

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

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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 monoterpene 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.

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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 Cwynar 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 monoterpene 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

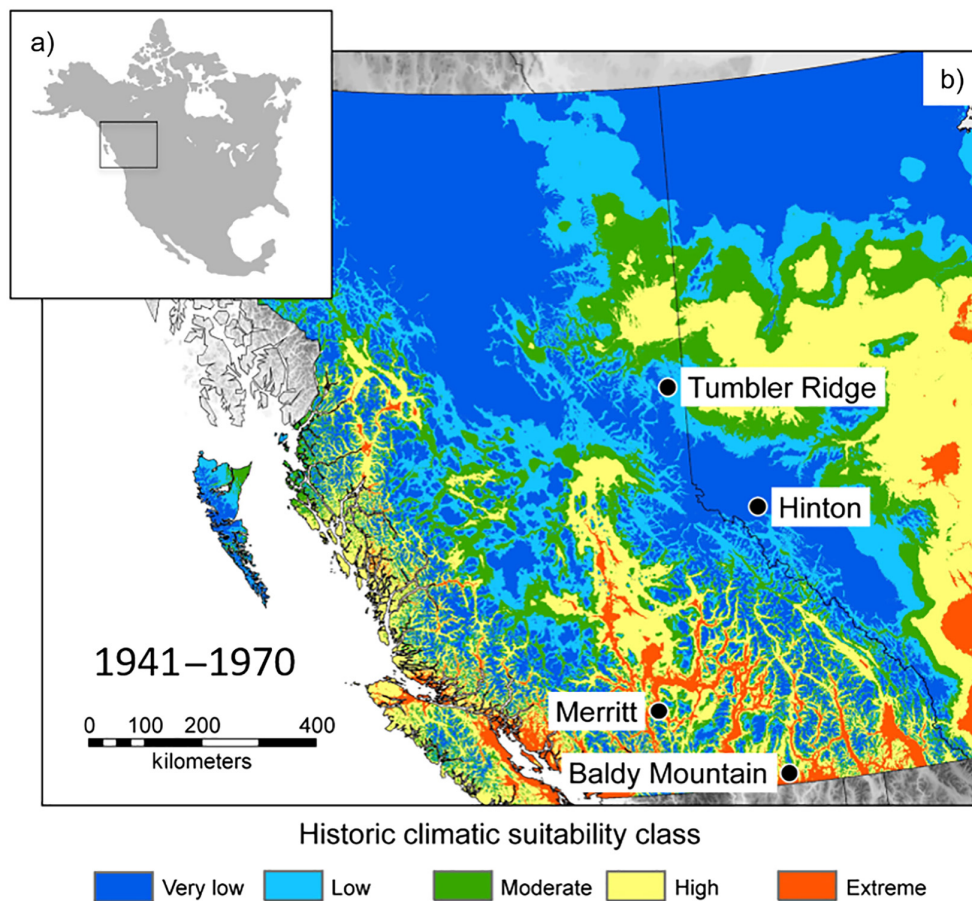


Fig. 1. (a) Study area within western North America and (b) location of lodgepole pine (*Pinus contorta* var. *latifolia*) populations with varying degrees of historic exposure to mountain pine beetle (*Dendroctonus ponderosae*) determined from calculations of historic climatic suitability (see Carroll et al. 2004) for the period 1941–1970. “Extreme” historic climatic suitability indicates climatically optimal habitat, whereas “low” and “very low” historic climatic suitability denote climatically unsuitable habitats.

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

Table 1. Geographic characteristics of experimental sites selected to assess the specificity of the defensive response of lodgepole pine (*Pinus contorta* var. *latifolia*) populations against the mountain pine beetle (*Dendroctonus ponderosae*).

Region	Site	Location	Elevation (m)	Historic climatic suitability†
Merritt	5	N 49.78, W 120.73	927	High
	6	N 49.98, W 120.59	995	
Baldy Mountain	1	N 49.11, W 119.17	1291	Moderate
	2	N 49.10, W 119.27	1422	
Tumbler Ridge	7	N 54.99, W 120.84	1027	Low
	8	N 54.74, W 120.55	1194	
Hinton	3	N 53.55, W 117.93	1252	Very low
	4	N 53.53, W 118.03	1380	

† Historic climatic suitability classes generated using the methods of Carroll et al. (2004) for the period 1941–1970.

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 on ice 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 (Franceschi 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 stereochemical configuration of monoterpenes differed among lodgepole pine populations, a random subsample of three trees from each site was selected to assess stereochemical 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, proportion basal area, and relative monoterpene abundance were arcsine(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 α -pinenes were present in both stereoisomers. There were no detectable concentrations of (+)- β -pinene, (–)-3-carene, (+)-limonene, or (+)- β -phellandrene. The mean ratio, (–):(+), of α -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 monoterpene 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 (–)- β -pinene, sabinene, myrcene, α -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*).

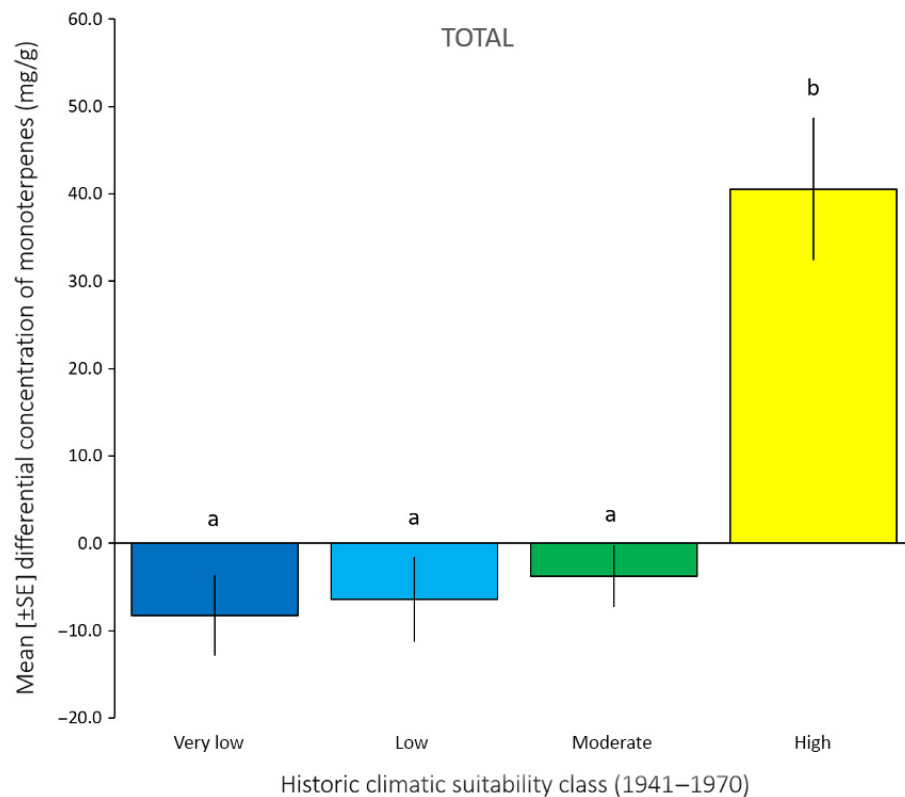


Fig. 2. Mean [\pm SE] differential concentration for total monoterpenes in phloem tissue, calculated by taking the difference between mountain pine beetle-simulation treatment and methyl jasmonate treatment at each tree, for four populations of lodgepole pine trees (*Pinus contorta* var. *latifolia*) each within four historic climatic suitability classes (see Carroll et al. 2004) for the period 1941–1970. Different letters denote significant differences based on Tukey's HSD post hoc comparison of means.

and (–)- β -phellandrene varied among HCSCs ($F_{3,86} = 7.45\text{--}13.25$, $P < 0.05$; Tables 3, 4), whereas there was no significant influence of historic exposure to MPB on the expression of α -pinenes, (+)-3-carene, or terpinolene ($F_{3,86} = 3.53\text{--}6.24$, $P > 0.05$; Tables 3, 4). Similar to the differential expression of total monoterpene 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

Table 3. Mean (SE) monoterpene 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	α -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	Low	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	Moderate	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	High	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	High	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.

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 4. Mean (SE) monoterpene 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	α -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	Low	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	Moderate	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	High	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]	120.09 [7.34]
6	MEJA	High	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.

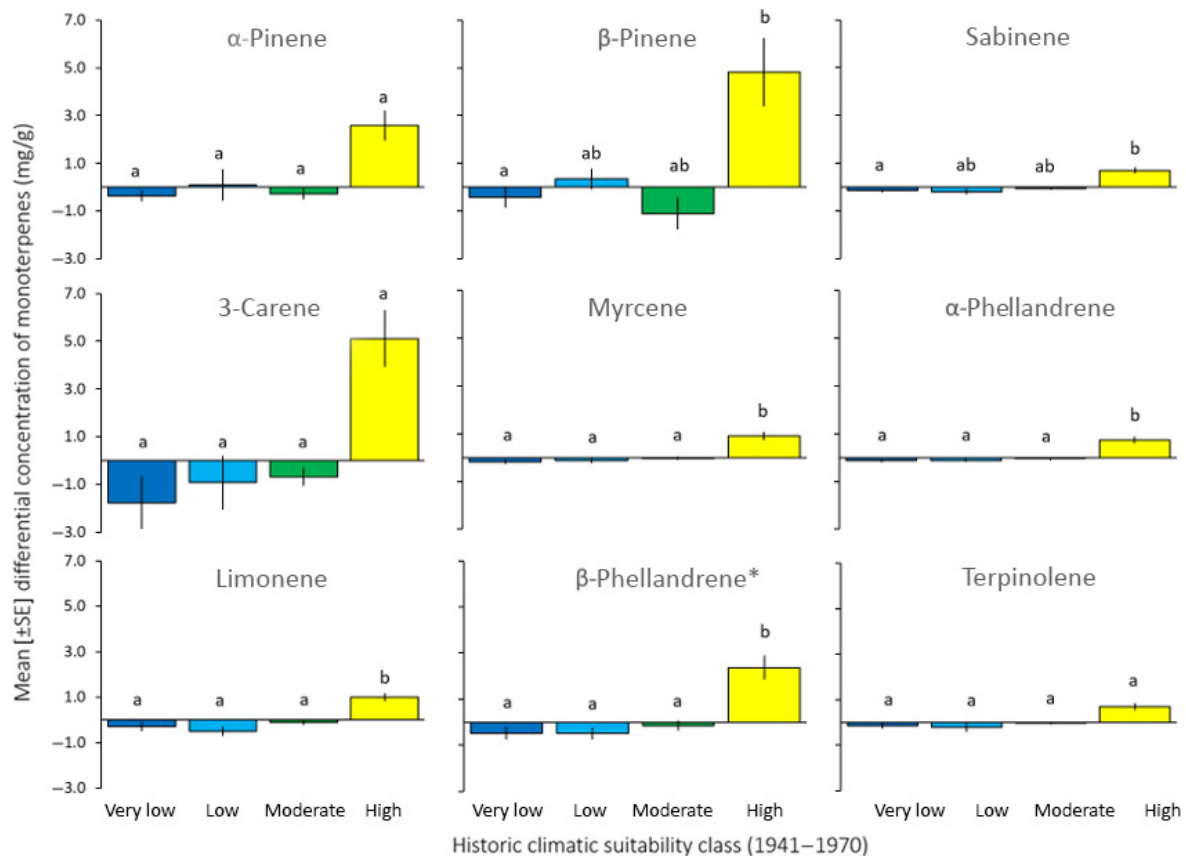


Fig. 3. Mean [\pm SE] differential concentration for individual monoterpenes in phloem tissue, calculated by taking the difference between mountain pine beetle-simulation treatment and methyl jasmonate treatment at each tree, for four populations of lodgepole pine trees (*Pinus contorta* var. *latifolia*) each within four historic climatic suitability classes (see Carroll et al. 2005) for the period 1941–1970. Different letters denote significant differences based on Tukey's HSD post hoc comparison of means. *Note that values for β -phellandrene have been transformed ($\times 10^{-1}$) for this graphic for equivalency of y -axis scale.

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 monoterpene 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 monoterpenes 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 monoterpenes 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 monoterpenes [(–)- 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 -pinenes, (+)-3-carene, or terpinolene. Each of these volatile monoterpenes 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*-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*-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*-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 plannipennis*, 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 (Jönsson 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 (Trân 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.

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DATA AVAILABILITY

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