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Research article

Defoliator outbreaks track with warming across the Pacific coastal temperate rainforest of North America

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The biogeography of irruptive insect herbivores is determined by host availability and climate conditions. As such, outbreak distributions are sensitive to climatic change, especially across large latitudinal gradients. Here, we investigate the outbreak distributions of two understudied defoliators, hemlock sawfly *Neodiprion tsugae* (Hymenoptera) and western blackheaded budworm *Acleris gloverana* (Lepidoptera), that have both recently impacted the greatest land area recorded across the Pacific coastal temperate rainforest since the establishment of aerial survey programs. We compiled polygon-based estimates of insect damage collected by aerial observers, forest inventory, and downscaled climatic data to develop gridded estimates of bioclimatic conditions across the extent of the Pacific coastal temperate rainforest, including the continental United States, British Columbia and Alaska. We leveraged these data to develop ensemble machine learning models with the goal of predicting the outbreak distribution of each insect. In this manuscript we: 1) describe the historical patterns of defoliator outbreaks, 2) identify and describe climatic conditions associated with outbreaks in both species and 3) assess whether historic outbreaks have tracked geographic shifts in climate conditions across the region. We demonstrate that outbreaks of hemlock sawfly and western blackheaded budworm have been observed across the Pacific coastal temperature rainforests of North America in each decade since the establishment of the Canadian and United States aerial survey programs. The distribution of outbreaks by both insects were best explained by host availability, a limited range of spring, summer, and winter temperatures, and minimum precipitation. Finally, we demonstrate that outbreaks have tracked the poleward shift in suitable climate over the last century. This study establishes a baseline understanding of the climatic constraints and biogeographic patterns of historic sawfly and budworm outbreaks across the Pacific coastal temperate rainforest and emphasizes the overarching importance of climate in driving the irruptive dynamics of these defoliator species.

Keywords: climate envelope, defoliators, hemlock sawfly, Pacific coastal temperate rainforest, population dynamics, western blackheaded budworm

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Introduction

Global disturbance regimes are escalating under shifting climate conditions (Seidl et al. 2017), with disturbances caused by outbreaks of forest insects affecting the greatest extent annually in forested ecosystems (Hicke et al. 2016, Kautz et al. 2017). Climate strongly influences insect population dynamics and projections of future climate suggest a substantial increase in conditions that promote insect population growth and degrade host tree vigor. The impacts of insect related tree damage and mortality events directly affect ecosystem process and function (Kurz et al. 2008, Seidl et al. 2017, McDowell et al. 2020) often with economic implications (Chang et al. 2012, Gregoire et al. 2015). The drivers of population dynamics and their effects are well documented in bark beetle systems (Raffa et al. 2008, Aukema et al. 2016, Biedermann et al. 2019), but insect defoliator systems are complex, system specific, and not as well understood (Pureswaran et al. 2018). An improved understanding of the climate constraints and biogeographic distributions of defoliator outbreaks are critical for predicting how outbreak regimes may change in response to future climate conditions and help society anticipate the extent, frequency, and possible impacts of contemporary and future outbreaks.

Defoliator insect populations often irrupt at regular intervals and outbreak cycles are governed by density-dependent processes, cross-scalar trophic interactions, and density-independent drivers such as weather and climate. As poikilotherms, insects are highly sensitive to temperature, which alters their development rate, generation time, fecundity, and survival (Bale 1991, Neven 2000, Gillooly et al. 2001, Deutsch et al. 2008, Pörtner and Farrell 2008, Robinet and Roques 2010). Forest insects are less sensitive to variation in hydrological regimes, although water availability regulates host availability, forage quality, and tree defenses, all of which influence outbreak cycles and population dynamics (Jactel et al. 2012, Flower et al. 2014, Kolb 2016, Trowbridge et al. 2021). Defoliator population cycles are generally cyclical and often follow seasonal to multi-annual temperature anomalies and are regulated by delayed feedback loops enforced by predator–prey, insect–parasitoid, insect–disease, or insect–host relationships (Royama 1992, Berryman 1996, Bjornstad and Grenfell 2001, Dwyer et al. 2004, Myers and Cory 2013). At the sub-continental scale, the extent, severity and synchrony of defoliator outbreaks are influenced by density-independent factors such as regional climate and host forage availability and connectivity (Peltonen et al. 2002, Cooke et al. 2007, Haynes et al. 2014, 2018). Population decline typically occurs after several years of outbreak conditions as the impact of negative density-dependent controls supersede the effects of positive controls. Often, negative controls are exerted by the spread of disease, a build-up of predators or parasitoids, or the depletion of host resources. The degree of host resource limitation and rate of recovery regulates outbreak recurrence, duration, and extent. Predicting outbreak cycles is particularly challenging and requires a detailed understanding of how insect populations respond within communities to climatic and host drivers through time. Here, we focus broadly on identifying climate conditions associated with the spatial patterns of historic defoliator outbreaks to improve predictive frameworks and guide future research and management activities.

The spatial distributions of native insects are constrained by species climatic tolerances, competitive fitness, and host range. The distributions of insect outbreaks and their regimes vary geographically through time following system specific favorable patterns in phenological synchrony, climate norms, and bioclimatic variability (Esper et al. 2007, van Asch and Visser 2007, Flower 2016). Historically, this variation occurred within a species extant range; however, ongoing climate change has spurred insect outbreaks in previously undocumented areas, in some cases affecting 'semi-naïve' host populations such as the temperature driven expansion of mountain pine beetle *Dendroctonus ponderosae* into upper-elevation whitebark pine *Pinus albicaulis* forests (Hicke and Logan 2009, Raffa et al. 2013, Howe et al. 2021), and boreal jack pine *Pinus banksiana* forests (Safranyik et al. 2010, Cullingham et al. 2011, de la Giroday et al. 2012, Burke et al. 2017, Cooke and Carroll 2017). More commonly, shifts in temperature lead to increases in the poleward extent of outbreaks (Battisti et al. 2005, Jepsen et al. 2008, 2011, Pureswaran et al. 2015, Robson et al. 2015, Dodds et al. 2018), elevational expansions (Battisti et al. 2006, Esper et al. 2007, Johnson et al. 2010, McCain and Garfinkel 2021), and changes in the frequency and extent of outbreak cycles (Paritsis and Veblen 2011, Flower 2016).

In the Pacific coastal temperate rainforest, broad-scale outbreaks of two defoliators, the hemlock sawfly *Neodiprion tsugae* and western blackheaded budworm *Acleris gloverana*, have defoliated forests across 10° of latitude since at least the 1940s (Mask 1992) and back-to-back outbreaks have affected nearly 20 000 km^2 since 2018 (FS-R10-FHP. 2018-2022). Both species feed on western hemlock *Tsuga heterophylla*, mountain hemlock *Tsuga mertensiana*, and Sitka spruce *Picea sitchensis*. Hemlock sawfly feed on mature needles whereas the western blackheaded budworm feed on current year's growth. Little is known about the bioclimatic distribution of sawfly or budworm outbreaks; most historical work focused on the effects of weather rather than climate and indicates that population dynamics in both species may be linked to weather conditions. Hemlock sawfly populations are hypothesized to be influenced by drought and indirectly mediated by a fungal pathogen (*Entomophthora sphaerosperma*; Hard 1976). Western blackheaded budworm population cycles have been reported to occur at 12 to 16 year intervals (Shepherd and Gray 2001), but geographic variation in this interval is unknown and the reported influence of weather is inconsistent. For example, outbreaks were suggested to occur following drought (Silver 1960) and warm summers (Hard 1974), while other studies found no association between the start of outbreaks and temperature (Silver 1963, Schmiege 1966). Further, outbreak collapse has been attributed to both warm (Schmiege 1966) and cold-wet summer conditions (Prebble and Graham 1945, Hard 1974). Inferences

from prior studies have been limited due to their focus on a single outbreak, their implementation at small geographic extents, and their lack of replication (e.g. fewer than 10 sites in any study). Here, we leverage data at broader spatial and temporal domains to investigate the relationship between climate and each species outbreaks to better understand system constraints and pave the way to predict patterns of future outbreaks across the region.

In this study, we construct ensemble machine learning models using aerial detection surveys of hemlock sawfly and western blackheaded budworm and downscaled climate data from 1901-present to: 1) describe the historical patterns of defoliator outbreaks across the Pacific coastal temperate rainforest, 2) identify and describe climate conditions associated with outbreaks in both species and 3) assess whether historic outbreaks have tracked geographic shifts in climate conditions across the region.

Material and methods

Data

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 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 hemlock sawfly and 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. Aerial detection data were available for different time periods in each region of our analysis (Alaska: 1989–2022, BC: 1960–2022, CONUS: 1997–2022).

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^{-1}) to 0.25 km^2 and transforming units to m^2 ha^{-1}. 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; m^2 ha^{-1}; log-transformed) for all models.

Climate

We compiled decadal climate data from raster-based estimates of annual and seasonal climate variables (1901–1910…2011–2020; 800 m raster; ClimateNA; Wang et al. 2016). We selected 14 candidate climate variables: Hogg's climate moisture index; precipitation as snow (cm); mean annual temperature (°C); mean annual precipitation (cm); number of frost-free days; spring, summer, autumn, and winter mean temperature (°C); spring, summer, autumn, and winter precipitation (cm); and minimum winter temperature (°C). Decadal climate data were intersected with the 0.25-km^2 grid and averaged per grid cell. Climate variables were selected based on hypothesized relationships and tested for inclusion in the final model (Supporting information). Ultimately, we selected minimum winter temperature, mean spring temperature, mean summer temperature, total summer precipitation, and total winter precipitation for inclusion.

Models

Ensemble model

We constructed classification ensemble (i.e. 'model stacking') models with the *ranger* implementation of random forest and the *XGBoost* implementation of 'extreme' gradient boosting. We tuned model hyperparameters based on a grid approach, although neither individual modeling approach is particularly influenced by hyperparameter selection. Based on tuning, we used Gini index as the split criterion for the random forest and grew 300 trees. We fit our gradient boosting models as probability boosted trees with the following parameters: 300 rounds (number of trees); a max depth of 9; η of 0.25 (step size shrinkage), and λ of 0.3 (L2 regularization term). Training data were selected for each ensemble model by randomly selecting 63% of observed presences per decade of observed sawfly and budworm defoliation and an equal number of absences to construct a balanced model. Predictions from each individual model (the random forest and gradient boosting) were averaged to compute a final prediction. We assessed model performances with confusion matrix metrics based on an independently sampled dataset. Since we report model performance across both the full dataset and an independent representative sample, we do not report out-of-bag performance metrics. Further, we used 1-AUC (area under the receiver-operator curve) dropout loss (Bücker et al. 2022) to assess variable importance, and accumulated local effects (Apley and Zhu 2020) to visualize relative mean predictions.

Model workflow

We constructed a series of separate ensemble models to predict the biogeographic distribution of hemlock–spruce forestlands and each insect in this study. First, we developed a simple model to predict the presence/absence of hemlock–spruce forestlands for data visualization purposes. We provide the methods and results of this model in the Supporting information. Second, we developed models to predict the spatial extent of outbreak populations of hemlock sawfly and western blackheaded budworm. Models were fit by selecting 63% of presences per decade (1961–1970 onward) and an equal number of absences. Models were constructed 10 times

for each insect species and average predictions and performance metrics are reported. Model selection was performed to select the best predictors and predictors were checked for multicollinearity (Spearman pairwise correlation < 0.7). Model selection details are provided in the Supporting information. Finally, based on our model predictions (decadal predictions from 1901–1910…2011–2022) and the thermal climate envelope based on our model results, we explored how the latitudinal range of areas suitable for western blackheaded budworm outbreaks has shifted over the duration of this study. We decided to focus on budworm outbreaks because we have a better historical record of the cyclical outbreaks in this species.

Modeling decisions and caveats

Analyses were restricted to hemlock–spruce defoliation attributed to either hemlock sawfly or western blackheaded budworm. This decision likely results in an underestimate of defoliation because western blackheaded budworm defoliation of spruce is similar to damage caused by other common defoliators, such as western spruce budworm, and thus may be incorrectly attributed; and there are several instances of unspecified 'unknown' or 'defoliator' reports in forests containing western or mountain hemlock. Further, the reported extent of sawfly and budworm defoliation across southeast Alaska is likely an underestimate due to the limited aerial survey coverage and frequent low cloud ceilings that obscure possible defoliation at higher elevations (see the Supporting information for more details).

Model confidence

Constructing spatiotemporally explicit models that predict the likelihood of insect outbreaks across large geographic extents is challenging, especially across areas with low spatial and unequal temporal coverage. We are most confident in our model predictions for southeast Alaska, Vancouver Island and the Olympic mountains in Washington. We are the least confident in our model predictions across the coastal mountains of British Columbia and at higher elevations for several reasons: 1) the coastal mountains in BC are sparsely populated and aerial detection survey coverage is extremely sparse; and 2) forestlands across these areas are among the wettest included in our study area. As a result, we are not as confident in predicted relationships across areas where precipitation is extremely high.

Packages

All analyses were conducted in R (ver. 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).

Data availability

Data products (compiled data, model predictions and analysis code) are available through Howe et al. 2024.

Results

Observed patterns of defoliation

Since 1960, 9135 km^2 of hemlock sawfly defoliation was reported primarily in southeast Alaska but also Vancouver Island. Eighty percent of this defoliation was reported during the most recent outbreak from 2015 to 2020 (Fig. 1). Western blackheaded budworm defoliation was reported across 34 057 km^2 of the Pacific coastal temperate rainforest spanning from the Olympic Peninsula, WA to the Cook Inlet, AK. Nearly a third (10 486 km^2) of the reported extent occurred during the most recent outbreak in southeast Alaska from 2018 to 2022.

Climatic constraints on outbreak populations of hemlock sawfly

The geographic distribution of hemlock–spruce forestlands putatively suitable to support outbreaks of hemlock sawfly defoliation was best explained by total summer precipitation greater than 34 cm, hemlock–spruce basal area greater than 2.5 log(m^2 ha^{-1} + 1), total winter precipitation between 45–102 cm, spring temperatures between 3.8° and 6.5°C, summer temperatures between 11.5° and 14.5°C, and minimum winter temperatures between −4.4° and 2.0°C (Fig. 2). Geographically, stands with suitable conditions to support outbreaks were primarily located in southeast Alaska (Fig. 3). In total, our sawfly outbreak distribution model correctly predicted, on average, 99.3% of observed hemlock sawfly defoliation (true positive rate; Table 1) and 94.6% of where there was no observed defoliation (true negative rate).

Climatic constraints on outbreak populations of western blackheaded budworm

The geographic distribution of hemlock–spruce forestlands suitable to support outbreaks of western blackheaded budworm defoliation was best explained by minimum winter temperatures greater than −2.5°C, summer temperatures between 12.0° and 14.5°C, total summer precipitation greater than 25 cm, spring temperatures between 1.6° and 6.5°C, total winter precipitation greater than 46 cm, and hemlock–spruce basal area greater than 2.7 log(m^2 ha^{-1} + 1) (Fig. 2). Geographically, stands with suitable conditions to support outbreaks were located throughout the study extent and included forests in the Olympic Mountains, northern Vancouver Island, Haida Gwaii and southeast Alaska (Fig. 4). In total, our budworm outbreak distribution model correctly predicted, on average, 98.4% of observed budworm defoliation (true positive rate; Table 1) and 91.9% of where there was no observed defoliation (true negative rate).

Evidence for shifting outbreak distributions

The budworm outbreaks detailed in this manuscript exhibited consistent response to climate conditions through time (Fig. 5A–B); however, their geography varied in response to

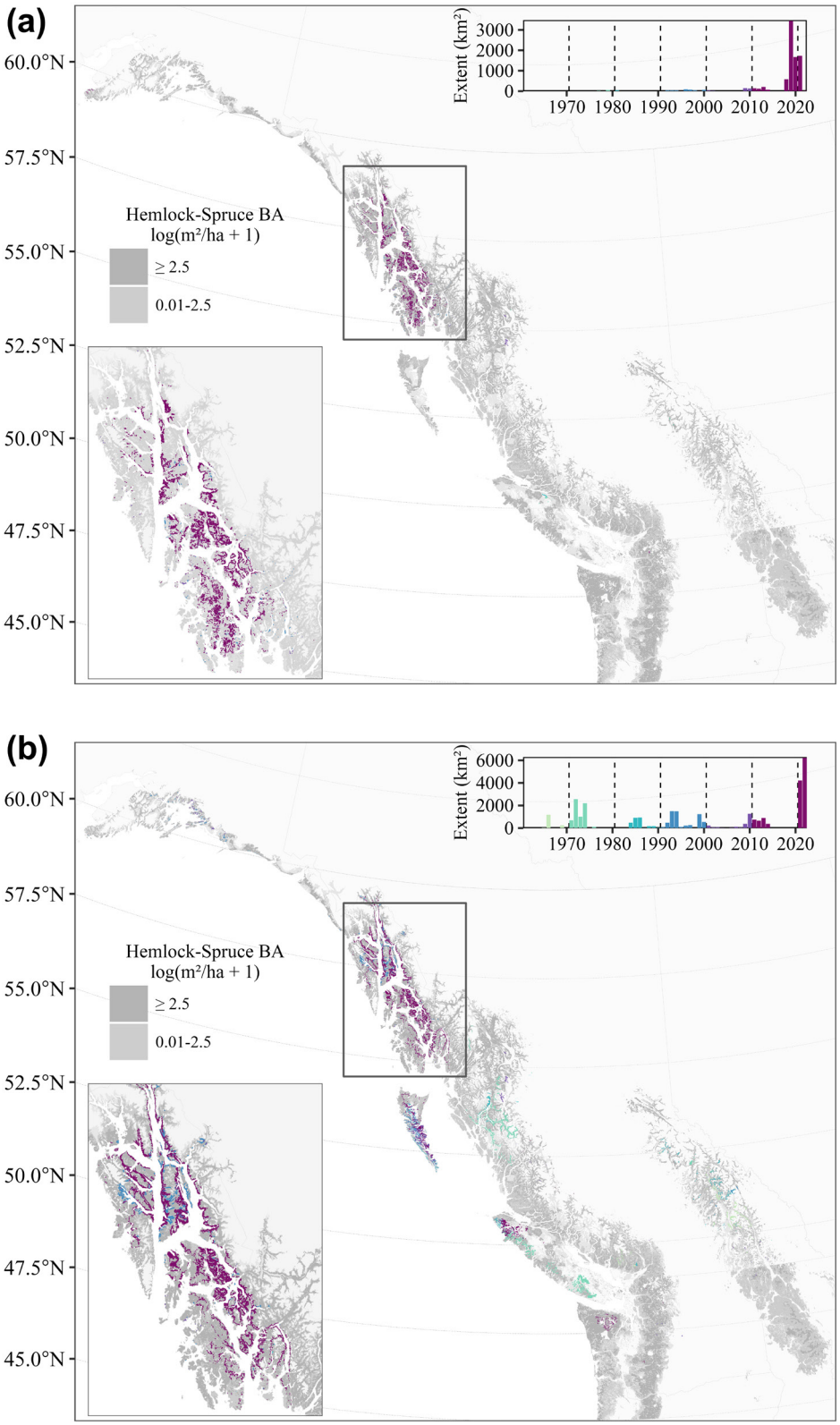

Figure 1. Observed distribution of forest defoliation from (a) hemlock sawfly and (b) western blackheaded budworm across the Pacific coastal temperate rainforest (Projection: NAD83/BC Albers [EPSG:3005]). Colors denote the last decade of recorded defoliation (time-series panel provides the key) and greyscale denotes our study area, binned by hemlock–spruce basal area.

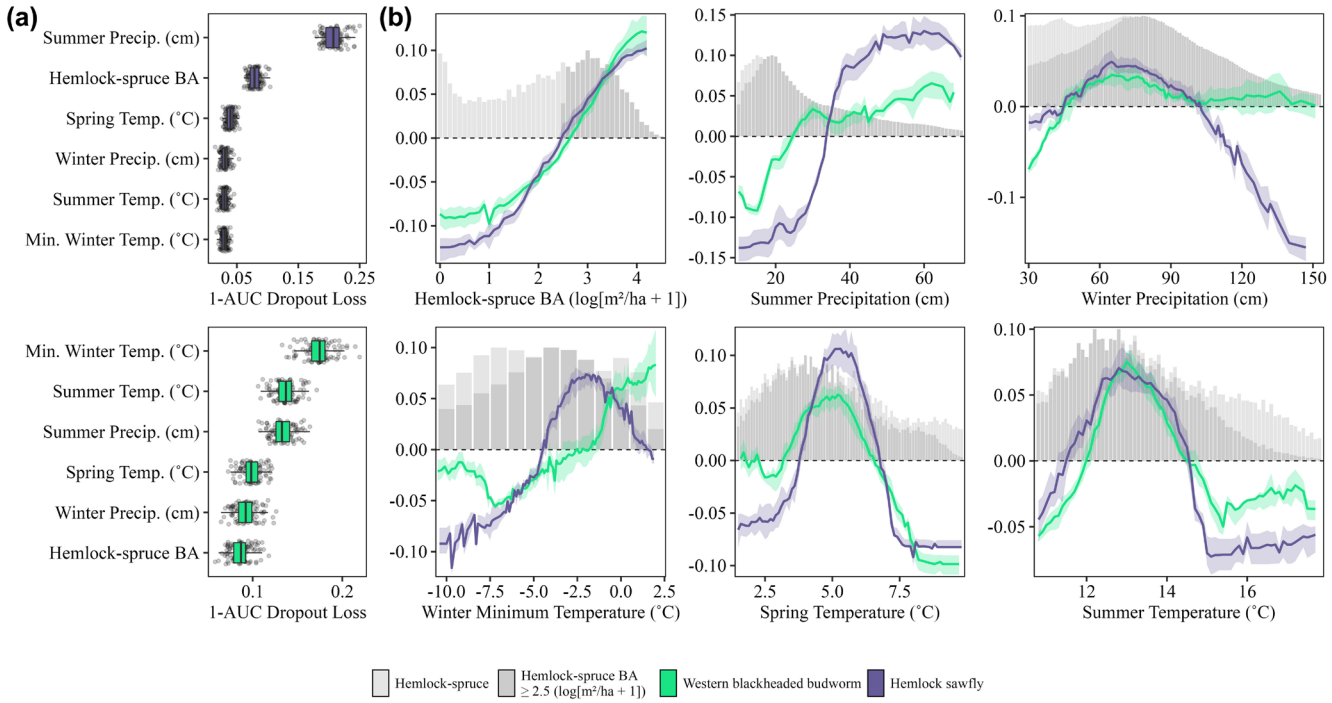

Figure 2. Putative climatic constraints on irruptive populations of hemlock sawfly and western blackheaded budworm. (a) Variable importance (1-AUC dropout loss) for best predictors of outbreaks for each species based on 100 iterations (10 constructed models and 10 iterations within each model). (b) Relative predicted relationships between each predictor and defoliator (lines) overlaid on the distribution (scaled between 0–0.1) of each predictor across hemlock–spruce forests, where light grey corresponds to all hemlock–spruce forestlands (basal area > 0 log [m^2 ha^{-1} + 1]) and darker grey corresponds to high hemlock–spruce basal area (≥ 2.5 log [m^2 ha^{-1} + 1]) forestlands.

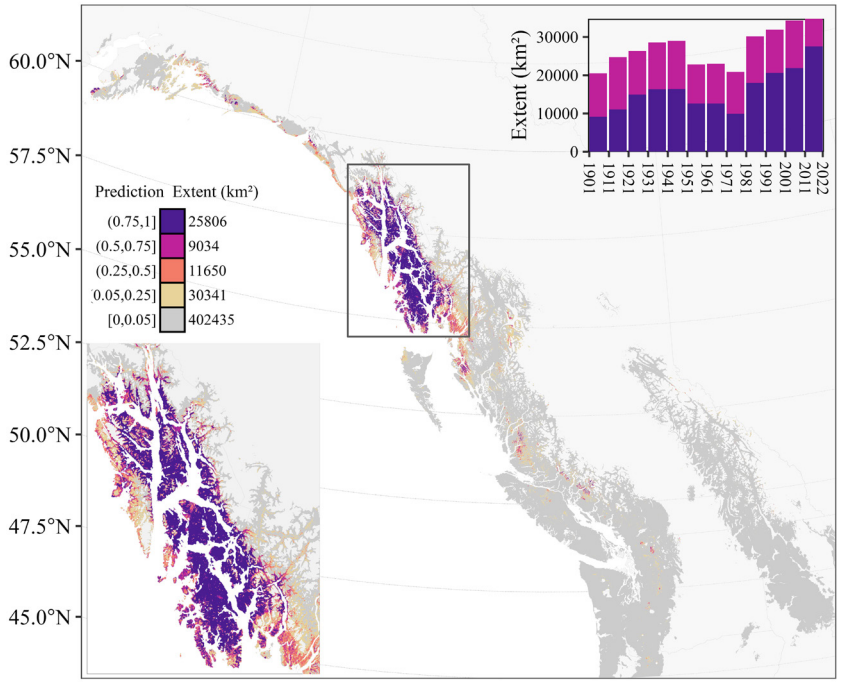

Figure 3. Predicted likelihood that hemlock–spruce forestlands could support irruptive populations of hemlock sawfly between 2011–2020 across the Pacific coastal temperate rainforest. Map insets provide a zoomed view of southeast Alaska and the predicted extent (km^2) of high hemlock–spruce basal area (≥ 2.5 log [m^2 ha^{-1} + 1]) forestlands that could support irruptive populations in each decade. Colors in the bar chart correspond to prediction intervals.

Table 1. Model performance evaluated with an independent dataset. Abbreviations: HSF = hemlock sawfly; BHBW = western blackheaded budworm; TP = true positives; FP = false positives; FN = false negatives; TPR = true positive rate; TNR = true negative rate. Evaluating true negatives is difficult based on the unequal temporal coverage of aerial detection flights. See the Supporting information for more details.

HSF	TP	FP	FN	TPR	TNR
Overall	26 294	7111	186	0.993	0.946
1971–1980	349	–	7	0.980	–
1981–1990	180	–	–	>0.99	–
1991–2000	1697	–	24	0.986	–
2001–2010	1443	–	24	0.984	–
2011–2022	38 259	–	51	0.999	–
BHBW	TP	FP	FN	TPR	TNR
Overall	84 995	34,942	1,398	0.984	0.919
1961–1970	5984	–	112	0.982	–
1971–1980	26 581	–	161	0.994	–
1981–1990	10 998	–	134	0.988	–
1991–2000	24 236	–	170	0.993	–
2001–2010	8977	–	171	0.981	–
2011–2022	59 361	–	251	0.996	–

regional climate variation (Fig. 5C). Similar analyses were not possible for sawfly outbreaks because geospatial data on past outbreaks was lacking. Over the last 12 decades, hemlock–spruce forestlands with susceptible forest structure (basal area ≥ 2.5 log[m^2 ha^{-1} + 1]) experienced warming temperatures. Across all susceptible hemlock–spruce forests, mean winter minimum temperature increased from −5.5°C in 1901–1910 to −3.1°C in 2011–2020, mean spring temperatures increased from 4.2 to 5.4°C, and mean summer temperatures increased from 12.5 to 13.7°C. Data do not indicate a change in total summer nor total winter precipitation during this period.

When we overlay historic climate conditions over the contemporary host tree distribution map, it is evident that rising regional temperatures have shifted the latitudinal distribution of suitable climate (Fig. 5, 6). The extent of susceptible hemlock–spruce forest that experienced suitable summer temperatures for budworm outbreaks (11.5°–14.5°C) has more than doubled since the early 20th century with the southern 25th percentile latitude shifting from 45.8° to 46.0° and the northern 75th percentile shifting from 48.5° to 49.7° between 1901–1910 and 2011–2020, respectively. Similarly, the extent of susceptible hemlock–spruce forest that experiences suitable winter minimum temperatures for budworm outbreaks (≥ −2.5°C) has also doubled since the early 20th century with southern 25th percentile latitude shifting from 46.5° to 47.4° and the northern 75th percentile shifting from 50.4° to 55.0° between 1901–1910 and 2011–2020. Collectively, these temperature shifts have putatively expanded the extent of hemlock–spruce forests climatically suitable for western blackheaded budworm outbreaks (i.e. predicted likelihood of outbreak ≥ 0.5) by 50% and have shifted the 25th percentile latitude of climatically suitable hemlock–spruce forests from 51.2° to 55.3° and the 75th percentile latitude from 56.8° to 57.5° between 1901–1910 and 2011–2020.

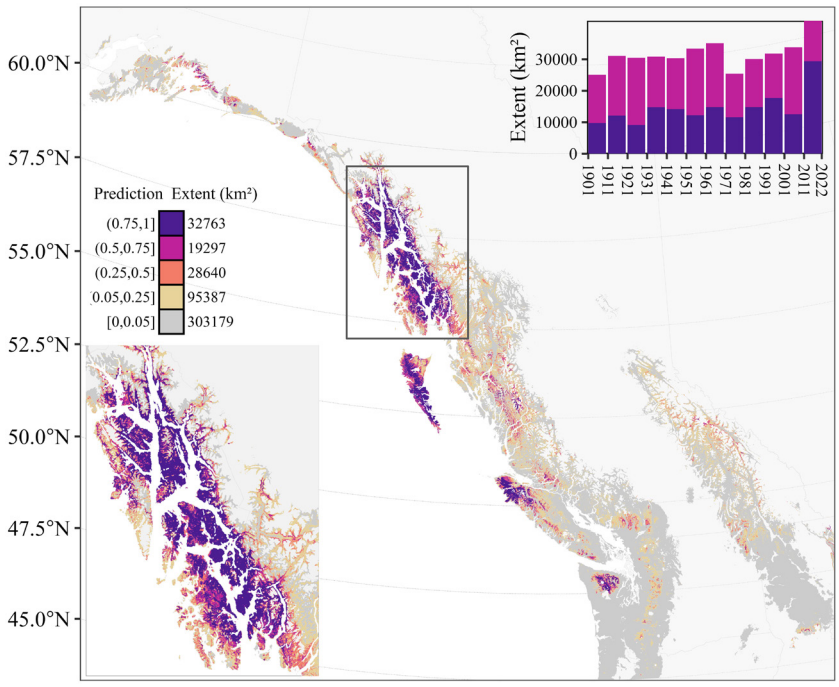

Figure 4. Predicted likelihood that hemlock–spruce forestlands could support irruptive populations of western blackheaded budworm between 2011–2020 across the Pacific coastal temperate rainforest. Map insets provide a zoomed view of southeast Alaska and the predicted extent (km²) of high hemlock–spruce basal area (≥ 2.5 log [m^2 ha^{-1} + 1]) forestlands that could support irruptive populations in each decade. Colors in the bar chart correspond to prediction intervals.

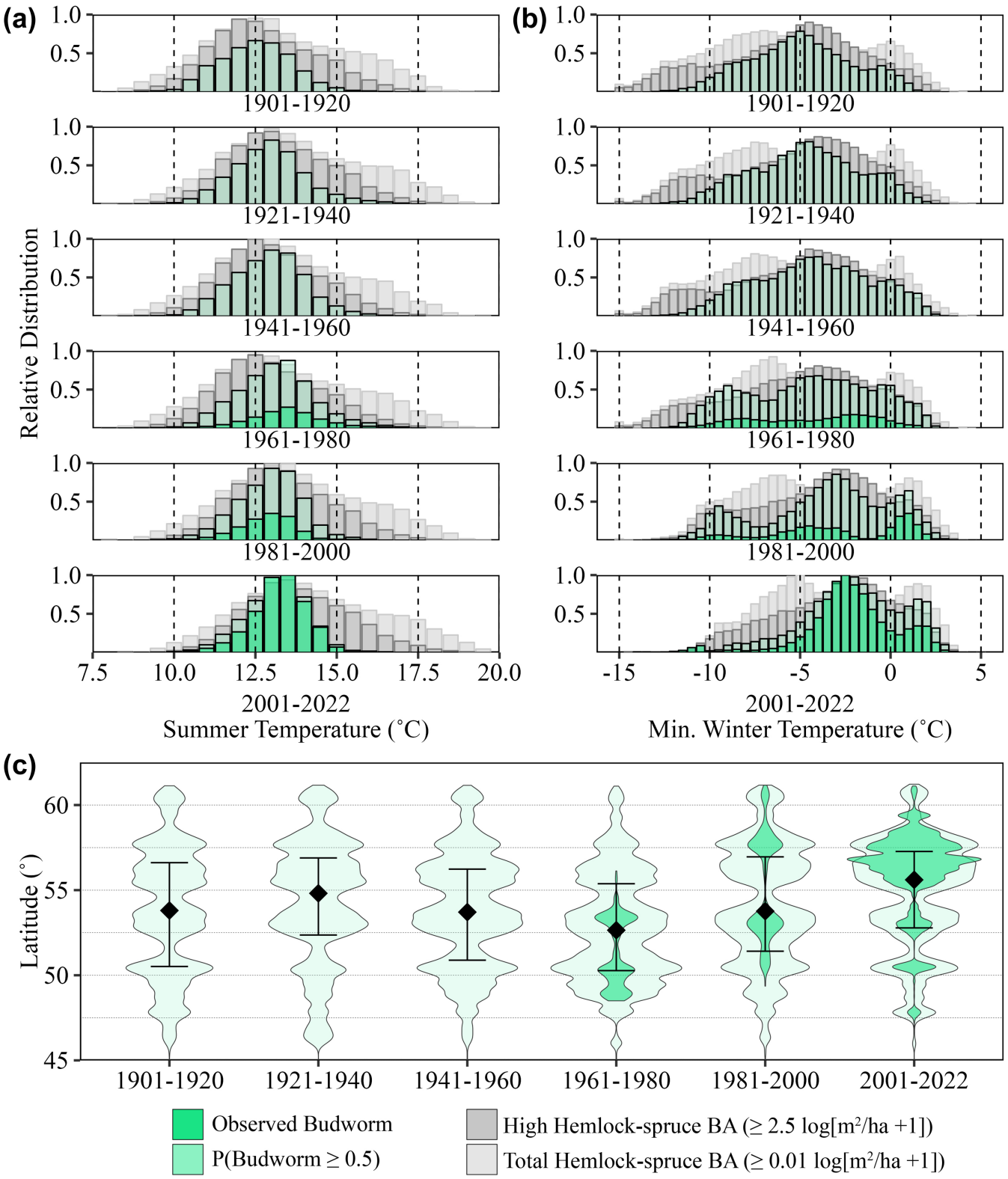

Figure 5. Relative distribution of (a) summer temperatures and (b) minimum winter temperature as compared to (c) the latitudinal distribution of predicted and observed western blackheaded budworm. Relative distributions are relativized between 0–1 overall (instead of within each time-period panel). Violin plots are relativized by their count (i.e. density). Points and error bars in C denote the 25th, 50th and 75th latitudinal percentiles of susceptible forests (hemlock–spruce basal area ≥ 2.5 log[m^2 ha^{-1} + 1]).

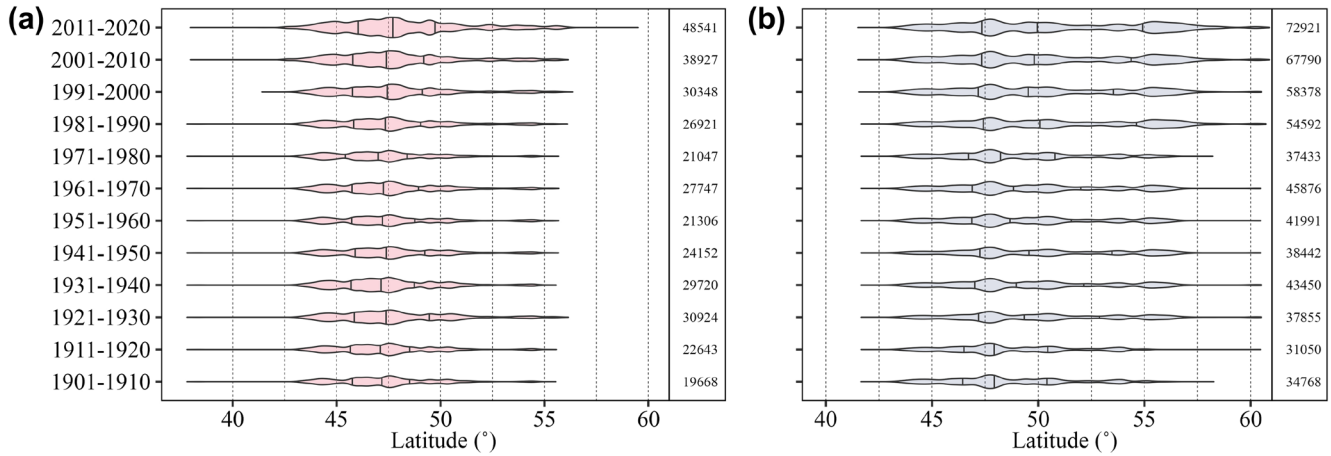

Figure 6. Latitudinal distribution of suitable (a) mean summer temperatures and (b) minimum winter temperatures for western spruce budworm outbreak populations per decade across high hemlock–spruce basal area ($\geq$ 2.5 log [m^2 ha^{-1} + 1]) forestlands. Right-side numbers indicate the extent of susceptible forestland (km^2). Vertical lines denote quartile breaks (i.e. 0.25, 0.5, 0.75)

Interestingly, warming across the region was associated with a cessation of budworm outbreaks on the southern portion of Vancouver Island with the last year of outbreak reported in 1975 (despite consistent aerial survey coverage). Suitable host forestlands (basal area $\geq$ 2.5 log[m^2 ha^{-1} + 1]) in this region (45°–50° latitude) saw an increase in minimum winter temperatures from −2.8°C in 1901–1910 to −1.3°C in 2011–2020, spring temperatures from 5.7° to 6.5°C, and summer temperatures from 13.9 to 15.5°C. These temperature shifts exceeded the suitable climate envelope for western blackheaded budworm outbreaks in many areas and nearly halved the extent of climatically suitable habitat since the last outbreak from 4176 km^2 between 1971–1980 to 2174 km^2 between 2011–2020.

Discussion

Hemlock sawfly and western blackheaded budworm outbreaks were observed across the Pacific coastal temperate rainforest of North America in each decade since 1960 with varying geographic extents. These outbreaks represent the greatest land area recorded since the establishment of the Canadian and United States aerial survey programs. In this manuscript, we demonstrate that these defoliator outbreaks occur within a bioclimatic envelope defined by host availability, a limited range of suitable spring, summer and winter temperatures, and minimum precipitation. Additionally, we present evidence that outbreaks have tracked the northward shift of suitable temperatures across this ecoregion. Results from this study support the notion that climate and host availability are fundamental determinants of irruptive insect herbivore distributions; however, different responses to climate variables highlight each species' unique natural history and variation in historic outbreak footprints. This study establishes a baseline understanding of the climatic constraints and biogeographic patterns of historic sawfly and budworm outbreaks across the Pacific coastal temperate rainforest and emphasizes the overarching importance of climate in constraining the irruptive dynamics of these defoliator species.

The biogeographic distributions of outbreak populations are regulated by a similar suite of drivers as individual species distributions. Since defoliators require host tree material, their distributions are primarily constrained by host distribution. Within the host distribution, temperature is the most important factor influencing individual insect and population distributions as it regulates maturation, reproduction, and stage-specific development rates and survival within the constraints of a species thermal tolerance (Bale 1991, Parmesan et al. 1999, Gillooly et al. 2001). Because population outbreaks are a product of density-dependent drivers and feedbacks, temperature regimes can have an outsized impact on outbreak dynamics. For example, summer temperatures influence larval developmental rates while winter temperatures influence overwintering mortality. Climatic fluctuations can contribute to initial population expansions and ultimately result in the positive feedback loops that typify population irruptions. Indeed, at a landscape scale, temperature is widely acknowledged for modulating both the location and periodicity of insect outbreak cycles (Ayres and Lombardero 2000, Battisti et al. 2005, Pureswaran et al. 2018, Biedermann et al. 2019). In this study, our findings conform to these biogeographic expectations; across the entire Pacific coastal temperate rainforest, hemlock sawfly and western blackheaded budworm outbreaks are intimately tied to a bioclimatic envelope defined by host availability and suitable temperatures.

The influence of high precipitation on defoliator outbreak distribution is less straightforward but is likely linked to the availability of high-quality host forage. It is well documented that defoliators prefer high-quality host forage (Mason et al. 1992, Foss and Rieske 2003, White 2018) and precipitation across this biome is strongly positively associated with host forest volume (Spribille 2002, North et al. 2004). Further, we suspect the observed negative relationship between the

highest winter precipitations and the suitability of hemlock–spruce forestlands to support irruptive populations is likely an artefact of the low aerial detection coverage at higher elevations across southeast Alaska and the Coastal Mountains of British Columbia, where the wettest winters were recorded. At a sub-continental scale, climatic precipitation appears to indirectly influence the biogeographic distribution of sawfly and budworm outbreaks, although our study is unable to disentangle alternative mechanisms or explanations such as larval water balance relations or fungal loads. The impacts of climatic precipitation on the biogeography of insect outbreaks is understudied, especially in this system and merit further investigation.

Enumeration of the bioclimatic bounds for historic western blackheaded budworm and hemlock sawfly outbreaks are especially noteworthy considering the degree of climatic change that occurred across the Pacific coastal temperate rainforest over the last century. Here, we document an increase in mean spring and summer and minimum winter temperatures across the ecoregion. The impact of warming temperatures on the outbreak distribution of budworm and perhaps sawfly across hemlock–spruce forests is already apparent; we demonstrate that budworm outbreak distribution has tracked the poleward shift in suitable climate. These findings are further corroborated by historical reports suggesting that outbreak centers of sawfly and budworm have shifted northward from Wrangel, AK (56.5°) in 1948–1955, to northern Kupreanof Island, AK (57°) in 1973–1975, and ultimately near Angoon, AK (57.6°) in the current outbreak (Mask 1992, FS-R10-FHP. 2018–2022). Similar patterns of outbreak range expansion have been documented in other taxa including the winter moth *Operophtera brumata* and western spruce budworm *Choristoneura occidentalis*, albeit with different suggested mechanisms. Outbreak range expansion of the winter moth is likely tied to warming winters and decreasing overwintering mortality (Jepsen et al. 2008), while outbreak expansion of western spruce budworm is putatively tied to warming springs and shifting phenological synchrony (Tai and Carroll 2022). Despite different mechanisms, the result is similar – a poleward range expansion of outbreaks within the greater context of the species distribution. Our findings provide another example of a poleward shift in outbreak distribution but not necessarily the species distribution, which we are unable to evaluate. Future dendrochronological studies will help clarify the historic distribution of defoliator outbreaks across this region.

Warm temperatures do not necessarily correlate to an increased likelihood of outbreak throughout an entire insect's distribution. At lower latitudes and elevations, warm climatic temperatures can disrupt regular population cycles and cause cyclical dynamics to collapse (Johnson et al. 2010). In this manuscript, we present evidence of an equatorward contraction in outbreak distribution that has potentially disrupted the 12–16-year cyclical dynamics of western blackheaded budworm populations across southern Vancouver Island (Shepherd and Gray 2001). Warming temperatures have also been suggested as a potential mechanism for the disruption of regular western spruce budworm irruption cycles across the low-lying forests of Vancouver Island (Alfaro et al. 2018). As above, future dendrochronological studies are necessary to investigate historic patterns and long-term trajectories of cyclical outbreak dynamics.

Our analyses of temperature and precipitation in this study are focused on decadal climatic regimes and are thus unsuitable for drawing conclusions on how weather influences the extent and severity of sawfly and budworm outbreaks. Lepidopteran outbreak cycles are often characterized by crucial stage-specific responses to weather. For example, western spruce budworm exhibits complex responses to warm temperatures; warm temperatures during the fall or early spring cause significant mortality to early instar larvae, but warm dry weather in the late spring increases larval survival (Nealis and Régnière 2021). Mechanistically, how fluctuations in temperature mediate sawfly and budworm outbreaks are uncertain as we lack a basic understanding of the thermal biology and stage-specific development rates of these insects. Meanwhile, drought is likely an important feature of outbreak dynamics in these systems. Sawfly population dynamics are reportedly mediated by a fungal pathogen that prefers wet and cool conditions (Hard 1976). Thus, warmer than average summers coupled with broad-scale drought between 2016 and 2019 across southeast Alaska may have contributed to the synchronous sawfly outbreaks across the region. The effect of drought on budworm population cycles is less clear, as drought has been loosely associated with the start of outbreaks (Silver 1960) and outbreak collapse has been attributed to cold–wet summers when disease is prevalent (Prebble and Graham 1945, Hard, 1974). Further research, especially at finer scales and in the laboratory setting, is required to understand insect life stage specific thermal tolerances and how weather influences the outbreak dynamics of these defoliators.

Model projections generated for each species based on climate and host tree availability suggest that suitable habitat for outbreak was much broader than areas mapped in aerial detection survey programs. Reconstructing past sawfly and budworm outbreaks throughout the Pacific coastal temperate rainforest is difficult as aerial detection coverage is spatially and temporally limited, as well as biased by increasing aerial detection coverage through time. For example, both recent outbreaks are the most extensive on record based on aerial observations, although aerial coverage especially in southeast Alaska is likewise the most extensive (FS-R10-FHP. 2018–2022). Despite these limitations, our model projections exhibit high fidelity based on known sawfly and budworm defoliation. Further, our historical projections of sawfly and budworm outbreaks conform to reports of several known outbreaks that are not included in our analysis because geospatial data were lacking (e.g. an extensive outbreak in southeast Alaska between 1948–1955 and smaller scale outbreaks in Alaska between 1973–1975, Hard 1974, Mask 1992). Regardless, data used in this study represent the most spatially and temporally comprehensive observations available to date. Model results allow us to distinguish climate tolerances associated with outbreaks in each species and provide

estimates of how climatically suitable habitat and observed outbreaks varied over the last century.

Quantification of the bioclimatic bounds for historic sawfly and budworm outbreaks are especially noteworthy for considering climate change implications on defoliator outbreaks across Pacific coastal temperate rainforests. Current projections suggest that mean annual temperatures could increase by 2.7°C (RCP 4.5) or 4.3°C (RCP 8.5) by 2100 across large expanses of the Pacific coastal temperate rainforest (Shanley et al. 2015). Mean winter temperatures are expected to increase from −3.6 to −1.5°C and summer temperatures from 8.9 to 12.2°C by 2060 across southeast Alaska (Lader et al. 2020). Warming temperatures are projected to coincide with increased annual rainfall and variability (i.e. more drought or extreme precipitation events) across much of Alaska (Lader et al. 2020, Bieniek et al. 2022). Rapid warming may cause cyclical outbreaks of sawfly and budworm to collapse or shift upslope. Additional work is needed to better understand species-level thermal tolerances, population-level adaptations to altered temperature regimes, and the spatial patterns of anticipated climate conditions across the Pacific coastal temperate rainforest.

Shifting climate conditions are altering insect outbreak dynamics across temperate forest ecosystems globally with substantial unforeseen effects to ecosystem processes. In this study, we document the northward expansion and southward contraction of defoliator outbreaks across the Pacific coastal temperate rainforest. Broad-scale outbreaks of insect herbivores can cause substantial losses in primary productivity, incur severe economic losses, and alter ecosystem trajectories (Cooke et al. 2007, Chang et al. 2012, Pureswaran et al. 2015). So far, the impact of recent sawfly and budworm outbreaks across the Pacific coastal temperate rainforest is unknown. Historical reports suggest that tree mortality rates are typically low following defoliation; however, rates increase substantially when sawfly and budworm outbreaks coincide (Hard 1974, Nealis and Turnquist 2010). While this has rarely been observed from the air, more than 7% of all grid cells impacted in outbreaks since 2016 were reportedly defoliated by both species. Our results demonstrate the overarching importance of climate in driving the biogeography and irruptive dynamics of these insect species and lay the groundwork for future studies investigating insect population dynamics, ecosystem effects, and the potential impacts of climate change. A better understanding of the geography and drivers of irruptive insects is paramount for assessing risk to our natural resources, guiding societal expectations of future disturbance regimes, and managing the impacts of broad-scale forest disturbances.

Conclusions

- Cyclical hemlock sawfly and western blackheaded budworm outbreaks have been documented across the Pacific coastal temperate rainforest since 1960.
- Defoliator outbreaks putatively occur within a bioclimatic envelope defined by host availability, a limited range of suitable spring, summer and winter temperatures, and minimum precipitation.
- Evidence from model projections and historical reports suggests that outbreaks have tracked the northward shift of suitable temperatures across this ecoregion.
- Climate change is projected to cause further significant increases in temperature across this ecoregion with unknown consequences for defoliator outbreak distributions.

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Author contributions

Michael Howe: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Elizabeth E. Graham**: Conceptualization (equal); Funding acquisition (equal); Project administration (supporting); Resources (supporting); Writing – review and editing (supporting). **Kellen N. Nelson**: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0gb5mkm6q (Howe et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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