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A shrinking envelope? Climate warming across the Pacific coastal temperate rainforest and its projected impact on a native defoliator

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Abstract
Temperature regulates the location, frequency, and extent of irruptive forest insect herbivore outbreak cycles. Across the Pacific coastal temperate rainforest, recent outbreaks by a native defoliator, western blackheaded budworm, have impacted the greatest land area recorded since the advent of aerial detection programs and led to widespread losses of canopy leaf area and forest growth. Evidence suggests that the geographic distribution of budworm outbreaks has tracked a poleward shift in suitable temperature across the ecoregion. In this manuscript, we compile aerial observer estimates of insect defoliation, forest inventory data, and historical and projected climate data under three emissions scenarios to hind- and forecast the distribution of budworm outbreaks from 1901 to 2100. Climate data indicate that seasonal temperatures have warmed and are projected to warm further across the ecoregion, while seasonal precipitation has and will remain relatively constant. Models indicate that a range of spring and summer temperatures primarily constrain the biogeography of budworm outbreaks, while minimum host availability, autumn and winter temperatures, and seasonal precipitation further contribute. Projected warming will shift a substantial portion of regional forestland beyond the upper temperature threshold of historic outbreaks. Thus, our forecasts suggest that budworm outbreak distribution will narrow under all three future climatic scenarios tested. Across much of the ecoregion, the distribution of forestlands suitable for budworm outbreaks is projected to shift poleward and upslope, eventually eclipsing its host's elevational distribution. The possible disruption of periodic defoliator outbreak disturbances in this system may have important ramifications for primary productivity, forest dynamics, and forest structure.

Keywords Defoliators · Population dynamics · Pacific coastal temperate rainforest · Western blackheaded budworm · Climate envelope · Forest insects

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1 Introduction

Periodic outbreaks of insect herbivores are a leading biotic disturbance across temperate and boreal forest ecosystems. Outbreaks by native insect herbivores can result in landscape-scale tree damage or mortality events (Hicke et al. 2016, 2020), that can cause significant losses to timber and fiber resources (Chang et al. 2012; Corbett et al. 2016; Hlásny et al. 2019), mobilize sequestered carbon (Kurz et al. 2008a, b; Hicke et al. 2011; Seidl et al. 2014), and even result in pervasive shifts to ecosystem form and function (Pureswaran et al. 2015; McDowell et al. 2020; Seidl and Turner 2022; Turner and Seidl 2023). Irruption frequency, location, duration, and extent are all sensitive to temperature and are thus influenced by anthropogenic climatic change (Bentz et al. 2010; Weed et al. 2013; Pureswaran et al. 2018; Jaime et al. 2024). Identifying biogeographic relationships between temperature and insect outbreaks is crucial for understanding how disturbance regimes may shift under projected climate conditions and help define current and future ecological constraints on land management.

Insects are poikilothermic and are thus highly sensitive to temperature, which is a key regulating factor of both individual insect and population dynamics. At the individual scale, temperature dictates survival, development rate, generation time and frequency, and fecundity (Bale 1991; Bentz et al. 1991; Neven 2000; Pörtner and Farrell 2008). Across landscapes and within populations, temperature dictates latitudinal and elevational distributions, insect-host tree phenological synchrony, predator-prey and tritrophic interactions, dispersal and synchrony, and likelihood of exhibiting irruptive population dynamics (Bale et al. 2002; Peltonen et al. 2002; van Asch and Visser 2007; Robinet and Roques 2010; Chuine 2010; Bozinovic et al. 2011; Kollberg et al. 2015; Walter et al. 2017). Since individuals of most insect species respond favorably to increasing temperature (Deutsch et al. 2008; Roitberg and Mangel 2016), climatic warming has long been predicted to exacerbate insect outbreaks and increase the frequency and extent of landscape-scale tree mortality events (Fleming and Volney 1995; Ayres and Lombardero 2000; Logan and Powell 2001; Williams and Liebhold 2002; Logan et al. 2003; Price et al. 2013). Indeed, since the beginning of the 21st century, large-scale insect outbreaks have decimated temperate and boreal forests, affecting more land area than any other disturbance including wildfire (Hicke et al. 2016).

Population responses to climate warming as well as their spatial and temporal dynamics at broad biogeographic scales are less straightforward (Haynes et al. 2014; Pureswaran 2018). For example, insect herbivores frequently display high levels of phenotypic plasticity in their response to temperature (Valtonen et al. 2011; Bentz et al. 2011; Fält-Nardmann et al. 2018; Butterson et al. 2021), which complicates efforts to predict how a population will respond to increasing temperature. Across landscapes, ecoregions, and even continents, increasing temperature has facilitated latitudinal and elevational range expansions for several well-documented irruptive forest insects including mountain pine beetle (*Dendroctonus ponderosae*) (Hicke and Logan 2009; de la Giroday et al. 2012; Raffa et al. 2013; Cooke and Carroll 2017), pine processionary moth (*Thaumetopoea pityocampa*) (Battisti et al. 2005, 2006), European spruce beetle (*Ips typographus*) (Marini et al. 2012), autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) (Jepsen et al. 2008), eastern spruce budworm (*Choristoneura fumiferana*)(Boulanger et al. 2024), and western spruce budworm (*Choristoneura occidentalis*)(Cooke and Carroll 2017; Srivastava et al. 2023). Further, warming temperatures have increased outbreak frequency and extent for European

spruce beetle (Seidl et al. 2014), caterpillars in the genus *Ormiscodes (Ormiscodes* spp.) (Paritsis and Veblen 2011), and western spruce budworm (Flower 2016). However, warming temperatures have also caused the regular outbreak dynamics of the pine tree-lappet (*Dendrolimus pini*), nun moth (*Lymantria monachal*) (Haynes et al. 2014), and larch budmoth (*Zeiraphera diniana*) to collapse (Esper et al. 2007; Johnson et al. 2010; Saulnier et al. 2017). Since insect populations exhibit such variable responses to climate warming, it is important to develop species-specific projections of future outbreak distributions.

Western blackheaded budworm (*Acleris gloverana*) is an irruptive defoliator that feeds on western hemlock (*Tsuga heterophylla*), mountain hemlock (*Tsuga mertensiana*), and Sitka spruce (*Picea sitchensis*). Outbreaks of western blackheaded budworm have been recorded across the Pacific coastal temperate rainforest, spanning from Washington to Alaska, and the most recent outbreak (between 2020 and 2023) was the largest recorded since the advent of aerial detection programs (USFS-R6,R10 2020–2023; BC 2020–2023). Outbreaks can cause substantial loss of host canopy leaf area and forest growth, and severe multiannual defoliation may result in tree mortality (Nealis and Turnquist 2010). Western blackheaded budworm outbreak distribution is related to host tree volume, minimum precipitation, and outbreaks have tracked a northward shift in suitable seasonal temperatures across the Pacific coastal temperate rainforest (Mask 1992, Howe et al. 2024).

Hemlock-spruce forests across the Pacific coastal temperate rainforest of North America are highly productive, containing extensive tracts of primary forest with substantial carbon stocks (Heath et al. 2011; Buma et al. 2016; Law et al. 2022, 2023). Historically, fine-scale gap-forming disturbances were the most common and stand-replacing disturbances were rare (Taylor 1990; Ott and Juday 2002; Daniels and Gray 2006). However, this expansive ecosystem is projected to warm significantly by the end of the century (Wolken et al. 2011; Shanley et al. 2015; Lader et al. 2020), raising concerns about future insect outbreak cycles and potential impacts to forest resources. To better understand how the distribution of western blackheaded budworm outbreaks might shift under projected climate conditions, we developed classification models using aerial detection insect maps, forest inventory data, and historical and projected climate data across the entire Pacific coastal temperate rainforest. Based on these models, we evaluated the bioclimatic drivers of outbreaks and generated spatially explicit hind- and forecasts of the distribution of western blackheaded budworm outbreaks from 1901 to 2100. Consideration of historic and projected outbreak distributions is vital for understanding the risks and possible impacts of defoliator insect outbreaks, and the resilience of hemlock-spruce forests across the Pacific coastal temperate rainforest.

2 Methods

2.1 Data processing

Study extent—We compiled data and conducted analyses at a 0.25 km^2 resolution across the Pacific coastal temperate rainforest (45˚- 62˚ latitude; −152˚ - −120˚ longitude). Grid cells were included in the study if they contained hemlock-spruce (by basal area; $N = 934{,}866$) or were predicted to be climatically suitable for hemlock-spruce (Howe et al. 2024; $N = 456{,}921$).

Aerial surveys—We compiled aerial detection survey data describing the extent of tree damage from insects and diseases. These data were collected by aerial observers in fixed-wing aircrafts by the United States Department of Agriculture (USDA) Forest Service (i.e., Alaska and the western Continental United States (CONUS); *United States Detection Survey Data*) and the British Columbia (BC) Ministry of Forests (*British Columbia Overview Survey Data*). We calculated the presence/absence of outbreak populations of western blackheaded budworm by intersecting annual polygon and point detection survey data with a 0.25 km^2 grid. Grid cells that contained any visible defoliation were listed as affected.

Forest structure—We compiled forest structure data from raster-based estimates of hemlock (*spp.*) and spruce (*spp.*) basal area over Alaska and CONUS (per acre; 240 m raster; published in 2012 [*Individual Tree Species Parameter Maps [US]*) and polygon-based forest inventory records published in 2020 (*Vegetation Resources Inventories [BC]*). Forest inventory data from the United States were aggregated by upscaling 240 m raster-based estimates of basal area (ft^2/acre) to 0.25 km^2 and transforming units to m^2/ha. Inventory data from BC were aggregated by summing the area-weighted mean (per hectare) of forest inventory polygons that intersected each 0.25 km^2 cell. We used total host basal area (hemlock + spruce; log[m^2/ha + 1] transformed) for all models.

Historical climate—We compiled 20-year climate data (1901–1920…2001–2020) from decadal raster-based estimates of annual and seasonal climate variables (1901–1910…2011–2020; 800 m raster; *ClimateNA*; Wang et al., 2016). Based on our previous work in this system (Howe et al. 2024) we calculated mean spring and summer temperature (˚C), mean autumn and winter temperature (˚C), total spring and summer precipitation (cm), and total autumn and winter precipitation (cm).

Projected future climate—We compiled 20-year climate projections (from ClimateNA) using the 8 General Circulation Model (GCM) ensemble (Mahony 2022). Emissions scenarios were based on the Shared Socioeconomic Pathways (SSP) from the Coupled Model Intercomparison Project (CMIP6) that was included in the 6th Intergovernmental Panel on Climate Change report (IPCC, 2023). We considered three emissions scenarios: medium-low (SSP 2–4.5˚C; 2.7˚C warming by 2081–2100); medium-high (SSP 3–7.0˚C; 3.6˚C warming by 2081–2100), and high (SSP 5–8.5˚C; 4.4˚C warming by 2081–2100). As above, we calculated mean spring and summer temperature (˚C), mean autumn and winter temperature (˚C), total spring and summer precipitation (cm), and total autumn and winter precipitation (cm).

2.2 Analysis

Overview— We used our spatially and temporally explicit dataset to explore how bioclimatic drivers explain western blackheaded budworm outbreak distribution (Table 1). Specifically, we predicted the presence/absence of western blackheaded budworm defoliation based on observed defoliation from 1961 to 1980, 1981–2000, or 2001–2020 and randomly selected absences from the same time periods as a function of host basal area (hemlock + spruce; log[m^2/ha + 1]) and 20-year estimates of mean spring and summer temperature (˚C), mean autumn and winter temperature (˚C), total spring and summer precipitation (cm), and total autumn and winter precipitation (cm).

Model— We constructed classification ensemble models with the *ranger* implementation of random forest (Wright and Ziegler 2017) and the *XGBoost* implementation of gradient

Table 1 Model (A) workflow, (B) formulation, and (C) performance

A) Workflow (50 models)	B) Formulation
Fit model ($N = 60{,}000$)	***Explanatory Variable***
Evaluate with test dataset ($N = 60{,}000$)	Budworm presence/absence
Predictor interpretation with test dataset (performance, variable importance, accumulated local effects, interaction strength & relative effects)	***Predictors***
	Hemlock-spruce basal area (log[m^2/ha + 1])
	Mean Spring & Summer Temp. (˚C)
Predict historical 20-year data ($N = 8{,}350{,}722$)	Mean Autumn & Winter Temp. (˚C)
Predict projected 20-year data ($N = 16{,}701{,}444$)	Total Spring & Summer Precipitation (cm)
Calculate relative mean predictions	Total Autumn & Winter Precipitation (cm)
C) Performance	
True positive rate	0.917
False positive rate	0.085
True negative rate	0.834
False negative rate	0.166
Brier score	0.093
Accuracy	0.875
Mean misclassification error	0.125

boosting (Chen et al. 2024). Both these approaches are tree-based models and are thus based on constructing many simple classification trees either in parallel (random forest; 'bagging') or sequentially by reducing residual error (gradient boosting; 'boosting')(Breiman 2001; Friedman 2001). We constructed an ensemble by fitting each model and averaging the predictions to compute a final prediction. We trained model hyperparameters based on a grid approach and report the selected hyperparameters in Supporting Information 1.

Model fitting & evaluation—Aerial detection programs in Alaska, British Columbia, and the continental United States do not capture all defoliation that occurs across the landscape (Coleman et al. 2018). As a result, we designed a bootstrap-inspired workflow where we constructed 50 individual models to develop robust predictions. We trained each model on a stratified dataset where we randomly drew 10,000 presences and 10,000 absences from each 20-year period in which budworm defoliation was observed (1961–1980, 1981–2000, and 2001–2020; total $N = 60{,}000$). We choose to construct 50 balanced models with equal presences and absences and temporal representation for several reasons: (A) aerial detection coverage is extremely low in some regions (e.g., coastal British Columbia) and a balanced model is more adept at predicting the potential range of defoliation as opposed to a model with a higher proportion of absences; (B) spatial coverage is variable among regions and time periods and thus stratified sampling helps prevent spatial overrepresentation (i.e., spatial bias); and (C) aerial flightlines are not equally available for each time period and region so we decided to construct our models akin to a presence-only sampling schema where absences were randomly drawn. We evaluated the performance of each model based on confusion matrix metrics (e.g., true positive rate, mean misclassification error, etc.) using independently drawn stratified datasets ($N = 50$) equal in composition to the training dataset.

Model effects—We assessed model effects based on each stratified test dataset ($N = 50$). We assessed predictor importance using 1-AUC (area under the receiver-operator curve) dropout loss (i.e., how much does performance decrease if each predictor is removed from the model)(Fisher et al. 2019), mean model effects (i.e., relative mean predictions while

controlling for other predictors) using accumulated local effects (Apley and Zhu 2020), and we evaluated predictor interaction strength using Friedman's h^2, a measure of how much prediction variability is explained by the sum of main effects where high h^2 denotes strong interactions (Friedman and Popescu 2008).

Simplified climatic envelope—Based on the modeled relationship between western blackheaded budworm outbreak distribution and each bioclimatic predictor, we identified prediction-based breakpoints corresponding to suitable (relative mean prediction ≥ 0) or unsuitable (relative mean prediction < 0) hemlock-spruce forestlands. Further, because relationships among seasonal temperature and precipitation are approximately linear across broad biogeographic scales, we simplified the predicted climatic envelope into six categories based on temperature and precipitation: (1) cool temperature, optimal precipitation; (2) cool temperature, low precipitation; (3) optimal temperature and precipitation; (4) optimal temperature and low precipitation; (5) warm temperature and optimal precipitation; and (6) warm temperature and low precipitation. Hemlock-spruce forestlands were designed as cool if either spring and summer (6.5˚C) or autumn and winter temperatures (1˚C) were below the prediction-based breakpoint, suitable if both seasonal temperatures were within breakpoint, and warm if spring and summer temperatures were above the breakpoint (10.5˚C). A comparison of the simplified and full predictor-based envelope is provided in Supporting Information 2.

Forecast assumptions—We predicted the likelihood of western blackheaded budworm outbreak distribution per future climate period and emissions scenario using each constructed model ($N = 50$) and averaged the predictions to compute a final prediction. Our forecast assumes that the observed relationship between outbreak distribution and mean spring and summer temperature is bound within the observed distribution of mean spring and summer temperatures across hemlock-spruce forestlands (i.e., the predicted lower and upper limits of mean spring and summer temperature are the product of a real phenomenon and do not simply track the distribution of temperatures in hemlock-spruce forests). In other words, we assume that budworm defoliation primarily occurs within a bioclimatic envelope and that warming temperatures do not have a universally positive effect on budworm population dynamics (i.e., hotter is not better). This distinction is relatively minor, but important for tree-based model forecasts since they are unable to extrapolate outside the predictor space.

Packages—All analyses were conducted in R (version 4.2.0). Integral packages included: tidyverse (wrangling; Wickham et al. 2019), terra (geospatial formatting; Hijmans 2024), sf (geospatial formatting; Pebesma 2018), stars (geospatial formatting; Pebesma and Bivand 2023), and mlr (machine learning framework; Bischl et al. 2016).

3 Results

Observed & projected climate change across hemlock-spruce forestlands—Since 1901–1920, hemlock-spruce forests across the Pacific coastal temperate rainforest have become warmer and wetter, and this trend is projected to continue under all three climate scenarios (Fig. 1; Table 2). In particular, mean spring and summer temperatures and autumn and winter temperatures have increased by over 1˚C and are projected to further increase 2–4˚C by the end of the century. Both total spring and summer precipitation and total autumn and

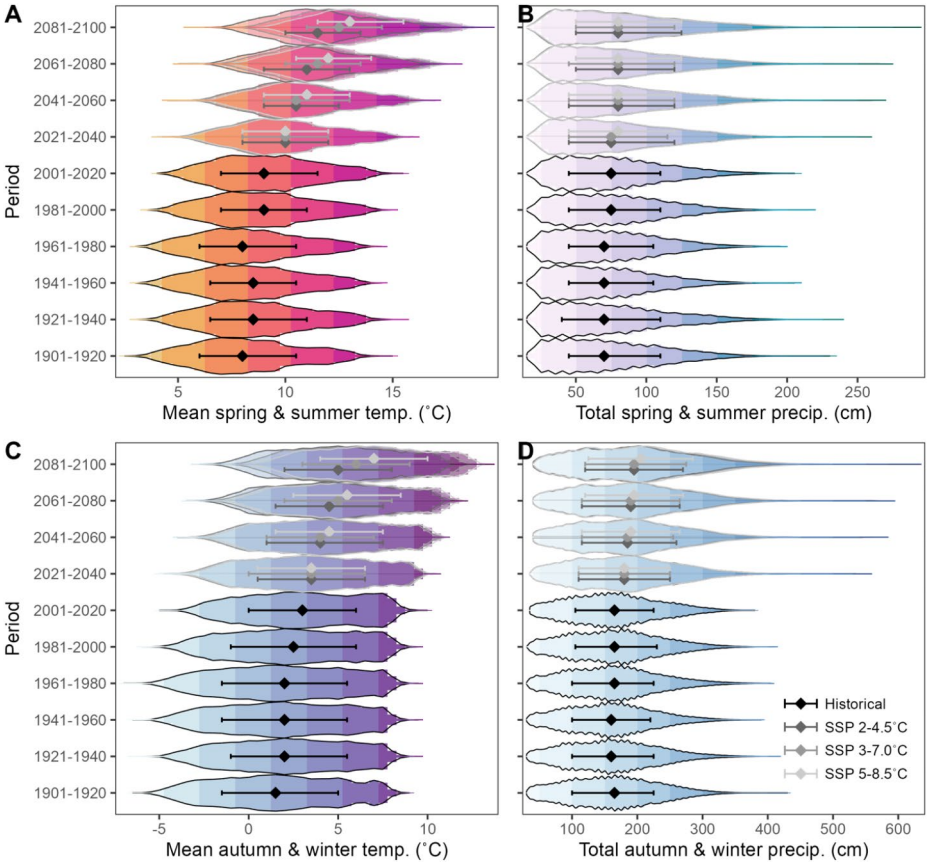

Fig. 1 Distribution of historic and projected seasonal temperature and precipitation for 20-year periods between 1900 and 2100 across Pacific coast hemlock-spruce forests. **(A)** Mean spring and summer temperatures (˚C); **(B)** Total spring and summer precipitation (cm); **(C)** Mean autumn and winter temperatures (˚C); **(D)** Total autumn and winter precipitation (cm). Grey scale denotes the emissions scenario for projections, points denote the median for each period/scenario, and lines denote the quintile range (0.2–0.8) for each period/scenario

winter precipitation have remained relatively constant but are projected to increase marginally by the end of the century.

Western blackheaded budworm outbreak distribution—Western blackheaded budworm outbreaks were best explained by an envelope of mean spring and summer temperatures (6.5–10.5˚C; Fig. 2) and minimum thresholds of mean autumn and winter temperature (1˚C), hemlock-spruce basal area (2.6 log[m^2/ha]), total spring and summer precipitation (60 cm), and total autumn and winter precipitation (140 cm). Overall, interactions among predictor variables explained a greater amount of prediction variation (~60%) than the sum of the main effects; i.e., there are strong interactions among predictors (Fig. 3; Table 3; Friedman's h^2). For example, there was a strong interaction between seasonal temperatures where western blackheaded budworm outbreaks were more likely to occur in hemlock-spruce forestlands where mean spring and summer temperatures were between 8.5–10.5˚C and mean autumn and winter temperature was above 4.5˚C. Models correctly predicted

Table 2 Historic and projected seasonal temperature and precipitation for 20-year periods between 1900 and 2100 across Pacific coast hemlock-spruce forests. Change (Δ) denotes difference from 1901–1920 (historic) or 2001–2020 (projected)

		Mean spring & summer temp. (˚C)		Mean autumn & winter temp. (˚C)		Total spring & summer precip. (cm)		Total autumn & winter precip. (cm)	
Period	Scenario	Observed	Δ	Observed	Δ	Observed	Δ	Observed	Δ
1901–1920		8.3		1.8		81.0		168.7	
1921–1940		8.8	0.5	2.4	0.6	81.6	0.6	169.3	0.6
1941–1960		8.5	0.2	2.2	0.4	77.7	−3.2	165.0	−3.7
1961–1980		8.4	0.1	2.1	0.3	79.2	−1.8	168.8	0.1
1981–2000		9.0	0.7	2.6	0.8	82.9	1.9	171.4	2.8
2001–2020		9.3	1.0	3.2	1.4	83.6	2.7	169.6	0.9
2021–2040	SSP 2–4.5˚C	10.1	0.8	3.7	0.5	85.6	2.0	187.3	17.7
	SSP 3–7.0˚C	10.0	0.7	3.5	0.3	85.4	1.8	186.6	17.0
	SSP 5–8.5˚C	10.2	0.9	3.7	0.5	86.5	2.8	187.6	18.0
2041–2060	SSP 2–4.5˚C	10.8	1.5	4.3	1.1	87.5	3.9	192.3	22.7
	SSP 3–7.0˚C	10.8	1.5	4.3	1.1	86.5	2.8	191.4	21.7
	SSP 5–8.5˚C	11.1	1.8	4.6	1.5	88.0	4.4	195.4	25.8
2061–2080	SSP 2–4.5˚C	11.2	1.9	4.8	1.6	88.4	4.8	196.9	27.2
	SSP 3–7.0˚C	11.7	2.5	5.2	2.1	88.2	4.5	196.7	27.1
	SSP 5–8.5˚C	12.2	2.9	5.7	2.5	90.0	6.3	199.9	30.3
2081–2100	SSP 2–4.5˚C	11.7	2.4	5.2	2.0	89.4	5.8	199.8	30.1
	SSP 3–7.0˚C	12.8	3.5	6.2	3.0	88.7	5.1	202.3	32.7
	SSP 5–8.5˚C	13.5	4.2	7.0	3.8	92.3	8.7	212.1	42.5

92% of budworm presences (true positive rate), 83% of absences (true negative rate), and misclassified 13% (mean misclassification error) of all observations (Table 1).

Simplified bioclimatic envelope for western blackheaded budworm outbreak distribution—Almost all observed western blackheaded budworm defoliation occurred within hemlock-spruce forestlands where mean spring and summer temperatures ranged from 6.5˚ to 10.5˚C (i.e., 94% occurred in hemlock-spruce forestlands overall; 93% between 1961 and 1980, 93% between 1981 and 2000, and 95% between 2001 and 2020). Defoliation was rarely observed in hemlock-spruce forestlands with mean spring and summer temperatures below (4% of hemlock-spruce forestlands) or above (2% of hemlock-spruce forestlands) this envelope. Further, nearly all observed defoliation outside the spring and summer temperature envelope was observed adjacent to suitable hemlock-spruce forestlands in either southeast Alaska (Fig. 4A: mean spring and summer temperatures < 6.5˚C) or on Vancouver Island (Fig. 4B; mean spring and summer temperatures ≥ 10.5˚C). In contrast, defoliation was more frequently observed in forestlands with cool autumn and winter temperatures (17% mean autumn and winter temperatures < 1˚C), with low precipitation (15% total spring and summer precipitation < 60 cm; 20% total autumn and winter precipitation < 140 cm), or low basal area (38% basal area < 2.6 log[m^2/ha + 1]). Based on the simplified bioclimatic envelope, 10% of defoliation was observed in hemlock-spruce forestlands with cool temperatures and optimal precipitation, 6% with cool temperatures and low precipitation, 63% with optimal temperatures and precipitation, 19% with optimal temperatures and low precipitation, 0% with warm temperatures and low precipitation, and 2% with warm tempera-

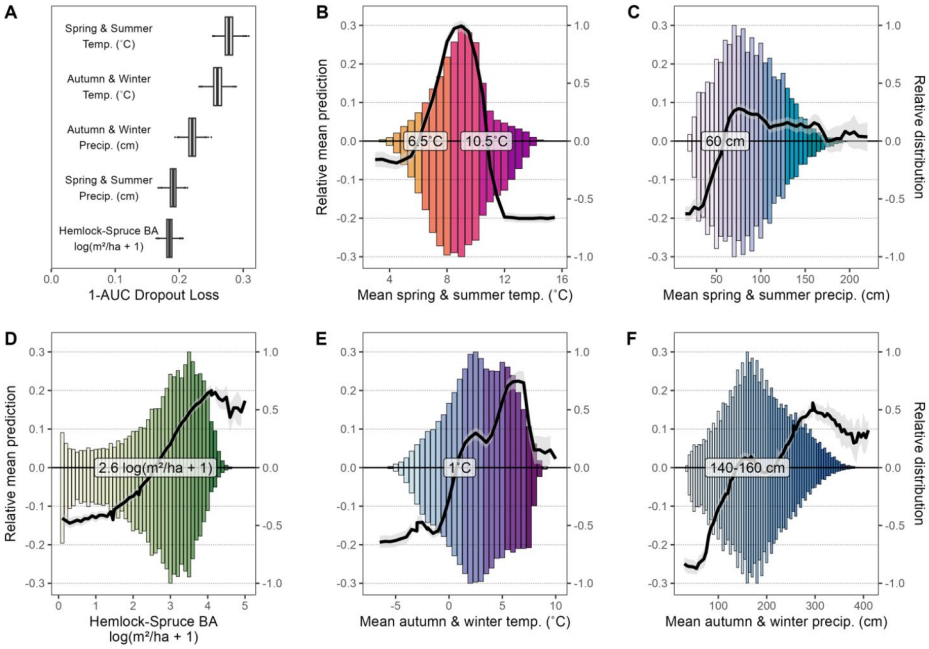

Fig. 2 Model results predicting western blackheaded budworm outbreak distribution with host tree basal area and spring-summer and autumn-winter temperature and precipitation. **A)** Variable importance for each predictor based on 1-AUC (Area Under the Curve) dropout loss. **B**-**F**) Relative mean predictions ± standard deviation (accumulated local effects) indicating positive and negative associations between predictor variable values and the probability of outbreak occurrence. Histograms depict the relative distribution of each predictor overall (negative values) and the average distribution in model training datasets (positive values; $N = 50$). Labels denote relative mean prediction thresholds that constrain the bioclimatic envelope

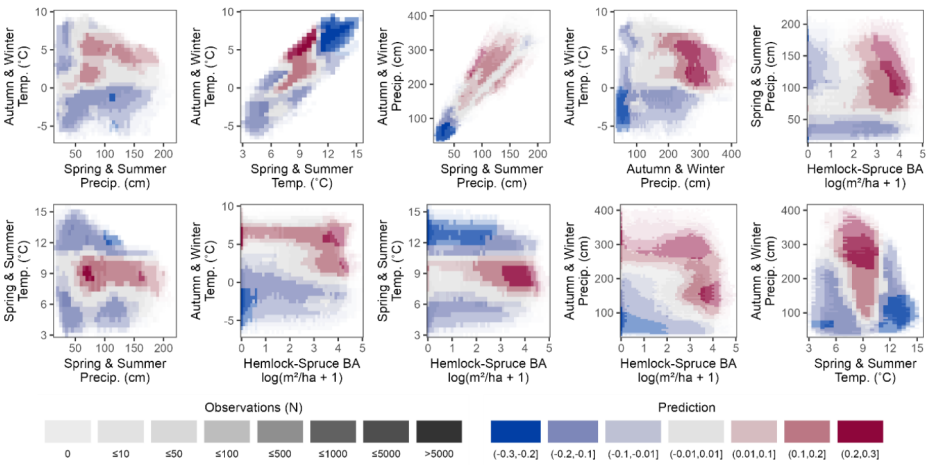

Fig. 3 Pairwise interactions among predictors that help explain the outbreak distribution of western blackheaded budworm. Interactions are arranged by greatest to least (Friedman's h^2; Table 3). Color denotes relative predictions and intensity (alpha) the number of observations present in the overall dataset

Table 3 Interaction strength (Friedman's h^2) of predictors included in the model. Overall, interactions among predictor variables explained a greater amount of prediction variation (~60%) than the sum of the main effects. Predictors are ordered by their one-way interaction strength

	Mean autumn & winter temp. (˚C)	Total autumn & winter precip. (cm)	Total spring & summer precip. (cm)	Mean spring & summer temp. (˚C)	Hemlock-spruce basal area (log[m^2/ha + 1])
Mean autumn & winter temp. (˚C)	0.46				
Total autumn & winter precip. (cm)	0.39	0.4			
Total spring & summer precip. (cm)	1.21	0.45	0.37		
Mean spring & summer temp. (˚C)	0.51	0.16	0.32	0.36	
Hemlock-spruce basal area (log[m^2/ha + 1])	0.30	0.18	0.38	0.24	0.24

tures and optimal precipitation. Collectively, these results indicate that spring and summer temperatures primarily constrain the biogeography of budworm outbreaks.

Predicted ramifications of observed & projected climatic change on the distribution of western blackheaded budworm outbreaks—Models predicted that the extent of hemlock-spruce forestlands suitable for western blackheaded budworm outbreaks increased by more than 5,000 km^2 from 1901 to 1920 (56,463 km^2) to 2001–2020 (62,127 km^2; Fig. 5). Correspondingly, hemlock-spruce forestlands identified as climatically suitable (i.e., based on the simplified climatic envelope) for budworm outbreaks increased by nearly 14,000 km^2 from 1901 to 1920 (74,108 km^2) to 2001–2020 (87,949 km^2). Warming temperatures across the Pacific coastal temperate rainforest are predicted to have a negative effect on the extent of western blackheaded budworm outbreak distribution based on all three emissions scenarios. By the end of the 21st century, the extent of western blackheaded budworm outbreak distribution is predicted to decrease (relative to 62,127 km^2 in 2001–2020) by nearly 50% (34,604 km^2; SSP 2–4.5˚C), two-thirds (Figs. 6 and 20,870 km^2; SSP 3–7.0˚C), or by more than 80% (10,598 km^2; SSP 5–8.5˚C). Similarly, the extent of hemlock-spruce forestlands that are climatically suitable for western blackheaded budworm outbreaks are projected to decrease by 2081–2100 (relative to 87,949 km^2 in 2001–2020) by more than half (42,207 km^2; SSP 2–4.5˚C), nearly 80% (Fig. 7; 18,274 km^2; SSP 3–7.0˚C), or by more than 90% (8,100 km^2; SSP 5–8.5˚C).

Broad scale decreases in the predicted extent of budworm outbreak distribution are related to the extensive warming that is projected to occur across the Pacific coastal temperate rainforest by the end of the 21st century (Fig. 1). The distribution of optimum spring and summer temperatures is projected to decrease in extent and shift upslope (Fig. 8), ultimately eclipsing the current elevational distribution of hemlock-spruce forestlands along nearly the entire latitudinal gradient of the Pacific coastal temperate rainforest.

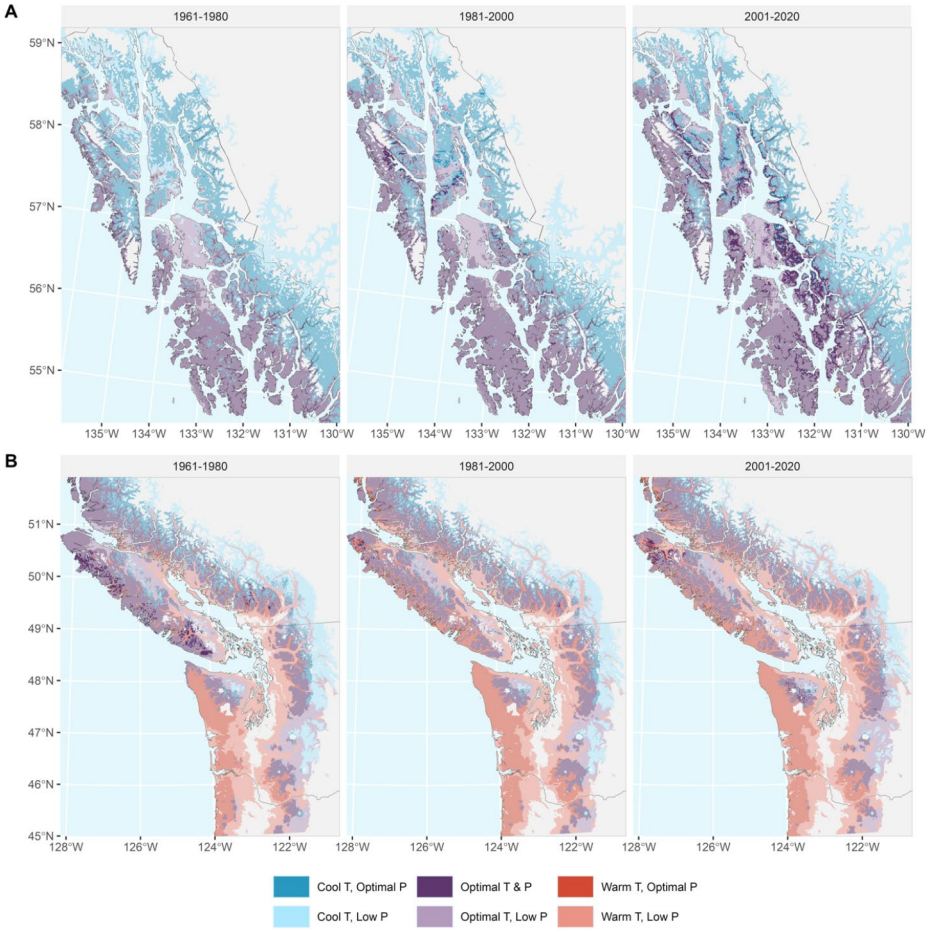

Fig. 4 Observed defoliation and simplified climatic envelope for western blackheaded budworm outbreak distribution for two regions: **A**) southeast Alaska; and **B**) the Cascades and Vancouver Island. The simplified climatic envelope is based on model-based breakpoints where T denotes temperature and P denotes precipitation. Color intensity (alpha) denotes presence/absence of western blackheaded budworm defoliation

4 Discussion

Quantifying and describing how outbreaks by insect herbivores are influenced by temperature across space and time is crucial for predicting and projecting future population irruptions. We describe how a range of spring and summer temperatures, minimum seasonal precipitation, autumn and winter temperatures, and host basal area help explain broad-scale biogeographic patterns in the outbreak distribution of a native defoliator across the Pacific coastal temperate rainforest ecoregion. Further, we document widespread observed and projected warming across our study area, consistent with other studies of the ecoregion (Shanley et al. 2015; Lader et al. 2020), and predict that continued warming will ultimately negatively impact the extent of western blackheaded budworm outbreak distribution. Spe-

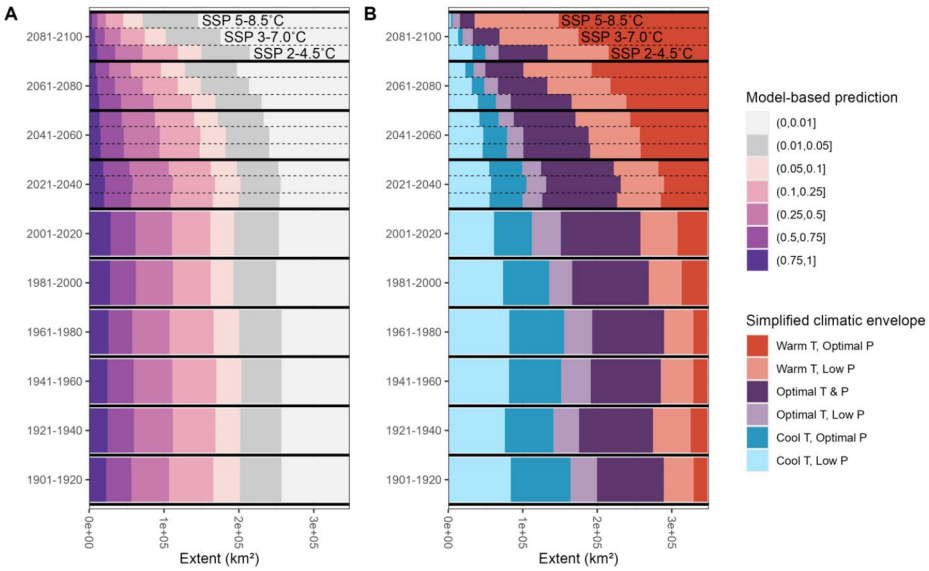

Fig. 5 Predicted extent (km^2) of western blackheaded budworm outbreak distribution based on **A**) predicted likelihood from the full model and **B**) simplified climatic envelope for historic and projected periods. The simplified climatic envelope is based on model-based breakpoints where T denotes temperature and P denotes precipitation

cifically, spring and summer temperatures in hemlock-spruce forests have already exceeded the optimal range for outbreaks in the southern Pacific coastal temperate rainforest, resulting in poleward and elevational shifts of the outbreak distribution. Model predictions based on three future climate emissions scenarios suggest this trend will continue across the entire latitudinal distribution of the Pacific coastal temperate rainforest, causing precipitous declines in the extent of climatically suitable hemlock-spruce forests by the end of the 21st century. Our findings highlight important ramifications for the frequency and extent of insect-caused disturbances across the Pacific coastal temperate rainforest and their potential impacts on high-value carbon reserves, among other ecosystem services.

Population irruptions by defoliators are a product of complex multi-scalar trophic interactions, feedbacks, and lagged density-dependence (Myers and Cory 2013). Most, if not all fine-scale dynamics such as phenological synchrony with host trees (van Asch and Visser 2007), predator-prey dynamics (Berryman 1996; Berryman et al. 2002), and host-pathogen interactions (Dwyer et al. 2004; Elderd et al. 2013) are influenced by broad-scale bioclimatic drivers that dictate the magnitude and extent of synchronous insect outbreaks and contribute to where outbreaks are biogeographically distributed (i.e., bioclimatic envelope of outbreaks). While this is a reductive approach and oversimplifies many of the mechanistic and demographic forces that shape irruptive dynamics, it is useful for evaluating potential climate change impacts, especially for those species (e.g., western blackheaded budworm) where we lack a basic understanding of thermal biology, development rates, stage-specific survival, dispersal processes, and trophic interactions. Despite these limitations, our results conform with other biogeographic analyses of prominent defoliators where winter temperatures limit the latitudinal and elevational ranges of defoliator outbreak distributions (Neu-

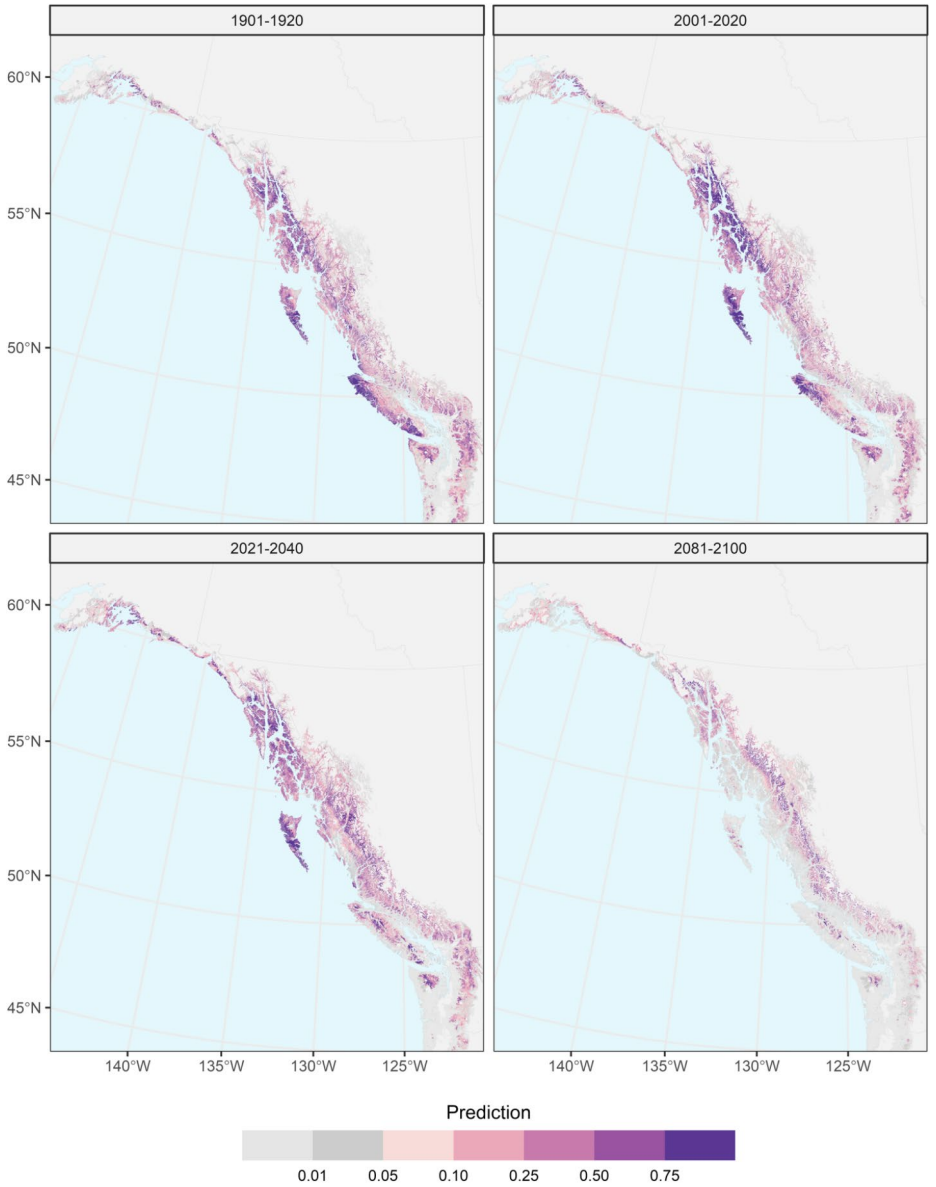

Fig. 6 Predicted extent (km^2) of western blackheaded budworm outbreak distribution based on historic and projected climate conditions. Projections are based on the SSP 3–7.0˚C emissions scenario (bottom). Maps for all 20-year periods and emissions scenarios (i.e., SSP 2–4.5˚C and SSP 5–8.5˚C) are provided in Supplement 3

vonen et al. 1999; Battisti et al. 2005; Jepsen et al. 2008; Srivastava et al. 2023; Boulanger et al. 2024), while spring and summer temperatures can limit the equator-ward range (Tobin et al. 2014; Thompson et al. 2017; Bourougaaoui et al. 2021; Boulanger et al. 2024). Our findings not only provide another example of a poleward and elevational range expansion

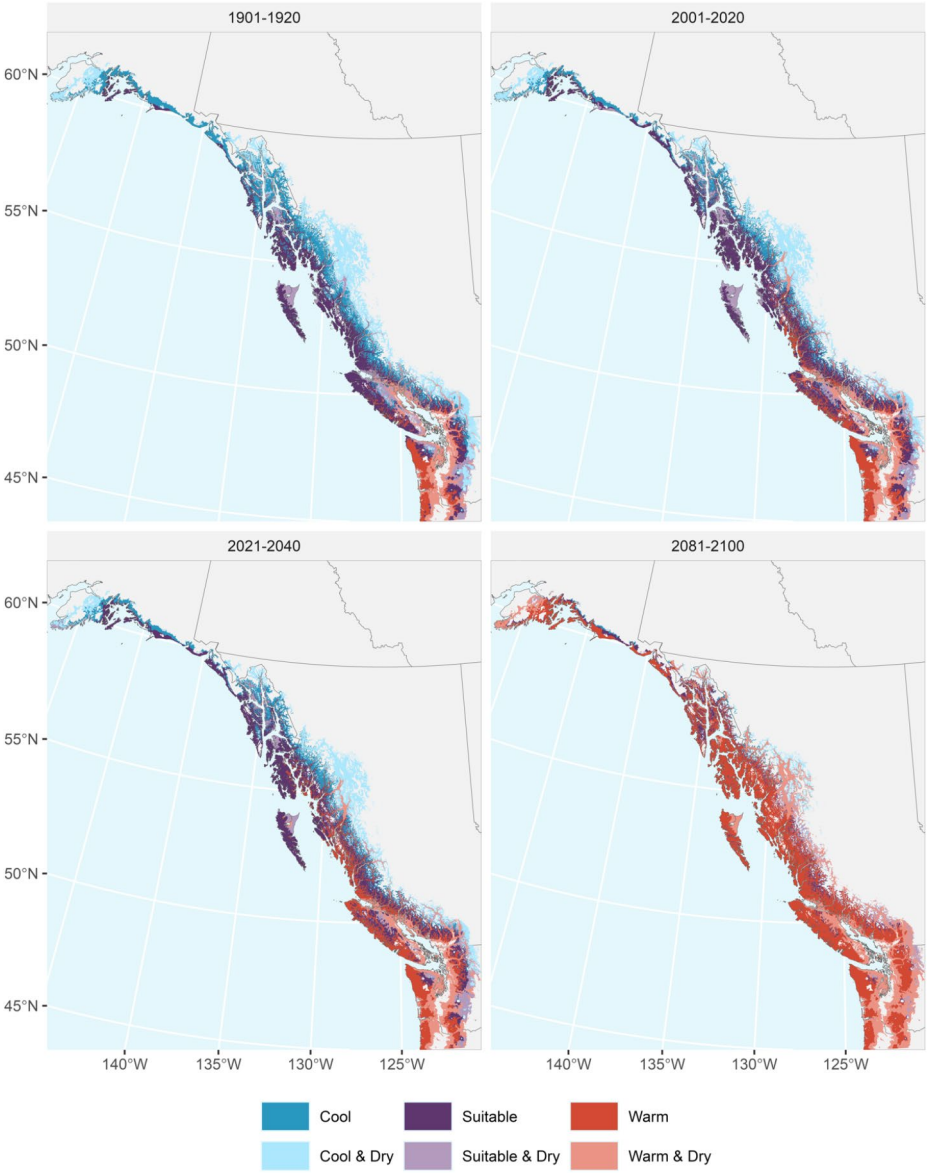

Fig. 7 Simplified climatic envelope for western blackheaded budworm outbreak distribution based on historic and projected climate conditions. The simplified climatic envelope is based on model-based breakpoints where T denotes temperature and P denotes precipitation. Displayed projections are based on the SSP 3–7.0˚C emissions scenario (bottom). Simplified climate envelopes for all 20-year periods and emissions scenarios (i.e., SSP 2–4.5˚C and SSP 5–8.5˚C) are provided in Supplement 4

by an irruptive forest insect herbivore, they also contribute to the small but growing list of defoliators that may be negatively impacted by increasing temperature.

How warm temperatures affect western blackheaded budworm population dynamics is unknown, although our broad-scale model-based finding that outbreaks occur within a

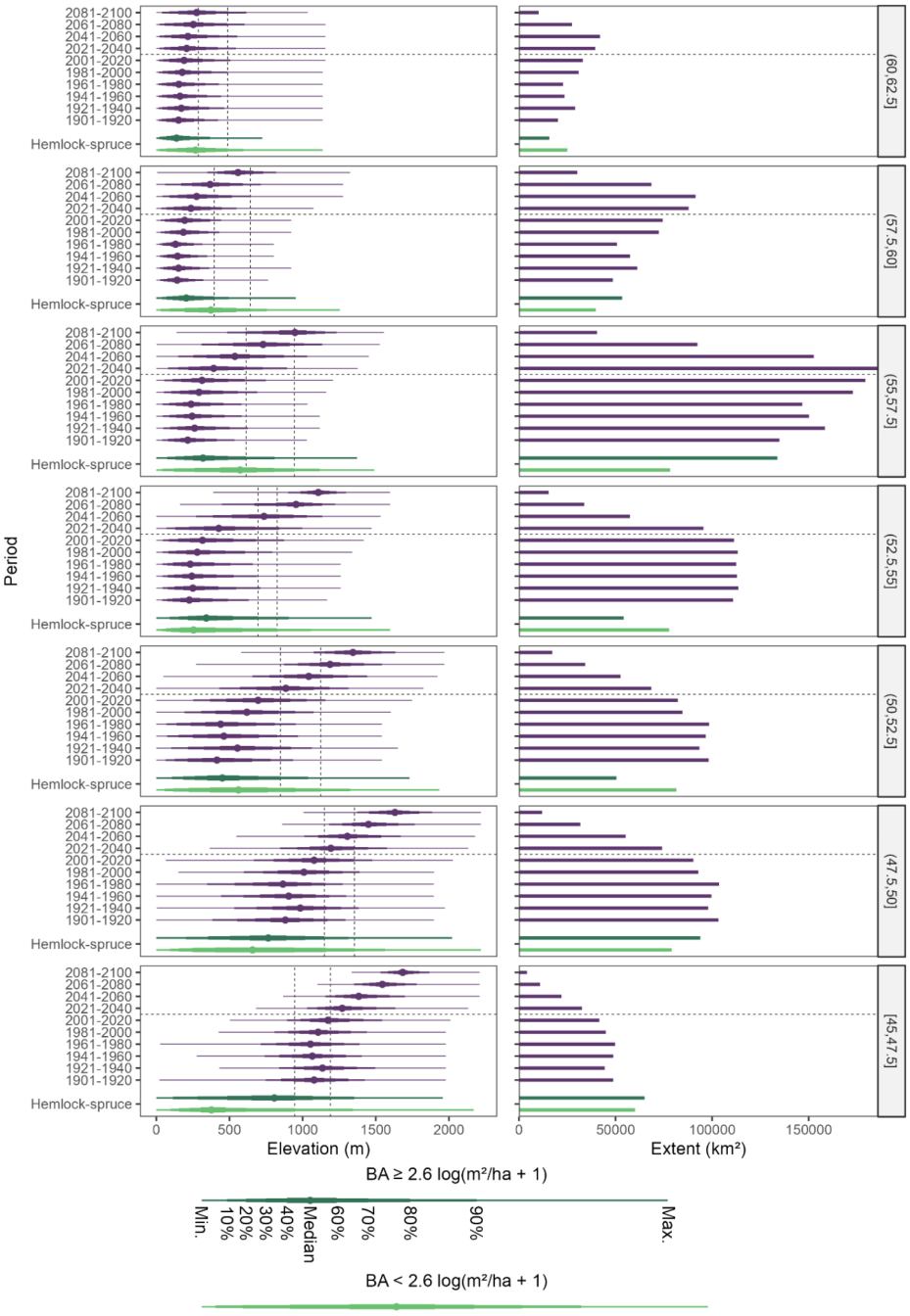

Fig. 8 Elevational distribution (left) and extent (right) of hemlock-spruce forestlands with mean spring and summer temperatures between 6.5–10.5˚C as compared to the distribution and extent of hemlock-spruce forestlands, stratified by latitude. Horizontal line delineates historical and projected conditions based on the SSP 3–7.0˚C emissions scenario. Vertical lines denote the 80% percentiles for high and low hemlock-spruce forestland basal area. Distributions based on other emissions scenarios (i.e., SSP 2–4.5˚C and SSP 5–8.5˚C) are provided in Supplement 5

temperature optima is supported by several field-based reports of extant outbreaks collapsing following anomalously warm temperatures (Schmiege 1966; Hard 1974). In other forest Lepidoptera, warm temperatures that exceed temperature optima have direct negative impacts on larval survival (Rouault et al. 2006; Robinet et al. 2015; Thompson et al. 2017; Banahene et al. 2018) or cause diapausing larvae to deplete energy stores (Han and Bauce 1997; Nealis and Régnière 2016, 2021). Warming temperatures have also been shown to have indirect negative effects on Lepidoptera populations by decreasing host quality (Holopainen et al. 2018), altering predator-prey dynamics (Furlong and Zalucki 2017; Damien and Tougeron 2019), or shifting the geographic window for phenological synchrony with host trees (i.e., phenological asynchrony)(Miller-Rushing et al. 2010; Renner and Zohner 2018; Visser and Gienapp 2019; Simmonds et al. 2020). Phenological asynchrony along an elevational gradient is one of the suggested mechanisms responsible for the collapse of regular larch budmoth outbreaks in the European Alps (Saulnier et al. 2017; Büntgen et al. 2020), in part because the bioclimatic envelope for outbreak populations (e.g., the outbreak epicenters) increased in elevation (Johnson et al. 2010), ultimately surpassing the elevational distribution of its host (Hartl-Meier et al. 2017). Collapse of cyclical population dynamics does not necessarily translate to a total cessation of outbreaks. For example, larch budmoth outbreaks were recently observed in the European Alps after more than 30 years of absence (Büntgen et al. 2020). Regardless of mechanism, our findings and projections suggest that western blackheaded budworm outbreak dynamics could follow a similar pattern as those of larch budmoth and ultimately collapse.

Population irruptions of insects are vital components of ecosystems (Yang 2012), whether they occur in aquatic systems (Ives et al. 2008), agricultural systems (Collett et al. 1998; Simpson et al. 1999), or forests (Ludwig et al. 1978; Royama 1992; Bjornstad and Grenfell 2001). Outbreaks by herbivorous insects can contribute to gap formation in forests, which are biodiversity hotspots for insects and vertebrates (Müller et al. 2008; Forsman et al. 2010; Vindstad et al. 2019; Przepióra et al. 2020) and are vital components of forest successional processes. Further, when insect populations reach irruptive levels they provide abundant food sources for birds and mammals (Koenig and Liebhold 2005; Wilson and Barclay 2006), with cascading effects throughout food webs (Eveleigh et al. 2007; Calderón-Sanou et al. 2021). Finally, insect outbreaks alter nutrient cycles through large inputs of frass and eventually carcasses, both of which are rich in nitrogen and contribute to plant and ecosystem productivity (Hunter 2001; Gratton et al. 2008). The potential collapse of western blackheaded budworm outbreak dynamics may have numerous negative and unforeseen consequences for ecosystem processes across the Pacific coastal temperate rainforest.

Projecting defoliator outbreak regimes across the Pacific coastal temperate rainforest is crucial because of the ecosystem's status as a preferred carbon reserve (DellaSala et al. 2022; Law et al. 2022). This productive ecosystem has high carbon storage capacity and accretion rates with a relatively low risk of carbon loss due to the historical rarity of severe or stand-replacing disturbances. Our models predict the outbreak distribution of western blackheaded budworm will narrow under future climate emissions scenarios due to warm spring and summer temperatures, yet budworm is only one of several irruptive defoliators in the Pacific coastal temperate rainforest. Population irruptions by hemlock sawfly (*Neodiprion tsugae*) and western hemlock looper (*Lambdina fiscellaria*) are reportedly influenced by drought (hemlock sawfly)(Hard 1976) or a combination of drought and warm temperatures (western hemlock looper)(McCloskey et al. 2009). Thus, the projected increase in

drought frequency across southeast Alaska (Lader et al. 2020), coupled with warming may increase the frequency and extent of outbreaks by either of these insects. Uncertainty in future outbreak dynamics may heighten the risk profile of carbon reserves and investment, especially if outbreaks become less predictable.

4.1 Knowledge gaps

Little is known about western blackheaded budworm thermal biology, stage-specific development rates, how temperature affects demography, or long-term trends in outbreak dynamics. Further research on virtually all aspects of western blackheaded budworm biology and population dynamics is necessary. Aside from basic questions relating to western blackheaded budworm biology, this work highlights the need for further research on insect outbreak distributions, especially at equator-ward range margins. Disentangling mechanistic constraints such as how heat limits insect performance (i.e., thermal performance curves), development, and population dynamics is vitally important for predicting and projecting how insects will respond to continued anthropogenically driven climate warming. Finally, the impact of defoliator outbreaks in the Pacific coastal temperate rainforest are not well described and thus quantifying defoliation-caused mortality rates, canopy loss and top kill, and their impacts on forest structure and ecosystem dynamics remains a priority.

4.2 Conclusions

Projecting insect population responses to climate warming and quantifying their possible impacts remains a high priority across global forest ecosystems. Here, we describe substantial projected warming across the Pacific coastal temperate rainforest and the impact on irruptive populations of western blackheaded budworm. Model results suggest that seasonal temperatures may exceed the bioclimatic constraints for regular population irruptions by this native herbivore, with unknown ramifications for the Pacific coastal temperate rainforest disturbance regime, nutrient cycles, or insectivores. We advocate for continued investigation of defoliation outbreak dynamics in the Pacific coastal temperate rainforest ecosystem given its importance as a carbon reserve and biodiversity hotspot. A better understanding of outbreak dynamics will help refine projections of carbon risk and evaluations of ecosystem resilience in the face of continued anthropogenic climatic change.

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Author contributions Michael Howe: Methodology, Formal analysis, Writing – Original Draft, Visualization. Elizabeth E Graham: Conceptualization, Writing – review & editing, Project administration. Kellen N Nelson: Conceptualization, Writing – review & editing, Supervision, Project administration.

Data availability All datasets used in this analysis are freely available. Code and model outputs available upon request.

Declarations

Competing interests The authors declare that they have no known competing financial or personal conflicts that could have influenced the work reported in this paper.

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