph 5973 Mass Spectrometer, using an Agilent DB-WAX column (J&W [Agilent, Santa Clara, California, USA] 122-7062, 60 m, 0.25 mm, 0.25 µm). The dry mass of each dissected sample varied with phloem thickness, with an average of 205 mg and a range of 80–300 mg.

To determine whether the stereochmical configuration of monoterpenes differed among lodgepole pine populations, a random subsample of three trees from each site was selected to assess stereochmical ratios of chiral monoterpenes that comprised >1% of the total: α-pinenes, β-pinenes, 3-carenes, limonenes, and β-phellandrenes. Samples of phloem from MPB-simulation treatments were excised and prepared in the same manner as above, but without the use of technical replicates. An Agilent CycloDEX-B column (J&W [Agilent, Santa Clara, California, USA] 112-2532, 30 m, 0.25 mm, 0.25 µm) was used for chiral analyses. The ratio [expressed as (−):(+) of each chiral pair of monoterpenes was then calculated, and these were compared among populations of lodgepole pines.

**Statistical analyses**

All data were prepared using Microsoft Excel version 16.0 (Microsoft, Redmond, Washington, USA, 2016), and all statistical tests were performed using R version 3.3.1 (R Core Team, Vienna, Austria, 2016). Technical replicates were averaged for each biological replicate (Hall et al. 2011, 2013a, 2013b, Schmidt et al. 2011), and the total concentration of monoterpenes (mg/g) expressed in response to MPB-simulation and MEJA treatments, and the absolute and relative concentrations of monoterpene constituents that comprised >1% of the total were calculated for each tree. To test our prediction that the quantity of induced monoterpenes expressed in response to simulated MPB attack, relative to a generic defensive response elicitor, will increase in lodgepole pine populations with increasing historical exposure to epidemic MPB, we calculated the difference in concentration of monoterpenes in response to the two treatments for each tree. Differences were calculated by subtracting the absolute concentration of monoterpenes (totals and individual constituents) expressed in response to MPB-simulation, from the concentration expressed in response...
to MEJA treatment for each tree (n = 88). This “differential concentration” enabled assessment of the specificity of the induced defensive response to MPB attack while controlling for among-tree and site variability. Differential concentrations greater than zero indicate a specific response by trees to MPB attacks.

All data were tested for normality and homogeneity of variances. Stereochemical ratio, proportional basal area, and relative monoterpenoid abundance were arcsin(square-root)-transformed to account for the truncated distribution of proportion data (Dowdy et al. 2004). Differential concentrations, chiral ratios, and mensurational characteristics were analyzed using a mixed-effects analysis in R (function = lme; packages = lmerTest, lme4), where the fixed effect of HCSC determined the specificity of the induced reaction between treatments. The random effect of site (n = 8), nested within HCSC, was included to account for spatial autocorrelation among trees within each stand. Post hoc comparison of means using Tukey’s HSD was made to determine significant differences among the four levels of HCSC.

RESULTS

During treatment applications, discolored or lesioned phloem was rarely encountered (two to three trees per stand), and only three trees in total were discarded in favor of neighboring trees. The plastic wrap and duct tape covering were effective in preventing treatment site exposure or contamination, and none were disturbed.

Mensurational characteristics were equivalent among the lodgepole pine populations considered in our study (Table 2). Stem density, total basal area, proportion basal area occupied by lodgepole pine and non-host species, and the diameter of experimental trees did not vary among HCSC ($P > 0.05$; Table 2).

The stereochemistry of induced monoterpenes was also consistent among lodgepole pine populations. Of the chiral monoterpenes considered, only $\alpha$-pinenes were present in both stereoisomers. There were no detectable concentrations of $(+)$-$\beta$-pinene, $(-)$-3-carene, $(+)$-limonene, or $(+)$-$\beta$-phellandrene. The mean ratio, $(-)$:$(+)$, of $\alpha$-pinenes $[\pm$SE] was 2.25 [0.03], and there was no effect of population on the chirality ($F_{3,16} = 0.08, P = 0.97$).

The differential expression of monoterpenes associated with the simulated MPB challenge and the generic defense elicitor differed among lodgepole pine populations. The differences in the absolute concentration of all induced monoterpenes that were expressed in response to MPB were dependent on HCSC ($F_{3,86} = 9.56, P = 0.027$). However, the influence of historic climatic suitability on the specificity of the defensive response to MPB was only evident in the “high” HCSC; total monoterpenoid production by trees in response to the simulated MPB challenge and the MEJA application did not differ in the “very low,” “low,” and “moderate” HCSCs (Fig. 2).

In addition to differences in the quantitative expression of total induced monoterpenes in relation to the putative degree of historic exposure to MPB, the differential induced response also varied qualitatively among lodgepole pine populations. The differential induction of $(-)$-$\beta$-pinene, sabine, myrcene, $\alpha$-phellandrene, $(-)$-limonene,

Table 2. Mensurational characteristics of eight lodgepole pine (Pinus contorta var. latifolia) stands assessed for the specificity of their defensive response against the mountain pine beetle (Dendroctonus ponderosae).

| Region     | Site | Trees/ha $[\pm$SE] | Total basal area (m$^2$/ha) $[\pm$SE] | Proportion lodgepole pine basal area $[\pm$SE]† | Mean lodgepole pine diameter (cm) at 1.3 m $[\pm$SE] |
|------------|------|-------------------|--------------------------------------|---------------------------------------------|---------------------------------------------|
| Merritt    | 5    | 1466 [240]        | 31.88 [4.22]                         | 0.83 [0.04]                                 | 23.5 [1.02]                                 |
|           | 6    | 2700 [585]        | 48.22 [6.38]                         | 0.99 [0.10]                                 | 26.7 [0.98]                                 |
| Baldy Mountain | 1   | 933 [202]         | 25.44 [5.48]                         | 0.82 [0.08]                                 | 24.3 [0.87]                                 |
|           | 2    | 533 [240]         | 15.26 [6.80]                         | 0.92 [0.04]                                 | 23.8 [0.69]                                 |
| Tumbler Ridge | 7   | 1866 [463]        | 57.09 [12.8]                         | 0.96 [0.09]                                 | 26.8 [1.07]                                 |
|           | 8    | 2166 [448]        | 48.89 [7.14]                         | 0.62 [0.09]                                 | 26.9 [1.05]                                 |
| Hinton     | 3    | 1400 [208]        | 46.75 [5.55]                         | 1.00 [0.03]                                 | 27.8 [0.95]                                 |
|           | 4    | 1300 [305]        | 41.73 [3.53]                         | 0.95 [0.04]                                 | 28.8 [1.07]                                 |

† Non-lodgepole pine basal area comprised Douglas-fir (Pseudotsuga menziesii), subalpine fir (Abies lasiocarpa), spruce (Picea spp.), larch (Larix spp.), and trembling aspen (Populus tremuloides).
and (−)-β-phellandrene varied among HCSCs ($F_{3,86} = 7.45–13.25$, $P < 0.05$; Tables 3, 4), whereas there was no significant influence of historic exposure to MPB on the expression of α-pinene, (+)-3-carene, or terpinolene ($F_{3,86} = 3.53–6.24$, $P > 0.05$; Tables 3, 4). Similar to the differential expression of total monoterpenes concentrations, the influence of historic climatic suitability for MPB on the specificity of the induction of individual monoterpenes was only evident in the “high” HCSC (Fig. 3).

**DISCUSSION**

Post-glacial asymmetric recolonization of western North America has caused MPB to select for the expression of a specific induced defensive response in populations of lodgepole pine with long-term association with its herbivory, but not in putatively naïve host populations. Rapid and concentrated accumulation of monoterpenes is the primary source of variability in resistance to MPB among lodgepole pine trees (Raffa and Berryman 1982, Boone et al. 2011), and our results show that this trait is enhanced in response to MPB in populations with the greatest degree of historic exposure to MPB. Lack of a strong or specific induced response by evolutionarily naïve lodgepole pines is likely the proximate cause of observed enhanced performance by MPB in newly invaded habitats (Clark et al. 2010, Cudmore et al. 2010, Robinson 2015), ultimately due to a lack of coevolution with MPB, which is the primary tree-killing biotic agent in lodgepole pine forests (Safranyik and Carroll 2006).

The determination of specificity in induced response is made possible by the calculation of differential concentrations. Most often, experiments
designed to compare the induced reaction of trees among populations do so by applying one experimental treatment to individual trees within a stand, and compare the stand-level means among treatment groups (e.g., Raffa and Berryman 1982, Boone et al. 2011, Clark et al. 2014, Raffa et al. 2013). However, neighboring trees may express significantly different concentrations of chemicals for a variety of reasons unrelated to treatments, such as water stress (Lewinsohn et al. 1993, Klepzig et al. 1995). By treating each tree with both treatments, our method calculates treatment effects at the tree level, controlling for inter-tree variation in overall induced response within a stand. The inclusion of MEJA (as opposed to wounding only, as in Clark et al. 2010, 2014) ensures a comparison

Table 3. Mean (SE) monoterpane concentrations (mg/g) expressed in response to mountain pine beetle simulation (MPB) or methyl jasmonate (MEJA) treatments by lodgepole pines (Pinus contorta var. latifolia) from eight stands assessed for the specificity of their defensive response against the mountain pine beetle (Dendroctonus ponderosae).

| Site | Treatment | HCSC | 2-Pinene | β-Pinene | Sabinene | 3-Carene | Myrcene |
|------|-----------|------|----------|----------|----------|----------|----------|
| 4    | MEJA      | Very low | 2.38 [0.35] | 6.03 [1.27] | 0.63 [0.07] | 7.69 [1.48] | 0.95 [0.09] |
|      | MPB       |        | 2.44 [0.42] | 6.01 [1.28] | 0.60 [0.05] | 7.22 [1.30] | 0.92 [0.08] |
| 3    | MEJA      |        | 2.44 [0.31] | 4.15 [1.12] | 0.74 [0.13] | 8.83 [2.72] | 1.11 [0.17] |
|      | MPB       |        | 1.63 [0.20] | 3.29 [1.11] | 0.46 [0.03] | 5.79 [1.16] | 0.79 [0.08] |
| 8    | MEJA      | Low    | 4.77 [2.10] | 3.54 [1.06] | 0.57 [0.10] | 6.95 [1.56] | 0.89 [0.13] |
|      | MPB       |        | 5.60 [3.22] | 3.79 [1.45] | 0.57 [0.04] | 7.71 [1.09] | 0.93 [0.11] |
| 7    | MEJA      |        | 2.68 [0.64] | 2.37 [0.41] | 0.85 [0.25] | 9.69 [1.59] | 0.96 [0.13] |
|      | MPB       |        | 2.02 [0.35] | 2.84 [0.38] | 0.47 [0.04] | 7.09 [0.91] | 0.66 [0.06] |
| 1    | MEJA      | Moderate | 3.23 [0.67] | 8.11 [2.33] | 0.70 [0.10] | 4.48 [1.36] | 1.05 [0.15] |
|      | MPB       |        | 2.96 [0.42] | 6.49 [1.64] | 0.68 [0.06] | 3.95 [1.24] | 1.08 [0.11] |
| 2    | MEJA      |        | 3.55 [0.86] | 5.92 [1.26] | 0.67 [0.08] | 5.52 [1.19] | 1.11 [0.13] |
|      | MPB       |        | 3.25 [0.82] | 5.32 [1.05] | 0.56 [0.05] | 4.69 [0.89] | 1.05 [0.10] |
| 5    | MEJA      | High   | 5.44 [0.71] | 9.42 [2.48] | 1.28 [0.16] | 8.69 [2.44] | 1.89 [0.21] |
|      | MPB       |        | 7.30 [0.72] | 12.52 [2.31] | 1.77 [0.15] | 11.59 [2.14] | 2.59 [0.22] |
| 6    | MEJA      |        | 4.05 [0.54] | 8.72 [1.85] | 1.14 [0.12] | 12.44 [2.89] | 1.52 [0.15] |
|      | MPB       |        | 7.34 [1.23] | 15.24 [3.77] | 2.05 [0.24] | 19.76 [4.14] | 2.62 [0.29] |

Note: HCSC, historic climatic suitability class.

Table 4. Mean (SE) monoterpane concentrations (mg/g) expressed in response to mountain pine beetle simulation (MPB) or methyl jasmonate (MEJA) treatments by lodgepole pines (Pinus contorta var. latifolia) from eight stands assessed for the specificity of their defensive response against the mountain pine beetle (Dendroctonus ponderosae).

| Site | Treatment | HCSC | 2-Phellandrene | Limonene | β-Phellandrene | Terpinolene | Total   |
|------|-----------|------|----------------|---------|----------------|-------------|---------|
| 4    | MEJA      | Very low | 0.71 [0.08] | 1.12 [0.17] | 31.07 [3.23] | 0.99 [0.15] | 51.71 [5.23] |
|      | MPB       |        | 0.71 [0.09] | 1.12 [0.18] | 31.80 [3.59] | 1.00 [0.12] | 51.97 [4.74] |
| 3    | MEJA      |        | 0.76 [0.12] | 2.38 [0.61] | 32.51 [4.90] | 1.19 [0.29] | 54.21 [7.18] |
|      | MPB       |        | 0.49 [0.05] | 1.80 [0.40] | 22.28 [2.10] | 0.88 [0.12] | 37.49 [2.17] |
| 8    | MEJA      | Low    | 0.60 [0.09] | 1.35 [0.31] | 25.81 [3.34] | 0.91 [0.18] | 45.53 [5.67] |
|      | MPB       |        | 0.58 [0.04] | 0.85 [0.06] | 24.95 [1.43] | 1.04 [0.13] | 46.17 [4.12] |
| 7    | MEJA      |        | 0.67 [0.10] | 1.26 [0.38] | 29.48 [4.17] | 1.44 [0.31] | 49.48 [6.14] |
|      | MPB       |        | 0.46 [0.05] | 0.76 [0.11] | 20.75 [1.93] | 0.89 [0.09] | 36.01 [2.54] |
| 1    | MEJA      | Moderate | 0.86 [0.12] | 1.82 [0.77] | 38.13 [5.10] | 0.70 [0.16] | 59.19 [8.92] |
|      | MPB       |        | 0.87 [0.09] | 1.77 [0.66] | 38.46 [3.72] | 0.67 [0.15] | 57.11 [5.99] |
| 2    | MEJA      |        | 0.79 [0.09] | 2.33 [0.78] | 33.68 [3.42] | 1.00 [0.15] | 54.76 [5.18] |
|      | MPB       |        | 0.69 [0.06] | 2.17 [0.68] | 30.45 [2.18] | 0.95 [0.13] | 49.28 [2.61] |
| 5    | MEJA      | High   | 1.49 [0.19] | 3.21 [1.09] | 56.60 [6.65] | 1.31 [0.27] | 89.79 [9.85] |
|      | MPB       |        | 2.06 [0.20] | 4.16 [1.15] | 75.70 [6.13] | 1.76 [0.22] | 120.90 [7.34] |
| 6    | MEJA      |        | 1.15 [0.12] | 1.69 [0.19] | 45.55 [4.63] | 1.53 [0.28] | 78.12 [7.49] |
|      | MPB       |        | 2.06 [0.29] | 2.71 [0.33] | 73.94 [9.81] | 2.46 [0.43] | 128.87 [14.09] |

Note: HCSC, historic climatic suitability class.
between biochemical responses to biotic agents, one generic to all plants (MEJA) and one specific to the study system (MPB). Additionally, in our study, similarities in stand structure and qualitative monoterpenic content (including chirality) support the conclusion that variation in the specificity of the induced response is due to the influence of MPB herbivory over time.

Although we predicted that the specificity of the induced response by lodgepole pine against MPB would increase with increasing historical exposure to herbivory, differences only emerged in lodgepole populations from the “high” historic climatic suitability region. This is likely due to a lack of a gradation of historic exposure to MPB with increasing HCSC. Prior to 1970, epidemic MPB infestations were never recorded in “very low” and “low” HCSCs, and only rarely recorded in the “moderate” HCSC; frequent outbreaks occurred only in the “high” and “extreme” HCSCs (Safranyik et al. 1975, Carroll et al. 2004, Taylor et al. 2006). We would expect an even greater degree of specificity in sites within the “extreme” category of historic climatic suitability (sensu Carroll et al. 2004); however, due to the recent unprecedented outbreak of MPB in the last two decades in western Canada (Safranyik et al. 2010), and the extensive salvage logging of these impacted areas, we were unable to locate suitable intact stands in this category.

Despite the differential increase in the total expression of induced monoterpenes in response to MPB by lodgepole pine populations with
greatest historical exposure to herbivory, the increase was not consistent among all major monoterpene constituents. This suggests that selection has favored specific monoterpene over others in the induced response against MPB attacks. Although earlier studies found that lodgepole pine susceptibility to MPB was entirely a function of a tree’s capacity for total monoterpene induction, with no significant qualitative variation in resin constituents (e.g., Raffa and Berryman 1982, 1983a, b, Boone et al. 2011), they did not consider putatively naïve populations and therefore were unable to consider the potential for selection by MPB to influence the qualitative form of the induced defensive response. This is particularly relevant when considering those monoterpene that are highly toxic to MPB. For example, limonene is particularly antagonistic to MPB (Raffa and Berryman 1982, Reid and Purcell 2011) and was expressed in much greater amounts in putatively evolutionarily experienced stands. The potential role, if any, for the relative increase in the expression of other monoterpene [(−)-β-pinene, sabinene, α-phellandrene, and (−)-β-phellandrene] in experienced lodgepole pine populations is presently unknown and worthy of additional research.

Interestingly, historic exposure to MPB herbivory did not significantly affect the differential expression of α-pinene, (+)-3-carene, or terpinolene. Each of these volatile monoterpene is exploited by MPB to facilitate host choice, aggregation, and colonization; (−)-α-pinene is the precursor for the synthesis of the main aggregation pheromone (−)-trans-β-verbenol and enhances host selection (Erbilgin et al. 2014, Taft et al. 2015, Burke and Carroll 2016), and 3-carene and terpinolene are synergists with (−)-trans-β-verbenol (Borden et al. 2008). It is possible that since these chemicals may assist MPB colonization, they have been less favored in coevolved populations of lodgepole pines. However, myrcene is also a synergist with trans-β-verbenol (Borden et al. 1987, 2008) and was significantly affected by HCSC in our study. This may point to its greater utility to hosts as an antagonistic chemical, over its utility to MPB as a synergistic kairomone.

Since the resistance of a stand of trees determines the population size at which MPB can breach the endemic/epidemic threshold (Safranyik and Carroll 2006, Boone et al. 2011), the lack of a specific coevolved defensive response in naïve lodgepole pine populations suggests that the high rate of spread and impacts observed in newly invaded forests (Cudmore et al. 2010, Robinson 2015) may have been exacerbated by non-specific, weakly coevolved defenses. This does not imply that adaptations by evolutionarily experienced lodgepole pine populations would render them immune, but instead MPB-specific defensive traits will raise the threshold beetle density required to initiate eruptions (Boone et al. 2011), thereby providing a selective advantage. However, given the propensity for positive feedbacks to amplify across scales for an eruptive herbivore such as MPB, when population densities increase sufficiently, outbreaks will occur regardless of tree resistance (Raffa et al. 2008). Indeed, once MPB populations breach the endemic/epidemic threshold, beetles will preferentially colonize even the most defensive trees (Boone et al. 2011, Bentz et al. 2015, Burke and Carroll 2017). Interestingly, as a consequence of forest management efforts that have increased the amount of susceptible hosts over the landscape in western Canada (Taylor and Carroll 2004, Taylor et al. 2006), the most recent MPB outbreak reached an unprecedented size and resulted in unusually high levels of tree mortality (Cudmore et al. 2010, Safranyik et al. 2010), potentially negating any selective advantage associated with coevolved lodgepole pine populations, and depending on genotypes of lodgepole pine trees selected for reforestation following control and salvage harvesting, may have implications for the susceptibility of the future forest.

Variation in host defenses against MPB have been implicated in its infestation dynamics in other pine systems. Weakly coevolved induced defenses in whitebark pines (Pinus albicaulis) have been suggested as the primary driver of widespread mortality in this tree species (Raffa et al. 2013). By contrast, recent research has revealed that Great Basin Bristlecone pine (Pinus longaeva) is highly resistant, and potentially immune, to MPB colonization (Bentz et al. 2017). However, this resistance resulted from highly concentrated and chemically diverse constitutive resin chemistry and not an induced response. This trait is likely a consequence of an extremely long lifespan, sometimes >4000 yr (Schulman 1958, Lanner 2007), creating pressures to be defensive against a wide range of potential pests and pathogens. Long-lived and slow-growing plants tend to
invest more in secondary metabolites for defense vs. growth (Herms and Mattson 1992).

Resin metabolites are synthesized in constitutive and traumatic (i.e., induced) resin ducts in the cortex and xylem of conifers (Franceschi et al. 2005, Zulak and Bohlmann 2010). Induced resin accumulation requires up-regulation of terpenoid synthases and, depending on which terpene synthases are involved, may lead to quantitative or qualitative changes in induced resin (Keeling and Bohlmann 2006, Zulak and Bohlmann 2010). It is likely that differences we observed among experienced and naïve lodgepole pine populations are due to enhanced sensitivity to pathogen-associated molecular patterns (Jones and Dangl 2006) in coevolved populations, leading to an increase in traumatic resin duct production and the up-regulation of terpene synthases. The detection of these patterns by the immune system of plants has been implicated as the primary source of evolutionary pressure and change in plant immune response (Chisholm et al. 2006). For example, Miya et al. (2007) discovered a kinase receptor in Arabidopsis that is specific to the presence of chitin, the major structural component of fungal cell walls and insect exoskeletons. Considering fungi and insects commonly attack plants (often in unison, as in the MPB system), it is very likely that these receptors evolved in response to herbivory and infection. Further tests using our methods which include non-pathogenic fungal controls and microdissections of stem tissues could elucidate this further.

It is not clear whether long-term exposure among lodgepole pine populations to MPB has selected for stronger induced defenses, or lack of exposure has selected against them. The induced defensive response by conifers is energetically costly (Christiansen et al. 1987), and the growing season in northern latitudes is short. Therefore, trees at higher latitudes may prioritize growth over terpenoid biosynthesis for defense in the absence of significant herbivory (Herms and Mattson 1992). Thus, a lack of exposure to herbivory among lodgepole populations beyond the historic climatically constrained range of MPB may have led to selection against defense traits. Since the last glaciation (~8000 yr before present), lodgepole pine spread northward mostly from southern refugia to colonize western North America (Wheeler and Guries 1982, MacDonald and Cwynar 1985, Cwynar and MacDonald 1987). Furthermore, the genus Dendroctonus has had a long evolutionary history with Pinus hosts (Kelley and Farrell 1998) and would likely have been associated with ancestral lodgepole pine populations within the glacial refugia. It is possible that the strong defensive traits were present in the expanding lodgepole pine populations post-glaciation, but were lost once the trees migrated into regions from which MPB was climatically excluded.

Results of this study suggest that due to climate change-induced range expansion (Carroll et al. 2004), MPB has become an invasive species within a contiguous population of its principle host arising from weak evolutionary relationships in putatively naïve host populations. In exotic invasive systems, the invader’s success is attributable to a lack of coevolution with the full suite of biotic elements of the invaded habitat (Jeffries and Lawton 1984, Gandhi and Herms 2010). For example, trophic insufficiencies, including inadequate host defenses, have recently been implicated in the rapid invasion and severe impacts of the emerald ash borer, Agrilus planipennis, in North American host-tree populations (Cipollini et al. 2011, Whitehill et al. 2011, Duan et al. 2014, Herms and McCullough 2014). In the case of MPB, similarities in ecosystem processes and trophic interactions in the native and newly invaded lodgepole pine forests (Cudmore et al. 2010, Safranyik et al. 2010, Robinson 2015) suggest that the susceptibility to invasion of novel lodgepole pine forests is primarily due to non-specific, weakly coevolved tree defenses, emphasizing the role of bottom-up forces in habitat invasion by herbivores. Improvements in the capacity to determine what traits contribute to the susceptibility of novel systems will allow for better mitigation of consequences of exotic introductions, and native invasions, in the future (Liu and Trumble 2007, Davis 2009, Dukes et al. 2009, Raje et al. 2016).

Holarctic forests are likely to experience more native invasions with further climate warming. In northern Europe, where asymmetric herbivore-host distributions are common, and forests extend far beyond the thermal range of most insects, there is a risk of imminent range expansion by both lepidopteran defoliators (Netherer and Schopf 2010) and bark beetles (Jonsson et al. 2009) within the contiguous populations of their current hosts. Recent work indicates that both the autumnal moth, Epirrita autumnata, and winter moth,
Operophtera brumata, have exhibited rapid northward expansion as an apparent consequence of climate warming (Jepsen et al. 2008, 2011). Similarly, the southern pine beetle (Dendroctonus frontalis Zimmermann), a highly destructive species related to MPB and native to the southeastern region of the United States and northern Mexico, has significantly expanded its range northward as a consequence of warming winter temperatures (Trän et al. 2007). Analysis of the widespread and varied effects of climate change on insects and pathogens by Weed et al. (2013) suggests that in many cases, impacts have been greater than predicted by previous assessments (see Ayres and Lombardero 2000, Logan et al. 2003), and impacts are even more pronounced in the tree-killing species of bark beetles (Raffa et al. 2015). An understanding of the traits that allow native insects to invade novel habitats of conspecific hosts will be increasingly important, as climates continue to warm.

ACKNOWLEDGMENTS

Funding for this research was provided by the British Columbia Future Forest Ecosystem Science Council (www.gov.bc.ca/nro), the Natural Sciences and Engineering Research Council of Canada Strategic Network—TRIA-Net Turning Risk Into Action for the Mountain Pine Beetle Epidemic (tria-net.srv.ualberta.ca/), and the University of British Columbia (www.ubc.ca). J. Burke, J. Bohlmann, and A. Carroll conceived this project, J. Burke conducted field collections, chemical and statistical analyses, and J. Burke, J. Bohlmann, and A. Carroll wrote the manuscript. The authors declare no conflicts of interest. Marc-Antoine LeClerc, Tristan Takaro, Richard Schwendener, and Romain Belvas assisted in field collections. Lina Madilao assisted in chemical analyses. A. Burke, G. Burke, T. Ramey, N. Sopinka, S. Aitken, D. Srivastava, D. Herms, M. Isman, J. Cronin, L. Kuglerová, and two anonymous reviewers provided comments on earlier versions of this manuscript.

LITERATURE CITED

Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262:263–286.

Battisti, A., M. Stastny, S. Netherer, C. Robinet, A. Schopf, A. Roques, and S. Larsson. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecological Applications 15:2084–2096.

Bentz, B. J., C. K. Boone, and K. F. Raffa. 2015. Tree response and mountain pine beetle attack preference, reproduction and emergence timing in mixed whitebark and lodgepole pine stands. Agricultural and Forest Entomology 17:421–432.

Bentz, B. J., S. A. Hood, E. M. Hansen, J. C. Vandygriff, and K. E. Mock. 2017. Defense traits in the long-lived Great Basin Bristlecone pine and resistance to the native herbivore mountain pine beetle. New Phytologist 213:611–624.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–613.

Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Canadian Journal of Forest Research 41:1174–1188.

Borden, J. H., D. S. Pureswaran, and J. P. Lafontaine. 2008. Synergistic blends of monoterpenes for aggregation pheromones of the mountain pine beetle (Coleoptera: Curculionidae). Journal of Economic Entomology 101:1266–1275.

Borden, J. H., L. Ryker, L. Chong, H. D. Pierce, B. D. Johnston, and A. C. Oehlschlager. 1987. Response of the mountain pine beetle, Dendroctonus ponderosae Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. Canadian Journal of Forest Research 17:118–128.

Braschler, B., and J. K. Hill. 2007. Role of larval host plants in the climate-driven range expansion of the butterfly Polygonia c-album. Journal of Animal Ecology 76:415–423.

Burke, J. L., and A. L. Carroll. 2016. The influence of variation in host tree monoterpane composition on secondary attraction by an invasive bark beetle: implications for range expansion and potential host shift by the mountain pine beetle. Forest Ecology and Management 359:59–64.

Burke, J. L., and A. L. Carroll. 2017. Breeding matters: Natal experience influences population state-dependent host acceptance by an eruptive insect herbivore. PLoS ONE 12:e0172448.

Burke, J. L., J. C. Maerz, J. R. Milanovich, M. C. Fisk, and K. J. K. Gandhi. 2011. Invasion by exotic earthworms alters biodiversity and communities of litter- and soil-dwelling oribatid mites. Diversity 3:155–175.

Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 221–330 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Challenges and Solutions:
Duan, J. J., K. J. Abell, L. S. Bauer, J. R. Gould, and R. van Driesche. 2014. Natural enemies implicated in the regulation of an invasive pest: a life table analysis of the population dynamics of the emerald ash borer. Agricultural and Forest Entomology 16: 406–416.

Dukes, J. S., et al. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Canadian Journal of Forest Research 39:231–248.

Erbilgin, N., C. Ma, C. M. Whitehouse, B. Shan, A. Najjar, and M. L. Evenden. 2014. Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naïve host ecosystem. New Phytologist 201:940–950.

Farrar, J. L. 1995. Trees of Canada. Fitzhenry and Whiteside Limited, Markham, Ontario, Canada.

Franceschi, V. R., T. Krekling, and E. Christiansen. 2002. Application of methyl jasmonate on Picea abies (Pinaceae) stems induces defense-related responses in phloem and xylem. American Journal of Botany 89:578–586.

Franceschi, V. R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist 167:353–375.

Gandhi, K. J. K., and D. A. Herm. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biological Invasions 12:389–405.

Graves, A. D., E. H. Holsten, M. E. Ascerno, K. P. Zogas, J. S. Hard, D. P. W. Huber, R. A. Blanchette, and S. J. Seybold. 2008. Protection of sprinkle from colonization by the bark beetle, Ips perturbatus, in Alaska. Forest Ecology and Management 256: 1825–1839.

Hagen, S. B., J. U. Jepsen, R. A. Ims, and N. G. Yoccoz. 2007. Shifting altitudinal distribution of outbreak zones of winter moth Operophtera brumata in sub-arctic birch forest: A response to recent climate warming? Ecography 30:299–307.

Hall, D. E., J. A. Robert, C. I. Keeling, D. Domanski, A. L. Quesada, S. Jancsik, M. A. Kuzyk, B. Hamberger, C. H. Borchers, and J. Bohlmann, 2011. An integrated genomic, proteomic and biochemical analysis of (+)-3-carene biosynthesis in Sitka spruce (Picea sitchensis) genotypes that are resistant or susceptible to white pine weevil. Plant Journal 65:936–948.

Hall, D. E., P. Zerbe, S. Jancsik, A. L. Quesada, H. K. Dullat, L. L. Madillo, M. M. S. Yuen, and J. Bohlmann. 2013b. Evolution of conifer diterpene synthases: diterpene resin acid biosynthesis in lodgepole pine and jack pine involves monofunctional and
bifunctional diterpene synthases. Plant Physiology 161:600–616.

Hall, D. E., et al. 2013a. Transcriptome resources and functional characterization of monoterpane synthases for two host species of the mountain pine beetle, lodgepole pine (Pinus contorta) and jack pine (Pinus banksiana). BMC Plant Biology 13:80.

Hanula, J. L., A. E. Mayfield, S. W. Fraedrich, and R. J. Rabaglia. 2008. Biology and host associations of redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae: Euphorbiaceae: Sphaerioxylon). Journal of Economic Entomology 101:1276–1286.

Herms, D. A., and D. G. McCullough. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annual Review of Entomology 59:13–30.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12:450–455.

Hickling, R., D. B. Roy, J. K. Hill, and C. D. Thomas. 2005. A northward shift of range margins in British Odonata. Global Change Biology 11:502–506.

Hudgins, J. W., E. Christiansen, and V. R. Franceschi. 2003. Methyl jasmonate induces changes mimicking anatomical defenses in diverse members of the Pinaceae. Tree Physiology 23:361–371.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46:10–18.

Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23:269–286.

Jepsen, J. U., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2008. Climate change and outbreeds of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreed range expansion. Journal of Animal Ecology 78:182–190.

Jepsen, J. U., L. Kapari, S. B. Hagen, T. Schott, O. P. L. Vindstad, A. C. Nilssen, and R. A. Ims. 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with subarctic birch. Global Change Biology 17:2071–2083.

Jones, J. D. G., and J. L. Dangl. 2006. The plant immune system. Nature Reviews 444:323–329.

Jönsson, A. M., G. Appelberg, S. Harding, and L. Bärring. 2009. Spatio-temporal impact of climate change on the activity and volitism of the spruce bark beetle, Ips typographus. Global Change Biology 15:486–499.

Keeling, C. I., and J. Bohlmann. 2006. Genes, enzymes and chemicals of terpenoid diversity in the constitutive and induced defence of conifers against insects and pathogens. New Phytologist 170:657–675.

Kelley, S. T., and B. D. Farrell. 1998. Is specialization a dead end? The phylogeny of host use in Dendroctonus bark beetles. Evolution 52:1731–1743.

Klepzig, K. D., E. L. Kruger, E. B. Smalley, and K. F. Raffa. 1995. Effects of biotic and abiotic stress on induced accumulation of terpenes and phenolics in red pines inoculated with bark beetle-vectored fungus. Journal of Chemical Ecology 21:601–626.

Kroken, P., N. E. Nagy, and H. Solheim. 2008. Methyl jasmonate and oxalic acid treatment of Norway spruce: anatomically based defense responses and increased resistance against fungal infection. Tree Physiology 28:29–35.

Lanner, R. 2007. The bristlecone book: a natural history of the world’s oldest trees. Mountain Press Pub. Co., Missoula, Montana, USA.

Lewinsohn, E., M. Gijzen, R. M. Muzika, K. Barton, and R. Croteau. 1993. Oleoresinosis in grand fir (Abies grandis) saplings and mature trees: modulation of this wound response by light and water stresses. Plant Physiology 101:1021–1028.

Liebhold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monograph 30:1–49.

Liebhold, A. M., D. G. McCullough, L. M. Blackburn, S. J. Frankel, B. Von Holle, and J. E. Aukema. 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. Diversity and Distributions 19:1208–1216.

Liu, D., and J. T. Trumble. 2007. Comparative fitness of invasive and native populations of the potato psyllid (Bactericera cockerelli). Entomologia Experimentalis et Applicata 123:35–42.

Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130–137.

MacDonald, G. M., and L. C. Cwynar. 1985. A fossil pollen based reconstruction of the late Quaternary history of lodgepole pine (Pinus contorta ssp. latifolia) in the western interior of Canada. Canadian Journal of Botany 15:1039–1044.

MacFarlane, D. W., and S. P. Meyer. 2005. Characteristics and distribution of potential ash tree hosts for emerald ash borer. Forest Ecology and Management 213:15–24.

Martin, D. M., D. Tholl, and J. Gershenzon. 2002. Methyl jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis, and terpenoid accumulation in...
developing xylem of Norway spruce stems. Plant Physiology 129:1003–1018.

Mattson, W. J., P. Niemela, I. Millers, and Y. Inguanzo. 1994. Immigrant phytophagous insects on woody plants in the United States and Canada: an annotated list. General Technical Report NC-169, USDA Forest Service, St. Paul, Minnesota, USA.

Miller, B., L. L. Madilao, S. G. Ralph, and J. Bohlmann. 2005. Insect-induced conifer defense. White pine weevil and methyl jasmonate induce traumatic resinosis, de novo formed volatile emissions, and accumulation of terpenoid synthase and putative octadecanoid pathway transcripts in Sitka spruce. Plant Physiology 137:369–382.

Miya, A., P. Albert, T. Shinya, Y. Desaki, K. Ichimura, K. Shirasu, Y. Narusaka, N. Kawakami, H. Kaku, and N. Shibuya. 2007. CERK1, a LysM receptor kinase, is essential for chitin elicitor signaling in Arabidopsis. Proceedings of the National Academy of Sciences USA 104:19613–19618.

Mock, K. E., B. J. Bentz, E. M. O’Neill, J. P. Chong, J. Orwin, and M. E. Pfrender. 2007. Landscape-scale genetic variation in a forest outbreak species, the mountain pine beetle (Dendroctonus ponderosae). Molecular Ecology 16:553–568.

Musolin, D. L. 2007. Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. Global Change Biology 13:1565–1585.

Netherer, S., and A. Schopf. 2010. Potential effects of climate change on insect herbivores in European forests: general aspects and the pine processionary moth as specific example. Forest Ecology and Management 259:831–838.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Evolutionary Biology 37:637–669.

Raffa, K. F., and E. B. Smalley. 1995. Interaction of pre-attack and induced monoterpen concentrations in host conifer defense against bark beetle-fungal complexes. Oecologia 102:285–295.

Rajeev K. R., R. V. R. Ferris, and J. D. Holland. 2016. Phylogenetic signal and potential for invasiveness. Agricultural and Forest Entomology 18:260–269.

Ramsfield, T. D., B. J. Bentz, M. Faccoli, H. Jactel, and E. G. Brockerhoff. 2016. Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts. Forestry 89:245–252.

Régnière, J. 1996. A generalized approach to landscape-scale forecasting with temperature-driven simulation models. Environmental Entomology 25:869–881.

Régnière, J., R. St-Amant, and A. Béchard. 2014. BioSIM 10 – user’s manual. Information Report LAU-X-155. Canadian Forest Service, Laurentian Forest Centre, Quebec City, Quebec, Canada.

Reid, M. L., and J. R. C. Purcell. 2011. Condition-dependent tolerance of monoterpenes in an insect herbivore. Arthropod-Plant Interactions 5:331–337.

Robinson, A. 2015. Spread and impact of an eruptive herbivore in a novel habitat: consequences of climate change – induced range expansion. Thesis.
The University of British Columbia, Vancouver, British Columbia, Canada.

Rochlin, L., D. V. Ninivaggi, M. L. Hutchinson, and A. Farajollahi. 2013. Climate change and range expansion of the asian tiger mosquito (Aedes albopictus) in northeastern USA: implications for public health practitioners. PLoS ONE 8:e60874.

Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 in L. Safranyik and R. J. Wilson, editors. The mountain pine beetle – a synthesis of biology, management, and impacts in lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Safranyik, L., A. L. Carroll, J. Régnière, D. W. Langor, W. G. Riel, T. L. Shore, B. J. Cooke, V. G. Nealis, and S. W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Canadian Entomologist 142:415–442.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle, and its associated blue stain fungi in western Canada. Pages 406–428 in D. M. Baumgartner, editor. Management of Lodgepole Pine Ecosystems Symposium Proceedings. Washington State University Cooperative Extension Service, Pullman, Washington, USA.

Sambaraju, K. R., A. L. Carroll, J. Zhu, K. Stahl, R. D. Moore, and B. H. Aukema. 2011. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. Ecography 35:211–233.

Schmidt, A., R. Nagel, T. Krekling, E. Christiansen, J. Gershenzon, and P. Krokene. 2011. Induction of isoprenyl diphosphate synthases, plant hormones and defense signalling genes correlates with traumatic resin duct formation in Norway spruce (Picea abies). Plant Molecular Biology 77:577–590.

Schulman, E. 1958. Bristlecone pine, oldest known living thing. National Geographic 113:355–372.

Taft, S., A. Najar, and N. Erbilgin. 2015. Pheromone production by an invasive bark beetle varies with monoterpen composition of its naive host. Journal of Chemical Ecology 41:540–549.

Taylor, S. W., and A. L. Carroll. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. Pages 41–51 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Challenges and Solutions: Proceedings of the Mountain Pine Beetle Symposium. Information Report BC-X-399, Canadian Forest Service, Pacific Forestry Centre, Kelowna, British Columbia, Canada.

Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Pages 67–94 in L. Safranyik and B. Wilson, editors. The mountain pine beetle – a synthesis of biology, management, and impacts in lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Trán, J. K., T. Ylioja, R. F. Billings, J. Régnière, and M. P. Ayres. 2007. Impact of minimum winter temperatures on the population dynamics of Dendroctonus frontalis. Ecological Applications 17:882–899.

Wallin, K. F., and K. F. Raffa. 1999. Altered constitutive and inducible phloem monoterpenes following natural defoliation of jack pine: implications for host mediated interguild interactions and plant defense theories. Journal of Chemical Ecology 25:861–880.

Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83:441–470.

Wheeler, N. C., and R. P. Guries. 1982. Population structure, genic diversity, and morphological variation in Pinus contorta Dougl. Canadian Journal of Forest Research 12:595–606.

Whitehill, J. G. A., A. Popova-Butler, K. B. Green-Church, J. L. Koch, D. A. Herms, and P. Bonello. 2011. Interspecific proteomic comparisons reveal ash phloem genes potentially involved in constitutive resistance to the emerald ash borer. PLoS ONE 6:e24863.

Zeneli, G., P. Krokene, E. Christiansen, T. Krekling, and J. Gershenzon. 2006. Methyl jasmonate treatment of mature Norway spruce (Picea abies) trees increases the accumulation of terpenoid resin components and protects against infection by Ceratocystis polonica, a bark beetle-associated fungus. Tree Physiology 26:977–988.

Zulak, K. G., and J. Bohlmann. 2010. Terpenoid biosynthesis and specialized vascular cells of conifer defense. Journal of Integrative Plant Biology 52:86–97.

Data Availability

All relevant data are within the paper and available from dataverse.harvard.edu, doi: 10.7910/DVN/X3JYB3.